

Don't Throw Bateman Out with the Bathwater!

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SYNOPSIS. Bateman identified two aspects of sexual selection. The first, called Bateman's principle, is that sexual selection favors increased promiscuity of males but not of females as a result of differences in parental investment in gametes. The second is that the variance in mate number of males is the fundamental cause of a sex difference in fitness variance. We argue that Bateman's insight about the source of sexual selection is more fundamental than his speculation about patterns of parental investment. We show that, when the sex ratio is 1:1, the average female must be as promiscuous as the average male, because each copulation involves one male and one female. Because mean male and female promiscuity are tied together in the same manner as mean male and female fitness, a sex difference in mating propensity must be the result of either (1) a sex difference in the covariance between matings and number offspring, or (2) Fisherian run-away sexual selection, wherein female reluctance to mate is a weak form of female choice. We show how female promiscuity can limit the evolution of male promiscuity, turning the central argument of parental investment theory on its head.

"The female, with the rarest exceptions, is less eager than the male . . . she is coy, and may often be seen endeavouring for a long time to escape."

"The intensity of intra-masculine selection is due to the greater dependence of the fertility of males on frequency of insemination." A. J. Bateman (1948)

Bateman (1948) identified the critical role of male fertility in sexual selection and suggested that variation among males in mate numbers was the fundamental cause of the sex difference in fitness variance. This sex-difference fitness variation is important to resolving what we have called the Quantitative Paradox of Sexual Selection (Shuster and Wade, 2003). As Darwin (1859) noted, in species with separate sexes, it is common for the males of closely related species to exhibit much greater differences in phenotype than the females, a macro-evolutionary pattern indicative of a very strong evolutionary force. Darwin identified male-male competition for mates or female choice of mates, to account for this taxonomic pattern. However, mechanism alone does not explain why the value of a trait to male reproductive fitness can handily outweigh opposing components of fitness in both sexes. How can sexual selection be one of the strongest evolutionary forces when it affects only one fitness component in only one sex and is opposed by selection in the other sex? Bateman's insight that males have a much greater fitness variance than females resolves this paradox. We can give it quantitative expression (see below) using the "opportunity for selection," a useful comparative measure of selection (Crow, 1958, 1962;

Shuster and Wade, 2003; Wade, 1979, 1995; Wade and Arnold, 1980).

Because males with the greatest numbers of mates will tend to have the highest fitness and because females invest more resources in gamete production than males (anisogamy), Bateman (1948, p. 364) further inferred that sexual selection favors increased male promiscuity: *"In most animals the fertility of the females is limited by egg production which causes a severe strain on their nutrition. In mammals the corresponding limiting factors are uterine nutrition and milk production, which together may be termed the capacity for rearing young. In the male, however, fertility is seldom likely to be limited by sperm production but rather by the number of inseminations or the number of females available to him."* He continued (Bateman 1948, p. 365) *"The primary feature of sexual selection is to be sure the fusion of gametes irrespective of their relative size, but the specialization into large immobile gamete and small mobile gametes produced in great excess (the primary sex difference), was a very early evolutionary step. One would therefore expect to find in all but a few very primitive organisms, and those in which monogamy combined with a sex ratio of unity eliminated all intra-sexual selection, that males would show greater intra-sexual selection than females. This would explain why in unisexual organisms there is always a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females. Even in derived monogamous species (e.g., man) this sex difference might be expected to persist as a relic."* These arguments are paraphrased in most textbooks and Bateman's principle is considered "one of the grounding truisms of behavioral ecology" (Knight, 2002; see also Trivers, 1972; Reynolds, 1996; Badyaev, 2004). However, recent work, especially that coupling behavioral studies with molecular markers for paternity analysis, has shown that female promiscuity is widespread and much less passive (Birkhead and Moller, 1998).

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What are we to do? Do we champion Bateman (1948) for his insight in identifying variance in mate numbers as the cause of a sex difference in selection intensity (Wade, 1979; Wade and Arnold, 1980; Shuster and Wade, 2003)? Or, do we vilify him for perpetuating a sexual stereotype of the indiscriminately eager male and the choosy passive female? We argue against throwing Bateman out with the bathwater because we view his insight about the source of sexual selection as more fundamental than his speculation about the consequences of patterns of parental investment. We show that average male and female promiscuity are tied together in the same manner as average male and female fitness. As a result, female promiscuity can limit male promiscuity and turn the central argument of parental investment theory on its head.

