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# THE INTENSITY OF SEXUAL SELECTION IN RELATION TO MALE SEXUAL BEHAVIOUR, FEMALE CHOICE, AND SPERM PRECEDENCE

BY MICHAEL J. WADE & STEVAN J. ARNOLD

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**Abstract.** In this paper we define sexual selection on males as the variance in numbers of mates per male and show how the intensity of this selection is affected by male sexual behaviour, female choice, sex ratio, and modes of sperm precedence. This definition coincides with Darwin's conception of sexual selection but differs from some post-Darwinian views. For systems of single-male paternity, we show that the intensity of total selection on male reproductive success equals the intensity of natural selection on female fertility, times the sex ratio, plus the intensity of sexual selection on males. The absolute intensity of sexual selection is unaffected by the system of sperm precedence. The application of the results to field studies is discussed.

## Introduction

In sexual species each offspring has one mother and one father. This simple observation forms the basis for Fisher's (1958) theory for the evolution of the sex ratio. It has the natural consequence that the total reproductive value at the end of the period of parental investment is equal in males and females, 'because each sex must supply half the ancestry of all future generations of the species'. An alternative formulation of this basic observation is that the average fitness of females must equal the average fitness of males multiplied by the sex ratio at breeding. This simple result suggests that there might also be some elegant relationship between the variances in fitness of the two sexes. Wade (1979) presents a first approach to this problem, and the aim of this paper is to extend Wade's earlier results and specify the nature of this relationship for a variety of known mating systems.

The relationship between variances in fitness of each sex is more complicated, and more subject to assumptions, than the relationship between means. Sexual reproduction ensures a simple relationship between mean fitnesses regardless of how one defines fitness and irrespective of the particulars of the mating system. In contrast, variances in fitness depend very much on the nature of the mating system (e.g. upon variance in harem size, mode of sperm precedence, etc.). Furthermore, aspects of the mating system, such as parental care, can affect different components of total fitness, so that the effects on variance depend on the definition of fitness. In order to keep our problem tractable, we have taken the number of surviving progeny resulting from a single season of reproduction as fitness and asked, what is the relation between variance in progeny number in the two sexes? Because reproductive

success is itself a major component of fitness, variance in reproductive success is directly related to the intensity of selection. Using this simple definition of fitness, we were able to deduce certain general properties of the relation between variances in the two sexes that are independent of the particular distribution of individual fitnesses.

Bateman (1948) argued that a sexual difference in the variance of fertility (progeny number) is a measure of the sex difference in the intensity of sexual selection. Using genetic markers to determine the number of offspring left by individual male and female *Drosophila* in the laboratory, Bateman observed that the variance in the number of offspring left by males was greater than that of females. He showed that this was primarily due to the variance in the numbers of females mated by different males.

In contrast, Trivers (1972) attempted to define the relative parental investment of the sexes in their offspring as the controlling force in sexual selection. Trivers proposed that the ratio of the maximal number of male gametes to the maximal number of female gametes be used as a measure of the potential for sexual competition.

Wade (1979) showed that Trivers's measure would not necessarily reflect the intensity of sexual selection. It was argued that since sexual selection is primarily an intrasexual phenomenon in its effects, the variance in reproductive success among males is a more appropriate measure of the intensity of sexual selection. (It was noted that natural selection, or random survival of offspring, can also cause variation in the number of progeny per family.) Wade also derived an expression for the variance in male reproductive success in terms of the variance in reproductive success among females. This derivation consti-

tuted an analysis of variance in which variance among males in number of progeny was resolved into two components: a component due to variance among females in reproductive success (progeny number) and a component due to variance among males in numbers of mates. This derivation confirmed Bateman's original empirical conclusion that 'Variance in numbers of mates is . . . the only important cause of the sex difference in variance of fertility'.

The purpose of the present report is to extend Wade's (1979) analysis and determine the extent to which the intensity of sexual selection is modulated by female choice, male sexual attributes, and the mode of sperm competition. The first two variables were explicit in Darwin's (1859, 1871) original formulation of sexual selection, but the third variable merits special comment. In many organisms with internal fertilization, the female may be inseminated by more than one male. In such cases the apportionment of paternity in the offspring of a female may differ dramatically between even closely related species (Parker 1970a). In some species the first inseminating male sires all offspring; in others the last male is the sire; while in others paternity is apportioned among all males in relation to their gametic representation at the time of fertilization. In a formal sense, external fertilization and mating systems in which the male has a wholly efficient method of guarding the female after insemination (Parker 1970a) may be considered examples of first-male paternity. This paper is directed, in part, to the question: which system of sperm precedence produces the most intense sexual selection?

Following some brief remarks on the present state of research on sexual selection, we will derive a mathematical model along the lines of Wade (1979) and discuss its implications. We emphasize at this time that the variables important to the primary result (see equation (17)) are measurable for many species even in the field. If the variance in the size of broods, the variance in the numbers of mates per male, or the variance in mating rates of males and the sex ratio of individuals of breeding age can be obtained, then the intensity of sexual selection can be measured with our formulation. In fact, our formulation provides an explicit definition of sexual selection. Furthermore, if a particular trait is the focus of both natural selection and sexual selection, the total selection intensity on the trait can be partitioned into separate components with our formulation. (Questions concerning the survivorship

of broods can readily be addressed with techniques outlined in Crow & Morton 1955.)

In general, present research into sexual selection is directed toward one of three broad goals: (1) prediction of mating systems from environmental variables, (2) reconstruction of the phylogeny of sexually selected traits, and (3) characterization of the sexual dynamics within populations in demographic and evolutionary time.

Studies such as those of Orians (1969), Crook (1970), Emlen & Oring (1977), and Lenington (1977) fall into the first category and are concerned with the effects of the non-social environment on social adaptations. This research attempts to answer questions of the sort: what types of mating systems are likely to evolve when resources are dispersed? The second approach is concerned with the diversity of sexually selected characters among related organisms and the elucidation of the selective pressures moulding their evolution (Darwin 1871; Richards 1927; Alexander 1964; Crook 1972; Selander 1972; Arnold 1977; Wells 1977). By comparing groups these authors direct their research to questions like 'why are mating displays so diverse?' and 'what are the separate steps in the evolution of complex courtships'?

Finally, with respect to the last goal, several authors have sought to derive the basic behavioural differences between the sexes (Bateman 1948; Parker et al. 1972; Trivers 1972; Borgia 1979; Alexander & Borgia 1979; Wade 1979). The goal here is to uncover general principles governing the interactions between the sexes and between sexual rivals, that is, governing sexual dynamics. Empirical studies with this aim usually focus on one or a few populations (Bateman 1948; Maynard Smith 1956; Parker 1970b; Hausfater 1975; Arnold 1976; Thornhill 1976; McCauley & Wade 1978; McCauley 1979). A mathematical characterization of sexual selection and response to this selection has been the aim of theoretical studies of sexual dynamics (Fisher 1958; O'Donald 1977; Wade 1979; Lande 1980).