THE OPPORTUNITY FOR SEXUAL SELECTION

Mean male fitness, W_δ , equals mean female fitness, W_φ , multiplied by the sex ratio, R , expressed as the ratio, N_φ/N_δ (Fisher, 1958). Note that the sex ratio, R , is also the average number of mates per male. It is also the inverse of R_o , the ‘operational sex ratio’ (Emlen and Oring, 1977). The quantity, R_o , heuristically captures the ecological concept of females as a male reproductive resource: the greater the excess of males over females at the time of breeding, the greater the intensity of reproductive competition among males for mates. However, R , the reciprocal of R_o , is necessary for calculating the variance in mate numbers among males, Bateman’s cause of sexual selection.

Like the relationship between male and female mean fitness, the variance in male fitness is a function of the variance in female fitness (Wade, 1979). To calculate the total variance in male fitness, V_δ , let p_k be the fraction of males that have k mates ($0 < k < N_{females}$), where, for example, p_0 is the frequency of males with no mates at all and, p_m equal to $\sum p_j = (1 - p_0)$, is the frequency of successfully mating males. Let the distribution of female reproductive success have a mean, X , and variance, V_φ , independent of the male(s), although this latter assumption can be relaxed (see Wade, 1979; Shuster and Wade, 2003). It follows that R equals $\sum j p_j$, the mean number of mates per male, and the variance in the number of mates per male is V_{mates} or $\sum p_j(j - R)^2$.

With these definitions, we can express the total variance in male fitness, V_δ as the average variance within the categories of mating males, $\sum p_j(jV_\varphi)$, plus the variance among the mating categories, $\sum p_j(jX - RX)^2$,

$$V_\delta = \sum p_j(jV_\varphi) + \sum p_j(jX - RX)^2 \quad (\text{Eq. 1a})$$

$$= RV_\varphi + X^2V_{mates}. \quad (\text{Eq. 1b})$$

Bateman’s (1948) insight is made explicit by equation 1b: V_δ exceeds V_φ because males vary from one another in mate numbers, *i.e.*, $V_{mates} > 0$. The effect of variation among males in mate numbers on male fitness is illustrated in Figure 1, where V_δ is so much greater than V_φ not only because a few males have

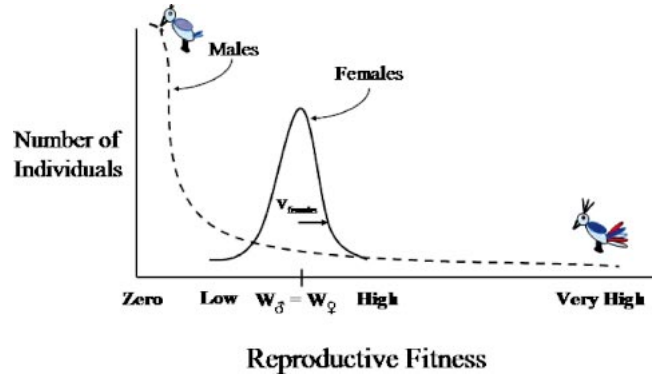


FIG. 1. Schematic diagram illustrating the effect of variation in mate numbers on the distribution of offspring among males. The opportunity for selection tends to be much greater when males vary from one another in numbers of mates.

large numbers of mates but also because so many males have no mates at all. Note the mean fitnesses of males and females are equal. However, the variance in absolute male fitness is not as useful as a comparative measure based on relative male fitness, called I , the opportunity for selection (Crow, 1958, 1962; Wade, 1979, 1995; Wade and Arnold, 1980). Because the relative fitness of an individual equals its absolute fitness divided by the population mean fitness, the variance in relative fitness equals the variance in absolute fitness divided by the square of mean absolute fitness.