All three approaches or goals are concerned with the effects of sexual selection and, consequently, a characterization of the intensity of this selection is of common concern. The intensity of selection will always be a simple function of the variance in fitness (see above). In the present case we require a function that specifies the variance in fitness in the two sexes and consequently the intensity of sexual selection in males and females. Strictly speaking, the variance in fitness only gives a measure of the opportunity for selection

in each sex. There must be a heritable basis for the observed differences if selection is going to be effective in producing genetic change.

### The General Model

The purpose of the following model is to evaluate the effects of differences in male sexual behaviour, female choice of mating partners, female fertility (e.g. clutch size), sex ratio, and sperm precedence on the intensity of sexual selection. In other words, we want to determine whether and how these five factors influence variance in the reproductive success of males. We begin by defining variables that characterize behavioural aspects of the mating system (e.g.  $m_j$  and  $s_{ij}$ , see below). We then derive and compare expressions relating variance in reproductive success of the two sexes under three different systems of sperm precedence in order to determine whether sperm precedence affects the intensity of sexual selection and how it exerts its effect.

Our major results relating variance in the reproductive success of the two sexes, equations (15) and (32), do not depend on the particular formulation of underlying variables that we have used (e.g. upon  $m_j$  and  $s_{ij}$  as formulated). We derive our major results from these variables simply to show that equations (15) and (32) can be derived from first principles. Alternative derivations are given in the Appendix courtesy of Dr James Crow.

The model we derive is general in the sense that it can be applied to a wide range of real mating systems. For example, we employ a very general formulation of female choice and make no particular assumptions about the nature of frequency distributions. However, the model only compares variance in reproductive success in a single season of mating. Thus, since differences in mortality schedules are not incorporated into the model, variance in success during a single season represents variance in life time success only for annual or semelparous populations. The model also makes two major assumptions about mate choice and mortality during the mating season. First, the model assumes that female choice of mating partners is uncorrelated with female fertility. In other words, the female's clutch size is unaffected by her choice of mates. Thus the model would have to be modified to accommodate the situation in which males provide parental care (see Wade 1979), males differ in the effect of this care on size and survivorship of broods, and females choose males on the basis of the care they might provide. The model can be

applied to systems with paternal care so long as female choice is not based on this male attribute. Second, the model assumes that male mortality during the mating season is uncorrelated with mating success. For example, we assume that high sexual activity by a male does not increase his chance of mortality during the mating season. There may be mortality during the mating season but it must be random with respect to mating success. Both of these major assumptions could be relaxed, and modified expressions could be readily derived. The consequences of not making these assumptions are discussed below.

We imagine insemination to be a two-stage process composed of an encounter phase and a mating phase. Thus a male may fail to inseminate a female(s) in a particular time interval either because his encounter rate is low or because he is discriminated against once he encounters females. The mating structure of populations of the soldier beetle *Chauliognathus pennsylvanicus* is one example (McCauley & Wade 1978) of female discrimination against males.

We first imagine that there are  $a$  different types of males and that each type of male is characterized by an encounter rate,  $m_j$  ( $j = 1, \dots, a$ ). This encounter rate is the number of females approached by a  $j$ -male in an interval of time during the breeding season. We further assume that females are approached at random during the breeding season without regard to breeding condition or previous sexual history; that is, males are assumed to exert no choice of mates and vary among themselves only in the rate at which females are approached. (All differences among females in attractiveness are suppressed by this formulation, but such differences could be accommodated by redefining encounter rates as  $m_{ij}$ , where  $i$  would represent the different categories of attractiveness among females.)

Let  $p_j$  be the frequency (proportion) of males that are  $j$ -males,  $\sum_{j=1}^a p_j = 1$ , and it follows that the average rate of encounter per male,  $\bar{m}$ , is equal to

$$\bar{m} = \sum_{j=1}^a p_j m_j \quad (1)$$

and the encounter rate of  $j$ -type males relative to the average male is

$$r_j = m_j / \bar{m} \quad (2)$$

We will similarly consider  $b$  different types of females, each present at a frequency  $q_i$  ( $i = 1, \dots, b$ ), whence  $\sum_{i=1}^b q_i = 1$ . The types of females are distinguished by their choice of mates. Females are permitted to exercise a choice of mates by defining  $f_{ij}$ , the failure rate given an encounter, to be the fraction of encounters between  $i$ -females and  $j$ -males that do not result in successful insemination. Likewise,  $(1 - f_{ij}) = s_{ij}$  can be defined as the success rate of encounters. The two variables  $m_j$  and  $s_{ij}$  can represent or derive from many different kinds of biological activities depending on the organism. For example,  $m_j$  could simply be a measure of male position in a lek. Conversely, if males actively search out relatively stationary females, then  $m_j$  might be the area searched by a  $j$ -male per unit time.

Assuming random encounters between the sexes, the probability of encounters,  $e_{ij}$ , between  $j$ -type males and  $i$ -type females is

$$e_{ij} = q_i p_j r_j \tag{3}$$

Note that if equation (3) is summed over all  $i$  and  $j$ , we obtain 1, as expected. (Direct male-male competition or female-female competition could be investigated by defining similar intrasexual encounter rates, but we will not do so here. Instead we subsume the results of male contests and female choice in the terms  $m_j$  and  $f_{ij}$ .)

The variations among males in encounter rates can be viewed as changing the apparent frequencies of the male types. The apparent frequency of a  $j$ -type male,  $p_j$ , becomes the effective frequency  $p'_j = r_j p_j$ , where  $\sum_{j=1}^a p'_j = 1$ . Similarly, in terms of successful encounters, each type of male,  $j$ , perceives the frequency of  $i$ -females as different from their apparent frequency,  $q_i$ , because of female choice. In terms of successful encounters or copulations, the frequency of  $i$ -females encountered by a  $j$ -male is  $q'_{ij} = q_i s_{ij} / \sum_{i=1}^b q_i s_{ij}$ , but to a  $k$ -male it is  $q'_{ik} = q_i s_{ik} / \sum_{i=1}^b q_i s_{ik}$ .

At the end of the breeding period each female produces some number of offspring. We assume that the resulting distribution of offspring number per female has a finite mean  $\bar{X}_f$  and variance  $\sigma_f^2$ . The number of progeny per female is a random variable uncorrelated with other aspects of the mating system. That is, we assume no correlation between female fertility and female choice as expressed in the term  $f_{ij}$ . Although such a correlation is often assumed in discussions of

sexual selection, we are working from first principles and prefer to leave the study of the evolution of such a correlation to a later time. Because females can mate with several males within one breeding season, we must specify the mode of sperm utilization in the production of a season's offspring. We examine three cases of particular interest: (1) first-male paternity, (2) last-male paternity, and (3) equal paternity to all inseminating males.

### First-Male Paternity

In order to study the effects of first-male paternity on the variance in male reproductive success, we require knowledge of the numbers of virgin females mated during each interval of the breeding season. For a given female, matings subsequent to the first are of no interest because these inseminations play no role in fertilization, nor do they influence offspring survival.

Different types of virgin females will mate at different rates because of variations in the choice variable,  $f_{ij}$ . The probability that an  $i$ -type female will mate in a given interval,  $\text{Pr}(\text{Mating}/i\text{-female})$ , can be obtained from  $\text{Pr}(\text{Mating between any male and an } i\text{-female}) = \text{Pr}(\text{Mating}/i\text{-female}) \times \text{Pr}(i\text{-female})$ . Rearranging the above and substituting from equation (3) gives

$$\text{Pr}(\text{Mating}/i\text{-female}) = \sum_{j=1}^a r_j s_{ij} p_j = S_i. \tag{4}$$

the probability that an  $i$ -type female will mate in any particular time interval, which is the success rate of  $i$ -females summed over the effective frequencies of males,  $p'_j$ . Hence,  $(1 - S_i) = F_i$  is the probability that an  $i$ -female fails to mate during a given interval.

Replacing  $\sum_{j=1}^a$  in equation (4) by  $\sum_{i=1}^b$  and substituting  $q_i$  for  $p_j$ , and dividing by  $p_j$  instead of  $q_i$ , we obtain the success rate of  $j$ -males,  $r_j S_j$ , which is the product of the approach rate  $r_j$  and the average acceptance rate by females,  $S_j$ .

If  $N_f$  is the total number of females of reproductive age, then, at the start of the breeding season, there are  $N_f q_i$  females of the type  $i$ , all of which are virgins. During each time interval of the season,  $S_i$  of the unmated  $i$ -females present at the beginning of the time interval are mated and  $F_i$  of the unmated  $i$ -females fail to mate. The decline in the numbers of  $i$ -type virgin females through the breeding season is presented in Table I.

Table I. The Mating Status of *i*-Type Females during the Breeding Season with First-Male Paternity

Time	Number of virgins at time <i>t</i>	Number of virgins mated in ( <i>t</i> , <i>t</i> +1)
0	$N_{fqi}$	$N_{fqi}S_i$
1	$N_{fqi}F_i$	$N_{fqi}S_i \cdot F_i$
2	$N_{fqi}F_i^2$	$N_{fqi}S_i \cdot F_i^2$
⋮	⋮	⋮
<i>t</i>	$N_{fqi}F_i^t$	$N_{fqi}S_i \cdot F_i^t$

For any interval (*t*, *t* + 1), the fraction of *i*-virgins mated by *j*-type males is given by

$$p_j S^*_{ij} = p_j r_j s_{ij} / S_i \quad (5)$$

where  $S^*_{ij} = r_j s_{ij} / S_i$  is the effective relative mating rate of *j*-males with *i*-females.

Expression (5) equals 1 when summed over all males (*j*). Over the entire season, *T*, the class of *j*-males will mate with a number of *i*-females,  $M_{ij}$ , which can be obtained by multiplying each of the entries in column 3 of Table I by the left side of equation (5) and summing over *t*. Hence,

$$M_{ij} = \sum_{t=0}^T q_i N_f S_i \cdot F_i^t \cdot p_j S^*_{ij} \quad (6)$$

Since  $F_i$  is always less than 1, this expression can be simplified to

$$M_{ij} = (N_{fqi}) (p_j) (S^*_{ij}) \quad (7)$$

where we assume that *T* is large enough so that virtually all *i*-females are mated. This is the number of *i*-females mated by *j*-males over the entire season, and it is simply the product of the total number of *i*-females and the effective mating rate of *j*-males with respect to *i*-females relative to the average effective mating rate of all males. Equations similar to (7) can be obtained for all types of females (*i*) and the total number of females mated by *j*-males is

$$M_{.j} = \sum_{i=1}^b M_{ij} = N_f p_j S^*_{.j} \quad (8)$$

where  $S^*_{.j} = \sum_{i=1}^b q_i S^*_{ij}$  is the seasonal effective mating rate of *j*-males relative to other males. Thus, differences among males in the rate of encounter of females and differences among females in their receptivity to male mating attempts exert their respective effects on male reproductive success by altering the effective male mating rates relative to the average.

In order to specify the variance in male reproductive success, we require the mean number of mates per *j*-male rather than the total number of mates of the entire class of *j*-males. Clearly, an average *j*-male will mate first with, and hence sire the offspring of, a fraction,  $1/N_m p_j$ , of the  $M_{.j}$  females. This fraction of all mated females is given by dividing equation (8) by  $(N_m p_j)$  for

$$S^*_{.j} / R \quad (9)$$

where *R* is the sex ratio of the breeding population expressed as the ratio of males to females.

The mean number of mates per male is  $(1/R)$ . Consequently, the variance in numbers of mates per male,  $\sigma_s^2$ , is

$$\begin{aligned} \sigma_s^2 &= \sum_{j=1}^a p_j (S^*_{.j} / R - 1/R)^2 = (1/R)^2 \\ &\times \sum_{j=1}^a p_j (S^*_{.j} - 1)^2 \end{aligned} \quad (10)$$

The variance in male mating rate,  $\sigma_{S^*}^2$ , is equal to  $\sum_{j=1}^a p_j (S^*_{.j} - 1)^2$ . Thus,

$$\sigma_s^2 = \sigma_{S^*}^2 / R^2 \quad (11)$$

Now,  $\bar{X}_f$  times expression (9) is  $X_{m,j}$ , the mean number of offspring fathered by a *j*-male, and the variance in offspring numbers of *j*-males,  $\sigma_{m,j}^2$ , is given by the variance about this mean. Because each female reproduces independently of all other females and each *j*-male mates with  $S^*_{.j} / R$  females, the variance in reproductive success among *j*-males is given by

$$\sigma_{m,j}^2 = \sigma_f^2 S^*_{.j} / R \quad (12)$$

Here we have assumed that there is no variation in numbers of mates among *j*-type males. This is a matter of definition. For the purpose of derivation, we have defined *j*-males such that there is no variation within the class in number of mates. (If there were within-class variation in numbers of mates, an additional term  $\bar{X}_f^2 \sigma_M^2$  would be added to the right hand side of equation (12), with  $\sigma_M^2$  representing the variance in numbers of mates among *j*-males. We are assuming  $\sigma_M^2$  to be effectively zero.)

We now have the mean and variance in reproductive success for males within any class and can calculate the total variance in male reproductive success using expression (12) and considering the among-class variance in mean success.

The grand mean of males,  $\bar{X}_m$ , is a weighted sum of the terms

$$\bar{X}_m = \sum_{j=1}^a p_j \bar{X}_f S^*_{.j}/R = \bar{X}_f/R \quad (13)$$

That is, the mean reproductive success of males is equal to that of the females divided by the sex ratio (Fisher 1958). This must be the case because each offspring has one male and one female parent.