The opportunity for selection on males, I_δ , is the variance in male relative fitness, which we obtain by dividing the variance in absolute male fitness, V_{mates} , from equation 1b by the square of mean male fitness, $(RX)^2$. We find

$$(V_\delta [RX]^2) = (RV_\varphi/[RX]^2) + (X^2V_{mates}/[RX]^2) \quad (\text{Eq. 2a})$$

$$I_\delta = (1/R)(I_\varphi) + I_{mates} \quad (\text{Eq. 2b})$$

$$I_\delta = (R_o)(I_\varphi) + I_{mates}. \quad (\text{Eq. 2c})$$

The ratio of the variance in mate numbers, V_{mates} , to R^2 , the square of the mean mate numbers, is I_{mates} , component of the total opportunity for selection that arises from the contribution of mating variance to relative fitness. We see from equation 2c that R_o is not the sex difference in the opportunity for selection although it is an important component of it.

When R equals 1 (and also R_o), we can reduce equation 2c to

$$I_\delta = I_\varphi + I_{mates}. \quad (\text{Eq. 3})$$

Subtracting I_φ from both sides of equation 3, we see that it is the contribution of sexual selection to male relative fitness, I_{mates} , that causes a sex difference in selection,

$$I_\delta - I_\varphi = I_{mates}. \quad (\text{Eq. 4})$$

Whenever males vary from one another in mate numbers, I_{mates} exceeds zero and provides a useful, standardized measure for comparing sexual selection

across taxa or mating systems (Wade, 1979, 1995; Wade and Arnold, 1980; Shuster and Wade, 2003). We expect that the sex difference in strength of selection will be correlated with the degree of sexual dimorphism because selection operates in different directions on males and females for the kinds of traits exaggerated in males that vary across closely related taxa (Darwin, 1859; Wade and Shuster, 2004).

THE OPPORTUNITY FOR SELECTION AND PHENOTYPIC CHANGE

The variance in relative fitness sets an upper bound on the total change in phenotype that can occur in a single generation. We can see this from the standard “breeders equation” of quantitative genetics, which governs the formal theory of phenotypic evolution in artificial and natural selection. The rate of change of mean fitness itself is

$$\Delta W/W = h_w^2 Cov(W,w)/W = h_w^2 I, \quad (\text{Eq. 5})$$

where we note that the covariance of absolute fitness with relative fitness, $Cov(W,w)$, divided by W , equals the variance in relative fitness, V_w or I . Phenotypic evolution, defined as change in the mean phenotype, Z , and expressed as ΔZ , occurs at a rate determined by h_z^2 , the heritability of the variation in phenotypic value(s), z , and the covariance between phenotypic value and relative fitness, w , $Cov(z,w)$:

$$\Delta Z = h_z^2 Cov(z,w). \quad (\text{Eq. 6})$$

Thus, total selection on all phenotypes must be partitioned across the variance in relative fitness, I . Differently put, only a fraction of the total variance in relative fitness can be leveraged by natural selection to produce change in any particular phenotypic and, furthermore, only a fraction of the variation in phenotypic value is heritable (*i.e.*, $0 < h_z^2 < 1$). As a general rule of thumb, the greater the number of traits under selection, the smaller the average change in the mean value of any particular phenotype, owing to negative phenotypic and genetic correlations among traits.

MEASURING I_δ AND I_\varnothing

In order to measure the opportunity for sexual selection, we must be able to measure the relative fitness of males and females or at least a reasonable proxy of it. Offspring numbers are often used as an indicator of fitness (see Shuster and Wade, 2003 for additional discussion) and we present a hypothetical scenario in Figure 2. Here, O represents offspring number and the first subscript represents the mother and the second the father. For example, the brood size of male 1 in Figure 2 equals $(O_{1,1} + O_{2,1})$ because he has offspring with two different females. The assignment of maternity and paternity can be difficult in some species without molecular markers. Average male fitness, W_δ , equals $\sum_\delta O_{i,j}/N_\delta$ and average female fitness, W_\varnothing , equals $\sum_\varnothing O_{i,j}/N_\varnothing$, where \sum_δ is the sum over the second subscript, j , and \sum_\varnothing is the sum over the first subscript, i . Since every offspring has one mother and one father,