The variance in male reproductive success,  $\sigma_m^2$ , is thus the weighted sum of the within-class variances plus the between-class variance, namely,

$$\sigma_m^2 = \sum_{j=1}^a p_j \sigma_{m,j}^2 + \sum_{j=1}^a p_j (X_{m,j} - \bar{X}_m)^2 \quad (14)$$

Substituting (12) and (13) into (14) yields

$$\sigma_m^2 = \sigma_f^2/R + (\bar{X}_f/R)^2 \sigma_{S^*}^2 = \sigma_f^2/R + (\bar{X}_f)^2 \sigma_s^2 \quad (15)$$

where  $\sigma_{S^*}^2$  is the variance in the effective mating rates of males and  $\sigma_s^2$  is the variance in numbers of mates per male. Thus male reproductive variance,  $\sigma_m^2$ , can be resolved into two components: a component due to variance in female fertility and a component due to male variance in mating rates. (Equation (15) is very similar to equation (6) of Wade (1979) for polygynous males; the variance in harem size is replaced by  $\sigma_s^2$ , the variance in numbers of mates per male.)

It is clear from equation (15) that whenever  $R \leq 1$ , the variance in male reproductive success will be equal to or greater than the variance in female reproductive success. The cause of any difference in variance must be the differences among males in the number of females successfully inseminated as is given by the second term on the right-hand side of equation (15). This formulation confirms Bateman's (1948) assertion that 'Variance in numbers of mates is . . . the only important cause of the sex difference in variance in fertility'. It also permits the process of sexual selection to be unambiguously defined and the influence of any trait on this process to be rigorously quantified (see Discussion).

Because reproductive success is a major component of fitness,  $\sigma_m^2$  can be viewed as a measure of the variance in fitness among males and, thus, a measure of the intensity of selection on males (Bateman 1948). This variance can be scaled in relation to average fitness in order to obtain a more conventional measure of the intensity of selection.

From equation (15) we can obtain a measure called the 'index of total selection',  $I_m$  for males and  $I_f$  for females (Crow 1958, 1962). Crow defined  $I$  by the formula  $I = V/W^2$ , where  $V$  was the variance in number of offspring per parent and  $W$  was the mean number of offspring per parent. Dividing equation (15) by  $\bar{X}_m^2$ , the square of the mean number of offspring per male, we obtain

$$\sigma_m^2/\bar{X}_m^2 = \sigma_f^2 R/\bar{X}_f^2 + R^2 \sigma_s^2 \quad (16)$$

or

$$I_m = R I_f + I_s \quad (17)$$

where  $I_m$  is the total intensity of selection on male reproduction,  $I_f$  is the total intensity of natural selection on female reproduction, and  $I_s$  is the intensity of sexual selection on males. This index,  $I_m$ , has the genetic meaning that 'if fitness were completely heritable, that is, if each offspring had exactly the average of his parents' fitnesses, the fitness of the population next generation would be that of the present generation multiplied by  $I$ . A trait or a gene that is genetically correlated with fitness will increase in proportion to this correlation' (Crow 1962, page 64).  $I_m$  is thus a measure of the opportunity for selection, and  $I_s$  can be a useful measure of the intensity of sexual selection on males irrespective of the heritability of fitness. It does not imply that a response to selection will necessarily follow. This point will be taken up later in the discussion.

This partitioning of reproductive variance (15) is most useful when effective mating rates of males can be observed in experimental or field situations. Under these circumstances the intensity of sexual selection on males can be calculated as

$$I_s = \sigma_{S^*}^2 \quad (18)$$

The intensity of sexual selection on males can be obtained with fewer assumptions if the actual numbers of broods sired by each male can be observed. Let  $\sigma_s^2$  be the variance in number of virgin females mated per male in a system of first-male paternity. More generally,  $\sigma_s^2$  is the variance in the mating success of males; that is, the variance in number of mates per male, where we count an inseminated female as a mate only if she bears the progeny of the male. Then, since  $\sigma_{S^*}^2 = \sigma_s^2/R^2$  from (11), it follows from the derivation of equation (15) or the Appendix that

$$\sigma_m^2 = \sigma_f^2/R + \bar{X}_f^2 \sigma_s^2 \quad (19)$$

This important result (19) can be restated using the convenient vocabulary of the animal breeder, where we refer to females having progeny as dams and males fathering progeny as sires. Thus equation (19) resolves the variance of reproductive success of sires into two components; a component due to variance in fertility among dams,  $\sigma_f^2$ , and a component due to variance among sires in number of dams,  $\sigma_s^2$ . In some breeding systems (e.g. polygynous birds) the latter component is simply variance in the harem size of males. Note that these variances include the class of females that mate but bear no progeny ('dams' with zero fertility) and the class of sexually active males that achieve no matings or progeny ('sires' with no dams). The first expression on the right side of equation (19) is the variance among males that have the same number of mates, and the second expression on the right is the variance among males that have different numbers of mates (see Appendix). Thus (19) is simply a nested analysis of variance in numbers of progeny per male.

Dividing both sides of equation (19) by  $\bar{X}_m^2$  to yield intensities of selection, as before, we obtain

$$I_m = RI_f + I_s \quad (20)$$

where

$$I_m = \sigma_m^2 / \bar{X}_m^2 \quad (21)$$

$$I_f = \sigma_f^2 / \bar{X}_f^2 \quad \text{and} \quad (22)$$

$$I_s = \sigma_s^2 / \bar{X}_s^2 = R^2 \sigma_s^2 \quad (23)$$

where  $\bar{X}_s$  is the mean number of mates per male or  $1/R$ . Thus the intensity of sexual selection on males,  $I_s$ , is equal to the variance in male mating success divided by the square of mean mating success. But, because the average number of mates per male must be  $1/R$ ,  $I_s$  also equals the variance in male mating success times the squared sex ratio.

These intensities of selection can be used to form two useful ratios. Let  $I_s/I_m$  be the relative intensity of sexual selection on males. It varies from 0, when there is no sexual selection on males, to 1, when there is no variance among females in fertility. This ratio measures the proportion of the total intensity of selection on male reproduction that can be ascribed to sexual selection. Another ratio is also of interest. Let  $I_m/I_f$  be the sexual ratio of reproductive intensities. Unlike  $I_s/I_m$ , this ratio may exceed 1. These ratios are particularly useful for comparing the relative intensities of selection in different

species or in the same population in different years. An example will be given in the Discussion.

Having considered the effects of first-male paternity, we will now turn our attention to cases of last-male paternity and equal paternity by all inseminating males.

### Last-Male Paternity

In this case, we must monitor the number of females that mate in an interval ( $t, t+1$ ) and do not mate again for the duration of the breeding season. During each interval ( $t, t+1$ ), a fraction,  $S_t = 1 - F_t$ , of  $i$ -females mate successfully with a male and a fraction,  $F_t$ , fail to mate. Of those  $i$ -females,  $N_f q_i S_t$ , that mate during the first interval of the breeding season ( $t=0, t=1$ ), a fraction equal to  $F_t^T$  will not successfully mate for the duration of the season. The numbers of these  $i$ -females for all intervals of the breeding season are recorded in Table II. When  $T$  is large, this problem is identical to that of the previous case, and we conclude that under the present assumptions first-male paternity is equivalent to last-male paternity in its effect on the intensity of sexual selection. Indeed, under these assumptions, all cases of single-male paternity are equivalent in their effect on the intensity of sexual selection.