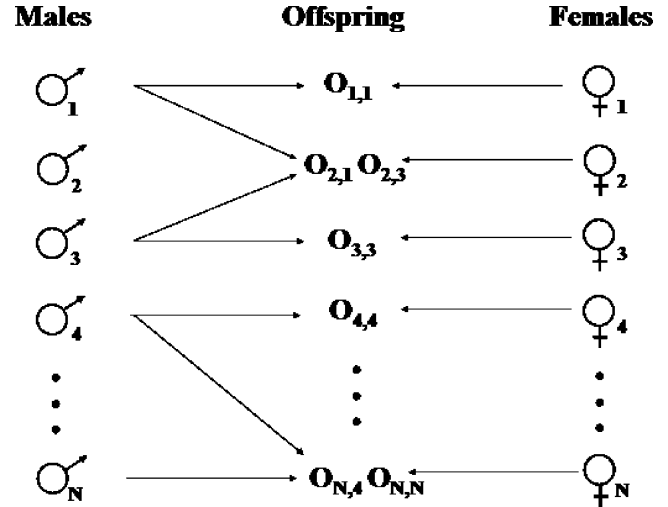


FIG. 2. The schematic diagram illustrates the apportionment of offspring among males and females. Each female i produces O_i offspring that are sired by one or more males as indicated by the arrows from the males and by the females as indicated by the second subscript. For example, male 1 has two mates, females 1 and 2; he is the sole sire of the offspring, $O_{1,1}$ of female 1, but shares parentage of the female 2's brood, $O_{2,j}$, with male 3 who sires $O_{2,2}$ of this female's offspring. Male 2 has no mates and sires no offspring. Paternity and maternity analysis of offspring may be necessary for making such assignments in natural populations.

$\sum_\varnothing O_{ij}$ must equal $\sum_\delta O_{ij}$, and we have $W_\delta = R W_\varnothing$. The sex-specific variances in fitness are

$$V_\delta = \sum_\delta (W_\delta - O_{i,j})^2/N_\delta \quad \text{and} \quad (\text{Eq. 7a})$$

$$V_\varnothing = \sum_\varnothing (W_\varnothing - O_{i,j})^2/N_\varnothing. \quad (\text{Eq. 7b})$$

Dividing equations 7 by the squared male and squared female mean fitness, respectively, gives us I_δ (*i.e.*, $V_\delta/[W_\delta]^2$) and I_\varnothing .

Variation among females in clutch numbers tends to increase the opportunity for selection on females and decrease the sex difference in the total opportunity for selection (Wade, 1979; Shuster and Wade, 2003). Selection is weaker on females when there is no variance in clutch numbers and stronger when there is variance in clutch numbers (Fig. 3). First, we partition the offspring of all females into two components: (1) k_i , the number of clutches of the i -th female; and, (2) $O_{i,l}$, the number of eggs in the l -th clutch of the i -th female. This permits us to partition the total variance in offspring numbers among females into two components, within and among clutches,

$$V_\varnothing = V_{within} + (O)^2 V_{clutch} \quad (\text{Eq. 8})$$

Where O is the mean number of eggs per clutch and W_\varnothing is the product of the mean clutch number, k , and O when clutch number and clutch size are independent. (The independence assumption can be relaxed [*cf.* Wade, 1979 or Shuster and Wade, 2003]) Dividing again by $(W_\varnothing)^2$, we find that

$$I_\varnothing = (1/k)^2 I_{within} + I_{clutch} \quad (\text{Eq. 9})$$

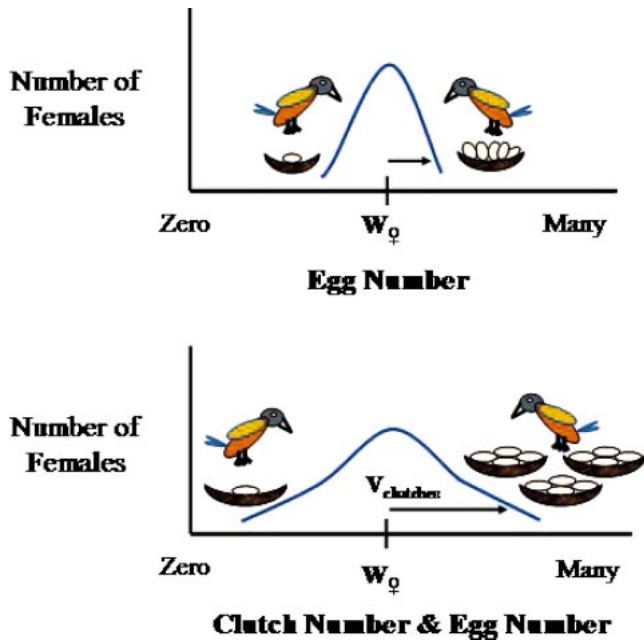


FIG. 3. Schematic diagram illustrating the effect of variation in clutch numbers on the distribution of offspring among females. The opportunity for selection tends to be much greater when female vary from one another in numbers of clutches laid.

Variation in clutch numbers among females changes the relationship between I_δ and I_φ .

THE SEX DIFFERENCE IN OPPORTUNITY FOR SELECTION, $\{I_\delta - I_\varphi\}$

The sex difference in the opportunity for selection, $\{I_\delta - I_\varphi\}$, equals I_{mates} in the simplest case as we showed above. It can also be expressed as

$$I_{mates} = HP \tag{Eq. 10}$$

where H is mean harem size of mating males (*i.e.*, $[R/(1 - p_0)]$) and P is Lloyd's (1967) measure of "Patchiness" or, equivalently,

$$I_{mates} = (1/P_m)I_H + I_{mating} \tag{Eq. 11}$$

where I_H is the variance in mate number among mating males (*i.e.*, not counting the non-mating males) divided by H^2 and I_{mating} is the variation in fitness between mating and non-mating males. The last equation is useful for determining how much of the variance in relative male fitness is owing to mating *versus* not mating in relation to the number of mates a male can acquire and guard, given that he mates (Wade and Shuster, 2004). Different aspects of the male phenotype might be involved in these two different aspects of male reproductive competition (*cf.* discussion in Shuster and Wade, 2003).

INTERPRETATION OF BATEMAN

To account for the sex difference in eagerness to copulate, a common interpretation of Bateman's Principle (Wilson, 1975; Thornhill and Alcock, 1983; Arnold, 1994; Levitan, 1998; Lorch, 2002) is this: If a

male mates with several females, he increases his offspring numbers, but in contrast, if a female mates with several males, her fitness is reduced. The decline in fitness for females is often attributed to time wasted mating, risk of mating, or risk of disease. Therefore, selection results in males that are promiscuous and females that are choosy. Let us quantify the definition of promiscuity for males and females, see how they are related to one another, and explore this expectation.

There are two common definitions of promiscuity. One definition, mate-number promiscuity (see Shuster and Wade, 2003, chpt. 4) is mate numbers, counting multiple matings by a given male with the same female as only one mating. Under this definition, a male or female must have multiple mating partners to be promiscuous. This definition may not be appropriate when sperm competition and fertilization are affected by the number and/or order of copulations that one or more males has with a single female (Shuster, 1991; Eberhard, 1996; Tram and Wolfner, 1998; Neubaum and Wolfner, 1999). Promiscuity is also defined in terms of the numbers of matings per male and per female, counting each mating, whether with the same or a different partner, as a single event. We call this mating-number promiscuity (Shuster and Wade, 2003, chpt. 4). Here, we use the second definition and define "promiscuity" for each sex as the average number of matings per individual in each sex. Let P_δ and V_{P_δ} represent the mean and variance of male promiscuity and, similarly, let P_φ and V_{P_φ} characterize the first two moments of the distribution of female promiscuity. Let c_i be the number of matings of the i -th male, who may have them with >1 female. With these definitions, we find that

$$P_\delta = \sum_\delta c_i/N_\delta \quad \text{and} \tag{Eq. 12}$$

$$V_{P_\delta} = \sum_\delta (c_i - P_\delta)^2/N_\delta \tag{Eq. 13}$$

If c_j is the number of matings of the j -th female, who may have them with >1 male, we find that

$$P_\varphi = \sum_\varphi c_j/N_\varphi \quad \text{and} \tag{Eq. 14}$$

$$V_{P_\varphi} = \sum_\varphi (c_j - P_\varphi)^2/N_\varphi. \tag{Eq. 15}$$

Because each mating involves one male and one female, we know that the total number of matings by males, $\sum_\delta c_i$, must be equal to the total matings by females, $\sum_\varphi c_j$. Thus, just like male and female mean fitness, average male and female promiscuity, P_δ and P_φ , respectively, are related through the sex ratio:

$$P_\delta = RP_\varphi. \tag{Eq. 16}$$

When R (*i.e.*, N_φ/N_δ) is equal to one, not only must W_δ equal W_φ , but P_δ must also equal P_φ . Clearly, it is not possible for males to be more promiscuous than females or have higher mean fitness unless $R > 1$. And yet, the consensus among even the most casual observers of sexual behavior is that males show greater