We must point out, however, that our model has ignored male mortality during the mating season. Although random mortality of males would not alter our conclusions, they would be changed if male mortality were correlated with male encounter rate. If the correlation between male mortality and male encounter rate is strongly positive, then males that encounter a large number of females during the first few intervals of the breeding season might not survive to the latter part of the season. With last-male paternity, this correlation would tend to equalize the numbers of mates obtained by fast and slow

Table II. The Mating Status of  $i$ -Type Females during the Breeding Season with Last-Male Paternity

Time	Number of females mating in ( $t, t+1$ )	Number of females not remating
0	$N_f q_i S_t$	$N_f q_i S_t \cdot F_t^T$
1	$N_f q_i S_t$	$N_f q_i S_t \cdot F_t^{T-1}$
2	$N_f q_i S_t$	$N_f q_i S_t \cdot F_t^{T-2}$
.	.	.
.	.	.
$t$	$N_f q_i S_t$	$N_f q_i S_t \cdot F_t^{T-t}$



males, with a resultant decrease in the variance in numbers of mates and the intensity of sexual selection. On the other hand, with first-male paternity, the decrease in the intensity of sexual selection will be much less because most of the effective matings occur early in the season.

In contrast, a negative correlation between male mortality and male encounter rate will enhance the intensity of sexual selection, and this effect will be strongest in the case of first-male paternity.

One likely cause of male mortality or injury during the breeding season is male contests for females or for territories (e.g. Darling 1937). In such cases, any correlation between mortality and encounter rates is likely to be positive rather than negative; males that extend themselves more in finding females may be more likely to incur injury or death. Thus in those cases where males do not obtain exclusive control of females, male-male competition can actually decrease the intensity of sexual selection relative to its intensity without male-male contests. This situation arises because a positive correlation between mortality and encounter rates lowers the variance in numbers of mates. Thus the intensity or rigour of sexual contests may not bear a direct relationship to the intensity of sexual selection. Although there is no necessary relationship, in certain circumstances we can expect one. For example, intense male-male contests may occur when combating males can gain exclusive access to females early in the mating season (see Shine 1979).

It is also clear that a positive correlation between male encounter rate,  $m_j$ , and female choice,  $f_j$ , will increase the intensity of sexual selection by increasing the variance in the effective numbers of mates among males,  $\sigma_j^2$ . Equations (16) and (17) can also be used heuristically to examine the effects of other possible combinations of male and female sexual traits on the intensity of sexual selection.

#### Equal Paternity by All Inseminating Males

Females of many organisms mate repeatedly with different males and store sperm in specialized organs, e.g. spermathecae. In some of these cases, sperm from different males apparently mix freely, and paternity is proportional to the male's gametic representation at the time of fertilization. In order to evaluate the effects of such instances of paternity by representation, we require the distribution of matings per female. We will assume throughout that the number of offspring sired by each inseminating male of a particular

female is  $\bar{X}_f/k$ , where  $\bar{X}_f$  is the number of offspring produced by the female and  $k$  is the number of mates taken by the female. This is equivalent to an assumption of paternity by representation with each male inseminating a particular female no more than once.

Letting  $F_i$  and  $S_i = 1 - F_i$  be the rates of failure and success of  $i$ -females in each interval of the season, as before (see equation (4)) we have

$$(I) F_i^{T-k} S_i^k \quad (24)$$

as the fraction of  $i$ -females mated  $k$  times during the season. Multiplying expression (24) by  $N_f q_i k$  gives the total number of matings engaged in by these females. A fraction of these matings, expression (5), are made by  $j$ -type males, and each of these males sires

$$(\bar{X}_f/k) (I) F_i^{T-k} S_i^k N_f q_i k (p_j S^*_{ij}) (1/N_m p_j) \quad (25)$$

offspring as a result. Expression (25) can be simplified and, when summed first over  $k$  and then over  $i$ , we recover the mean number of offspring sired during the breeding season by a  $j$ -type male,

$$\bar{X}_f S^*_{.j} / R \quad (26)$$

which is identical to the product of  $\bar{X}_f$  and expression (9), the average number of offspring sired by a  $j$ -male with first- or last-male paternity. Clearly, the grand mean of all males is equal to that given in equation (13). We conclude that paternity by representation has no effect on the mean numbers of offspring sired by the various types of males. In other words,  $j$ -males will have the same expected number of progeny under a system of paternity by representation as they would under a system of single-male paternity. The system of sperm precedence does, however, influence the variance in male reproductive success, as we show below.

In order to calculate the variance in progeny number under a system of equal paternity by all inseminating males, again let  $\bar{X}_f$  and  $\sigma_f^2$  be the mean and variance of female reproductive success. If each inseminating male sires  $1/k$  of the offspring produced by an  $i$ -female mated  $k$  times, then the contribution to the variance in male reproductive success by each of these matings is

$$(1/k)^2 \sigma_f^2 \quad (27)$$

We multiply expression (27) by expression (25) and divide by  $\bar{X}_f(1/k)$  to calculate the component of variance among  $j$ -males resulting from matings with  $i$ -females mated  $k$  times each, or

$$(\sigma_f^2/k^2) (I) F_i^{T-k} S_i^k N_f q_i k (p_j S^*_{ij}) (1/N_m p_j) \quad (28)$$

This expression reduces to

$$(\sigma_f^2/k) \left(\frac{T}{k}\right) F_i^{T-k} S_i^k q_i S^*_{ij}/R \quad (29)$$

We recognize that the harmonic mean number of matings for  $i$ -females,  $H_i$ , is given by

$$H_i = 1/\sum_{k=1}^T (1/k) \left(\frac{T}{k}\right) F_i^{T-k} S_i^k \quad (30)$$

where we must assume that there are no females which do not mate at least once. Hence, summing expression (29) first over  $k$  and then over  $i$ , we derive the variance in reproductive success among  $j$ -males,  $\sigma_{m,j}^2$ , which is equal to

$$\sigma_{m,j}^2 = (\sigma_f^2/R) \left(\sum_{i=1}^b q_i S^*_{ij}/H_i\right) \quad (31)$$

Because  $H_i$  is always greater than or equal to 1, paternity by representation will clearly diminish the intensity of total selection relative to the cases of single-male paternity (compare equation (31) with equation (12)). And, this effect is the result of a decrease in the within-class reproductive variance of males. That is, males that achieve the same number of effective matings are more uniform in their number of progeny produced than they would be under a system of single-male paternity. Paternity by representation does not alter the among-class component of variance, that is the component of variance due to variance in numbers of effective matings or sexual selection.

With expressions (18) and (23) we can calculate the total variance in male reproductive success,  $\sigma_m^2$ . Because the mean reproductive success for each male class remains the same as in the previous cases (see expression (26)), the total variance in male reproductive success is given by

$$\sigma_m^2 = \sigma_f^2/RH + (\bar{X}_f/R)^2 \sigma_{S^*}^2 \quad (32)$$

where  $H$  represents the weighted harmonic mean over both sexes. Dividing by  $\bar{X}_m^2$ , as before, to obtain an expression in terms of intensities of selection, we find that

$$I_m = RI_f/H + I_s \quad (33)$$

### An Application of the Model to a Natural Population

Payne (1979) has recently stressed the need for empirical data on variance in reproductive success in the two sexes and provided the appropriate data for a population of red-winged blackbirds (*Agelaius phoeniceus*). An application of our

model to Payne's results (Table III) amplifies and extends his conclusions.

The major assumptions of our model as applied to Payne's data are as follows. (1) The temporal domain of the model is a single season of reproduction. Thus the calculated intensities of selection refer to a single season and not to the entire life cycle. (2) All adults capable of reproduction are included in the tallies of reproductive and mating success. Payne's population is composed of three classes of males: adult males holding territories, adult males without territories, and first-year males without territories. Payne's observations clearly show that the first two classes contest for reproductive success. Obviously they should be included in the tallies. For our analysis, we have also included first-year males since Payne's observation that such males will attempt copulation with female dummies suggests that they are sexually competent and capable of mating given the opportunity. (3) A male is the sole sire of progeny in his territory (the consequences of relaxing this assumption are discussed below). This assumption may have been violated. Payne did not observe copulations by non-territorial males, but this, of course, does not eliminate the possibility of stolen copulations (Bray et al. 1975). Furthermore, the system of sperm precedence is unknown in this species. Thus it is difficult to evaluate the genetic consequences of stolen copulations should they occur. (4) Male mortality during the breeding season and the number of fledglings per mate are both uncorrelated with male mating success. Violation of the latter assumption complicates calculation of the intensity of sexual selection, as we shall see.

With these assumptions in mind we can calculate the intensities of selection for reproductive success in the two sexes and the intensity of sexual selection (Table III). The sexual difference in selection on reproduction is best evaluated in terms of intensities rather than variances. Thus the ratio of variances for the two sexes ( $\sigma_m^2/\sigma_f^2$ ) is 1.03 in 1975 and 2.49 in 1977. But because the sex ratio is greater than one in both years, the males actually experience a greater intensity of selection than these variance ratios indicate. Thus in 1975 the intensity of selection on males is 4.51 times greater than that on females and in 1977 it is 9.14 times greater.

The intensity of sexual selection on males can also be calculated from Payne's data, since he reports the mating success of males. Thus in the two years, sexual selection accounted for 59 to 81% of the total intensity of selection on male

Table III. Reproductive Success and Mating Success in a Population of Red-Winged Blackbirds in Two Years (Data from Payne 1979 and Personal Communication)

Female Reproductive Success									
Year	Number of fledglings/adult female					$\bar{X}_f$	$\sigma_f^2$	$I_f$	$R$
	0	1	2	3	4				
1975 ( $N = 29$ )	14	0	2	6	7	1.72	3.14	1.06	2.10
1977 ( $N = 40$ )	13	3	7	9	8	1.90	2.45	0.68	1.93

  

Male Reproductive Success														
	Number of fledglings/adult male										$\bar{X}_m$	$\sigma_m^2$	$I_m$	$I_m/I_f$
	0	1	2	3	4	5	6	7	11					
1975 ( $N = 61$ )	49	0	1	3	5	1	0	2	0	0.82	3.22	4.78	4.51	
1977 ( $N = 77$ )	64	0	1	2	1	3	1	3	2	0.99	6.09	6.22	9.14	

  

Male Mating Success										
	Number of mates/adult male					$\bar{X}_s$	$\sigma_s^2$	$I_s$	$I_s/I_m$	
	0	1	2	3	4					5
1975 ( $N = 61$ )	47	3	7	4	0	0	0.48	0.89	3.85	0.81
1977 ( $N = 77$ )	63	1	5	5	1	2	0.52	1.46	5.41	0.59

reproduction. In other words, the majority of the variance in reproductive success of males is accounted for by differences in numbers of mates.

In Payne's data set  $I_f$ ,  $I_m$ , and  $I_s$  can be calculated directly. Sometimes, however, there may be data for direct calculation of only two of these quantities. In such cases, the third quantity can be indirectly estimated by substitution into equation (17). The expression  $I_m - RI_f$  will estimate  $I_s$  plus a term due to covariance of mating success with female fertility (Wade 1979). If we attempt this indirect estimate of  $I_s$  with Payne's data we obtain 2.55 for 1975 and 4.91 for 1977; these estimates are less than the direct estimates for both years. These discrepancies might be due to sampling errors in the estimates of  $I_f$  and  $I_m$  or to a negative correlation between numbers of females per harem (mating success) and the mean number of fledglings per female. Sampling errors are the probable cause since Payne did not find statistically significant correlations between mating success and female fertility (Payne, personal communication).

The validity of assuming that a territorial male sires all the progeny hatched in his territory is difficult to evaluate. Since the mates of vasc-

tomized male red-winged blackbirds can lay fertile eggs (Bray et al. 1975), the possibility of stolen copulations can not be discounted. Failure to observe stolen copulations does not refute their occurrence, since this is exactly the kind of behaviour that is most difficult to observe. What is the consequence of assuming that it does not occur? Payne suggested that 'male variance was higher than estimated through some females mating promiscuously with certain males'. This conclusion follows if some small fraction of the males achieve the majority of stolen copulations. If, however, stolen copulations are distributed among many males (e.g. among the large number of year-old males erroneously classified as obtaining no mates), the effect will be to lower the variance in mating success,  $\sigma_s^2$ . In other words, assuming no stolen copulations in a population where they actually occur will probably lead to an overestimate of male reproductive success, rather than an underestimate as Payne argues.

#### Discussion

Our major result is the mathematical demonstration that variance in the reproductive success of

males can be partitioned into two useful components: one due to variance in the fertility of females and one due to variance in number of mates per male. The latter component is the main proximate cause of a difference between the sexes in the intensity of selection on reproduction, as Bateman (1948) supposed. These two components may be the most useful sufficient parameters in the characterization of mating systems.

In his important paper on sexual selection, Trivers (1972) stressed the importance of variance in reproductive success. We agree that this is a key variable and we have shown how it is related to the intensity of sexual selection. Trivers (1972, page 141) also stressed the role of sex differences in parental investment: 'What governs the operation of sexual selection is the relative investment of the sexes in their offspring'. Small parental investment by males may be the ultimate factor predisposing males for sexual competition. However, if we wish to estimate the intensity of sexual selection in an existing population, other variables are more useful in characterizing the process. Our results stress the importance of variance in female fertility, sex ratio, sperm precedence, and variance in numbers of mates per male as proximate factors determining the variance in reproductive success of males.

#### **Variance in Reproductive Success: Intensity of and Response to Selection**

The relationship between variance in reproductive success and the intensity of selection is not always transparent in the current literature. In the simplest formulation we imagine two types of male, with characteristic reproductive successes or fitnesses. In this case the difference between these two fitnesses constitutes the magnitude or intensity of selection acting on the population (Haldane 1932). When we generalize this formulation to accommodate more than two types of individuals, we can no longer represent the intensity of selection as a simple difference. But the intensity of selection can be represented as a simple function of variance in fitness, since variance in fitness is selection (Crow 1958). Since reproductive success is not simply a phenotypic trait with some unspecified relationship to fitness, but is itself a major component of fitness, variance in reproductive success is directly related to the intensity of selection.