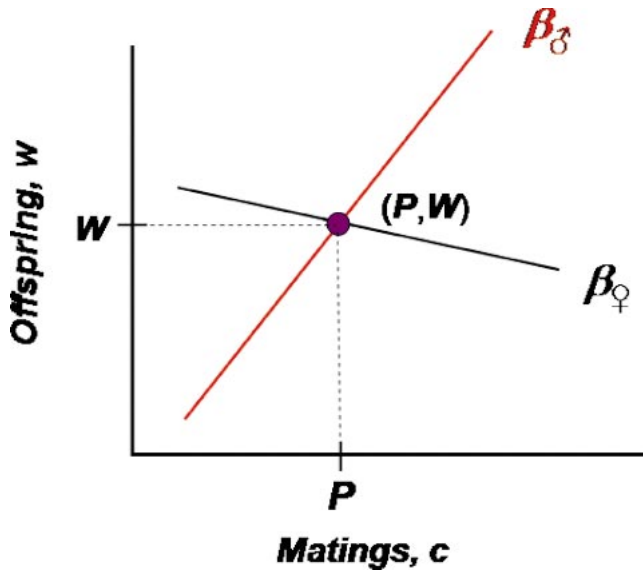


FIG. 4. The sex difference in the covariance between number of matings and number of offspring. It must often be the case that $\beta_{\varnothing}(c,w) < 0 < \beta_{\sigma}(c,w)$, which is the condition for selection to favor increased copulation in males but decreased copulation in females (see eq. [6] in text).

interest in mating than females. What is the source of the sex-difference in interest in mating?

Sexual conflict over mating arises because of a sex-difference in the covariance between number of copulations and fitness. For males, this covariance is defined as

$$\text{Cov}_{\sigma}(c, w) = \frac{\sum_{\sigma} c_i w_i}{N_{\sigma}} - P_{\sigma} W_{\sigma} \quad (\text{Eq. 17})$$

and, for females, it equals

$$\text{Cov}_{\varnothing}(c, w) = \frac{\sum_{\varnothing} c_j w_j}{N_{\varnothing}} - P_{\varnothing} W_{\varnothing} \quad (\text{Eq. 18})$$

Note that, when R is one, $P_{\sigma} W_{\sigma}$ must equal $P_{\varnothing} W_{\varnothing}$. If the covariance between mating numbers and fitness is positive for both sexes, then both sexes will be selected to be more promiscuous. In contrast, if the covariances are both negative, then promiscuity will be selected against in both sexes. Hence, any sex-difference in the interest in mating must result from selection resulting from differences in the sign of the covariance between number of matings and fitness. That is, it must often be the case that $\text{Cov}_{\varnothing}(c,w) < 0 < \text{Cov}_{\sigma}(c,w)$, which is the condition for selection to favor increased mating in males but decreased mating in females (see equation 6 above and Fig. 4). As a result of the sexually antagonistic selection on interest in mating, speaking colloquially instead of quantitatively, males may evolve to be “promiscuous” while females become “coy.”

It is possible that a reluctance to mate on the part of females is a weak form of female mate choice, such that only the largest or most vigorous males are suc-

cessful in mating with the most reluctant females (e.g., McCauley and Wade, 1978). If so, the most eager or vigorously courting males will not only have more mates but their mates will tend to be, on average, more reluctant or coy to mate. If both the male and female mating tendencies are heritable, then sons will be more eager and daughters will be more coy in the manner of Fisher’s run-away process of sexual selection.