It is important to distinguish between selection and response to this selection. Response to selection depends on heritable differences but selection itself does not. In the theoretical literature,

the change in fitness each generation is commonly expressed relative to the average fitness in the population. When differences in fitness are completely heritable, the change in fitness each generation relative to the average will be equal to the variance in fitness divided by the square of the average fitness (Crow 1958). In this case the ratio of variance in fitness to the squared average is both a measure of the intensity of selection and a measure of the predicted response to selection. When fitness is not completely heritable, as will commonly be the case, this ratio still represents the intensity of selection, even though average fitness will change by some fraction of the former amount each generation. In the extreme case, there may be no heritable differences in fitness. Nevertheless, selection can still be said to act on the population even though there will be no response to selection. Consequently our formulation of the intensity of sexual selection does not depend on heritability of the traits in question. We simply specify the intensity of selection and leave open the problem of characterizing the response to selection. The dynamic equations that would describe response to sexual selection will be most complicated because sexual selection is by its nature frequency-dependent.

#### **An Operational Definition of Sexual Selection**

We define 'sexual selection' on males as 'variance in numbers of mates that bear the male's progeny',  $\sigma_m^2$ . Because this definition is put in terms of the statistical consequences of sexual selection, rather than in terms of the agents that cause it or the evolutionary effect of the selection (response to selection), it is a most useful definition for theoretical and applied purposes. For example, with this definition we can express our fundamental result (equation (17)) in words: the intensity of total selection on male reproductive success equals the intensity of natural selection on female fertility, times the sex ratio, plus the intensity of sexual selection on males. This is also an operational definition of the components of selection, since all four summary statistics can be estimated in many natural and experimental populations. In contrast, a definition in terms of the agents of selection (female mating choice and male contests) gives the field worker the difficult task of actually ascribing selection to specific causes. A definition in terms of response to selection is still more difficult to implement, since genetic parameters such as heritabilities and genetic correlations must be estimated as well.

We believe that this definition of sexual selection captures the essence of Darwin's conception (Darwin 1859, 1871, 1876). Darwin did not simply equate sexual selection with differences in reproductive success and natural selection with differences in survivorship, as is commonly supposed (e.g. Selander 1972). Nor did he view sexual selection as a form of natural selection; he viewed each as a separate process. With regard to the distinction between sexual and natural selection, Darwin (1871) explicitly ascribes differences in fertility given mating to natural selection rather than to sexual selection. Thus differences in male genitalia that affect the number of progeny resulting from a given mating constitute natural selection, not sexual selection. For Darwin, sexual selection was variation among males in numbers of mates, and such differences might be caused by female choice of mating partners or by contests between rival males for mating success. Thus  $\sigma_3^2$  faithfully reflects this conception; sexual selection is variance in mating success, where mating success is measured in numbers of mates that bear progeny.

Our definition does not coincide with some post-Darwinian definitions of sexual selection. Thus Huxley (1938) changed Darwin's meaning when he called epigamic selection a subcategory of sexual selection that included aspects of natural selection (differences in fertility given mating).  $\sigma_3^2$  includes what Huxley called intra-sexual selection but only part of what he called epigamic selection (see Bateman 1948 for a discussion). Ehrman's (1972) definition of sexual selection as 'all mechanisms which cause deviation from panmixia' also violates Darwin's conception, and we consider her definition too sweeping to be useful.

#### Explication of Variables in the Model

We stress that our model is a static description of the components of reproductive success and their effects on sexual selection. It does not describe the evolution of sexual traits, nor is it explicitly concerned with the heritability of those traits. We expect offspring numbers and mating success to be heritable in many instances, but only empirical work with natural populations can provide answers. Our model simply describes how sexual behaviour and other variables affect the intensities of natural and sexual selection.

In the present model we have used two variables to characterize male and female mating success, namely,  $m_j$ , or the rate at which a particular

class of males,  $j$ , encounters females, and  $s_{ij}$ , or the probability that an encounter between a  $j$ -male and an  $i$ -female will result in mating and insemination. These two variables can represent or derive from many different kinds of biological activities, and the choice of activity for measurement of  $m_j$  or  $s_{ij}$  depends on the organism. For example, if females choose males on the basis of male position in a lek, then  $m_j$ , the encounter rate of  $j$ -type males with females, could be simply a measure of male position. On the other hand, if males actively seek relatively stationary females, then  $m_j$  would be given by the area traversed or searched by a  $j$ -male per unit time.

The probability of mating success (insemination) given an encounter,  $s_{ij}$ , also subsumes a variety of possibilities and so has a utility that transcends the peculiarities of any particular social system. The variable carries a double subscript and so indicates that particular combinations of males and females may differ in mating success as a consequence of both male and female attributes, namely, sexual acceptability of the males and sexual receptivity of females. The relevant male attributes may be found in male courtship behaviours and could include intensity or persistence of display or delivery of chemical aphrodisiacs (Arnold 1977). In many insects, for example, the rate of antennating by the male can influence female receptivity. Such differences in persuasion might apply equally to all females, or their effectiveness might vary in relation to female attributes; that is, females might differ in resistance to particular forms of persuasion. In general, female mating choices must be based on some attribute that varies among the males, even simple possession of real estate or materials, in order to exert an effect in the model; such male attributes need not be heritable.

Differences among males in mating success may also arise as a consequence of sexual contests between males. Such contests will generally have both offensive and defensive aspects (Darwin 1859, 1871; Fisher 1958; Parker 1970a). These two aspects were termed sexual interference and sexual defence by Arnold (1976), and differences in male attributes may affect either or both of them. Thus males might differ in ability to interfere with the ongoing matings of other males and hence in capacity to usurp matings. Such sexual interference lowers the mating success of the defender, while raising the success of the interloper. Males might also differ in ability to defend against interference; that is,

there may be differences in capacity for sexual defence. All of the effects of the above possibilities are collected together and exert their influence in the model by changing the rate of successful mating,  $s_{ij}$ .

In some organisms, sexual interference may occur most frequently during the precopulatory display, that is, after male-female encounter but prior to insemination. In these cases, the capacities of males for sexual interference and sexual defence are important components of  $s_{ij}$ . In at least some species (e.g. toads, *Bufo bufo*, Davies & Halliday 1977, and elephant seals, *Miromanga angustirostris*, Cox & Le Boeuf 1977), females are believed to behave in such a way as to promote male contests prior to mating. Furthermore, female receptivity is likely to depend in a complex way upon physiological condition and past history. When considered with the male attributes discussed above, this implies that  $s_{ij}$  may be extremely difficult to partition into component parts (female choice and male contest). It may always be easier or necessary to observe directly a sufficient number of encounters between males and females to determine the probability of successful encounter. Alternatively, if the intensity of selection is the main point of interest, it may be easier to observe the consequences of the mating system, tabulate variances and means, and then solve for unknowns in equation (15).

With the present model, we can also permit females to choose males on the basis of male sexual attributes by assuming a correlation between male encounter rate,  $m_j$  (or  $e_{ij}$ ), and mating success given an encounter,  $s_{ij}$ . A positive correlation will increase the intensity of sexual selection by increasing the variance in effective mating rates,  $\sigma_{S^*}^2$  (see equation (15)). Note that the expression for the mating success rate of  $j$ -type males,  $S_j^*$ , contains the sum of products of encounter rate,  $e_{ij}$ , and success rate given encounter,  $s_{ij}$ . Female choice exerts its effects in the model through the latter term. Thus if females choose males with high encounter rates,  $e_{ij}$  and  $s_{ij}$  will be positively correlated, and the sum of products of these terms will be greater than it would be in the absence of correlation. Consequently, the variance in the effective mating rates of males,  $\sigma_{S^*}^2$ , will be inflated by female choice, and the intensity of sexual selection will be increased. A negative correlation would decrease the intensity of sexual selection; this would be the case if females chose males with the lowest encounter rates.

The runaway effects of sexual selection, first discussed by Fisher (1958), are limited by the extent of correlation between female choice and male attributes, and do not occur when this correlation is absent. The effect of female choice can be seen explicitly in our model; it affects the variance among males in the number of mates.

### The Effect of Sperm Precedence on the Intensity of Selection

We found that all cases of single-male paternity are equivalent in their effects on the intensity of sexual selection. This is one of our major results. In order for first- and last-male paternities to differ in their effects, one must invoke differential mortality among the males during the mating season. Such mortality alters the variance in mating success by affecting the relative proportions of different types of males as well as the mean encounter rate with females,  $\bar{m}$ . If all males incur identical increments in mortality or, equivalently, in sexual incapacity, these quantities are not affected and the intensity of sexual selection remains unchanged. A positive correlation between male mating rate and male mortality lowers the intensity of sexual selection in cases of last-male paternity but increases it in cases of first-male paternity. This is because such a correlation increases the effective frequency of 'slow' males late in the mating season. With last-male paternity, all females are still effectively available for insemination at this time, whereas with first-male paternity, few unmated and available females remain. Alternatively, one could imagine these same variables,  $p_j$  and  $\bar{m}$ , changing if the encounter rates were functions of time. O'Donald (1973, 1977) has conducted many simulations cogently illuminating the effects of early breeding on sexual selection.

Compared to single-male paternity, we see from equation (26) that paternity by representation of all inseminating males has no effect on the intensity of sexual selection because the variance in numbers of mates is unchanged. Rather, paternity by representation (sperm mixing) affects total selection by reducing the variation among males that achieve the same number of effective matings (see equation (32)). Consequently, sperm mixing lowers the sexual ratio of intensities,  $I_m/I_f$ , and thus the sex difference in reproductive success is lowered. However,  $I_f/I_m$ , the relative intensity of sexual selection on males, is actually increased.

### Application to Actual Populations

The present results provide some short-cuts useful in field studies of sexual selection. The most elusive quantity for estimation will often be the total variance among males in reproductive success (Howard 1979). This variance is critical in determinations of the intensity of total selection on males, but to estimate it directly one would have to enumerate the paternities of a large sample of progeny. In some circumstances this is quite feasible; for example, when progeny reside near their fathers or when modern electrophoretic or karyotypic techniques are applicable. In many circumstances, however, direct enumeration of paternities is difficult or impossible, although the intensity of total selection may be of major interest. In such circumstances, it may often be possible to estimate indirectly the total variance in male reproductive success by using equation (15) or (32). In the case of single-male paternity, it is sufficient to know the mean and variance of the number of progeny per female irrespective of their mates, the sex ratio (which should include sexually competent males even if they do not hold territories), and the mean and variance of the number of effective matings per male (again including those sexually competent males that fail to achieve matings). These quantities can then be substituted into equation (15) to calculate the total variance in male reproductive success or into equation (17) to calculate the total intensity. In the case of paternity by representation (sperm mixing), one must also know the harmonic mean number of matings per female to perform the analogous calculations.

When working with actual data and when population size is stable, the variances should be normalized to a mean number of two progeny per parent (methods given in Crow & Morton 1955). This normalization procedure depends strongly on the pattern of mortality. The two extreme cases considered by Crow & Morton (1955) were death of entire broods versus independent survivorship of individual offspring.

The intensity of sexual selection on males can be calculated directly if the mating success of a large sample of males can be observed. Two empirical approaches are possible. One can tabulate the mating success of males over the entire reproductive season and take its variance (Table III). Or, one can observe the mating rates of individual males and take the variance of this distribution, if it is reasonable to assume that individual mating rates are constant during the season. In either case one must have data on

effective matings (matings that actually yield progeny for the mating male). Alternatively, one can indirectly estimate the intensity of sexual selection if there are data on the total intensity of selection on males and the intensity of selection on female fertility by using equation (17).

Our results also clarify several issues raised by Payne & Payne (1977) in their important review of quantitative studies of sexual selection in birds. First, they point out that the sex ratio necessarily complicates a comparison of reproductive variance in the two sexes. Our partitioning of male reproductive variance removes this difficulty by incorporating sex ratio (see equation (15)). Second, they advocate comparisons of coefficients of variation in reproductive success (that is, standard deviations divided by means). We suggest instead that variance in reproductive success be divided by the square of mean success if the intensity of selection is the point of interest in a comparison. Such scaling of variance by the square of the mean yields a measure of selection intensity with straightforward theoretical meaning (Crow 1958) and also has the same statistical virtues as coefficients of variation. Our results also offer some instruction to such comparisons. In many mating systems the intensity of selection will be greater in males than in females as a mathematical necessity. Nevertheless, sampling errors can yield the opposite result in empirical work, and Payne & Payne (1977) provide some examples. In order to interpret such results correctly, it is necessary to consider not only the mathematical consequences of the mating system with models like those provided here, but also the effects of sampling errors.

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### Appendix

We are grateful to Professor James F. Crow for suggesting the following derivation. The variance in the number of progeny among males,  $V_m$ , can be viewed as having two components: (1)  $V_b$ , the variance between males with different numbers of mates and (2)  $V_w$ , the variance between males with the same number of mates. Considering these individually,

$$V_b = k^2 V_s \quad (\text{A1})$$

where  $V_s$  is the variance in the number of inseminations per male and  $k$  is the number of progeny per insemination (or mate), or  $\bar{X}_f$ .

The variance in the number of progeny of males due to variability in fertility of inseminated females is

$$V_w = \bar{n} V_f \quad (\text{A2})$$

where  $\bar{n}$  is the mean number of independent females inseminated per male.

We now consider special cases:

1. Each female is mated once and only once (or only the first or last insemination leads to progeny). Then  $\bar{n} = N_f/N_m = 1/R$  and we have

$$V_m = V_f/R + k^2 V_s \quad [\text{same as (15)}] \quad (\text{A3})$$

and

$$I_m = R I_f + I_s \quad [\text{same as (17)}] \quad (\text{A4})$$

2. If only a fraction  $P_s$  of females are inseminated,  $\bar{n} = P_s/R$ , and

$$I_m = R I_f / P_s + I_s \quad (\text{A5})$$

$I_f$  is now the index among inseminated females, not for all females.