An alternative explanation, other than this run-away scenario, is that males may adopt behaviors that limit the promiscuity of their mates, even at the expense of their own mate numbers. Because P_{σ} equals RP_{\varnothing} , if P_{σ} exceeds 1, then so does RP_{\varnothing} , and the multiplicity of insemination that follows multiple copulations by females with more than one partner leads to inevitably to sperm competition. Thus, it is difficult to consider promiscuity without also considering cryptic female choice and sperm competition.

QUANTITATIVE ESTIMATES OF SPERM COMPETITION INTENSITY

“Sperm competition can be defined as competition between the ejaculates of different males over fertilization of a given set of eggs” (Parker, 1990, p. 120; see also Levitan, 1998). In species with internal fertilization, it takes place within the reproductive tract of multiply inseminated females (Birkhead and Møller, 1998). For such species, the mean and variance of the distribution of copulations across females to a first approximation determines the average opportunity for sperm competition. This is especially true when ejaculates are considered equivalent tickets in a lottery of fertilization. However, although multiple copulations by females are a necessary component of sperm competition, variations within or among males in the number, volume, or order of ejaculates as well as in the competitive ability of ejaculates could clearly change the outcome of sperm competition, making paternity analysis of resulting offspring essential. Here, for the sake of simplicity and in the absence of guiding data, we will assume that one copulation is like another and treat them as equivalent in their likelihood of fertilization.

The number of copulations between the i -th male and the j -th female is c_{ij} . Summing over all females (i.e., over all j), $c_i = \sum_j c_{ij}$, we have the total number of matings of the i -th male or P_i . Summing over all males (i.e., over all i), $c_j = \sum_i c_{ij}$, we have the total number of matings of the j -th female or P_j . Thus, of the P_j ejaculates carried by the j -th female, $(P_j - c_{ij})$ are from males other than the i -th male. The sperm of the i -th male experiences sperm competition from other males within the j -th female as $c_{ij}(P_j - c_{ij})$. If we sum this over all females and divide by the total number of copulations or ejaculates of the i -th male, $\sum_j c_{ij}(P_j - c_{ij}) / \sum_j c_{ij}$, we have m_{pi}^* , the sperm competition that this male experiences per copulation as a result of his mating behavior across the population of females. We can show that this is a function of $P_{i\varnothing}$, the promiscuity of the mates of this male:

$$m_{P_i}^* = \frac{\sum_j c_{ij}(P_j - c_{ij})}{\sum_j c_{ij}} \quad (\text{Eq. 19a})$$

$$m_{P_i}^* = \frac{\sum_j c_{ij}(P_j) - \sum_j c_{ij}^2}{\sum_j c_{ij}} \quad (\text{Eq. 19b})$$

$$m_{P_i}^* = P_{i\varphi} + \frac{\text{Cov}_i(c, P_\varphi)}{c_i} - k_i, \quad (\text{Eq. 19c})$$

where c_i is the mean number of copulations by the i -th male per female, $\text{Cov}_i(c, P_\varphi)$ is the covariance for the i -th male of his copulations with the promiscuity of his mates, and k_i is the mean crowding of copulations by the i -th male across females. The $\text{Cov}_i(c, P_\varphi)$ term is interesting because it is here that a male could adjust his mating behavior in accordance with his perception of the behavior of each of his mates. Equation 19c describes the sperm competition experienced by the i -th male. Clearly, the greater the average promiscuity of his mates, $P_{i\varphi}$, the greater the intensity of sperm competition he experiences. Thus, female promiscuity affects male-male competition for fertilization. Male behaviors or adaptations that reduce the average promiscuity of females may increase the likelihood of successful fertilization by reducing sperm competition.

Mate guarding is an effective strategy for mitigating the intensity of sperm competition by reducing $P_{i\varphi}$. The sperm competition experienced by the i -th male can be made *more intense* if $\text{Cov}_i(c, P_\varphi)$ is positive, which occurs when the i -th male copulates most frequently with the most promiscuous of his mates. It can be made *less intense* if $\text{Cov}_i(c, P_\varphi)$ is negative and the male copulates most frequently with the least promiscuous of his mates. This covariance term may be important to the evolution of mechanisms for the removal of the sperm of competing males. The more positive the average value of this covariance is across males, the more sperm competition will predominate as a component of sexual selection. The more negative the average value of this covariance is, the less important sexual selection via sperm competition will be. The final term, k_i , measures the distribution of copulations by the i -th male across his mates. It is required for variance in c_{ij} and is discussed in greater detail in Shuster and Wade (2003). The most important evolutionary outcome of copulation is fertilization (Fig. 2) and we relate fertilization to offspring numbers in the following section.

There are mating systems, like leks, in which females visiting the lek are virgins and only the multiply chosen males are remating and promiscuous. In these systems, if females visit a lek, mate once, and go away to raise offspring, the average number of mates per female is 1 and, if the sex ratio is unity, the average for males is also one, even though some males are more promiscuous than others. Here, female mating

behavior limits male mean promiscuity and obviates sperm competition.

FERTILIZATIONS, FITNESS OUTCOME OF SPERM COMPETITION, AND FEMALE PROMISCUITY (PROCEPTIVITY)

With random fertilization in proportion to copulation or ejaculate number, the number of offspring of the j -th female sired by i -th mating male is given by $O_j(c_{ij}/P_j)$. If the covariance between offspring number and promiscuity, $\text{Cov}_\varphi(O, P)$, is zero for females, then there is no fitness benefit or cost to a female from repeated matings. In this case, the *average offspring gained per copulation* by a male in the population equals

$$O_\delta = W_\varphi/H_{P_\varphi} \quad (\text{Eq. 20})$$

where H_{P_φ} is the *harmonic mean number of mates per female*. That is, the increment in male fitness associated with additional matings depends upon the harmonic mean promiscuity of females. Whenever, V_{P_φ} (cf. equation 15) > 0 , H_{P_φ} is always less than P_φ . Thus, female promiscuity is limiting to males and, whenever females vary in their tendency to copulate, those females with the fewest numbers of mates disproportionately determine their value to males of seeking additional mates. This implies that, when virgin females are relatively abundant, males might be under strong selection to seek additional mates. However, in contrast to general expectations about male promiscuity, when only mated females are available, the fitness gain to a male in seeking additional matings may be low. Furthermore, if by seeking additional matings a male increases the average promiscuity of his mates, $P_{i\varphi}$ (cf. equation 19a), by leaving them unattended. Thus, contrary to Bateman's often paraphrased statement that, "*In the male, . . . fertility is seldom likely to be limited by sperm production but rather by the number of inseminations or the number of females available to him,*" selection will usually select *against* an increase in male promiscuity.

As an example, consider two males, A and B, mating with females whose average number of offspring is W_φ . Let male A mate with only one female and guard his mate so that $(1/H_{A\varphi})$ is 1; as a result, W_A equals W_φ . Let male B mate with two females but does not guard either one. If one of his unguarded females mates twice with some other male, and the other female mates three times, then $(1/H_{B\varphi})$ is $(1/2)([1/2] + [1/3])$ and W_B equals $0.833W_\varphi$. Thus, despite having two mates, male B has a lower fitness because his mates are more promiscuous than those of male A, which has a single, guarded mate. It is matings with females with the lowest promiscuity that give a male the largest increment in fitness.

CONCLUSIONS

We can quantify Bateman's insight concerning the relationship between male mate numbers and sexual selection through equation 3, $I_\delta = (1/R)I_\varphi + I_{\text{mates}}$

However, we also show that, because the sexes are equally promiscuous, $P_{\delta} = RP_{\phi}$, the common interpretation of Bateman's insight requires additional careful consideration. In particular, we find that sexual conflict over interest in mating arises because of a sex difference in sign of the covariance between copulation and relative fitness, $\text{Cov}_{\phi}(c, w) < 0 < \text{Cov}_{\delta}(c, w)$. Since sperm competition becomes a potentially important factor whenever P_{ϕ} exceeds 1, it becomes critical to evaluate how female promiscuity can limit the gain in male fitness that attends an increase in mate numbers. We find that, if obtaining additional mates implies an increase in the promiscuity of females already mated, then seeking additional matings may not be favored in males.

A definite relationship between mating behavior and fitness is easier to assume in theory than it is to document in practice. We need more data on offspring paternity in order to incisively relate theory to patterns observed in nature.

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