

ON THE OPPORTUNITY FOR SEXUAL SELECTION, THE BATEMAN GRADIENT AND THE MAXIMUM INTENSITY OF SEXUAL SELECTION

Adam G. Jones^{1,2}

¹*Department of Biology, Texas A&M University, 3258 TAMU, College Station, Texas 77843*

²*E-mail: agjones@tamu.edu.*

Received November 19, 2008

Accepted January 8, 2009

Bateman's classic paper on fly mating systems inspired quantitative study of sexual selection but also resulted in much debate and confusion. Here, I consider the meaning of Bateman's principles in the context of selection theory. Success in precopulatory sexual selection can be quantified as a "mating differential," which is the covariance between trait values and relative mating success. The mating differential is converted into a selection differential by the Bateman gradient, which is the least squares regression of relative reproductive success on relative mating success. Hence, a complete understanding of precopulatory sexual selection requires knowledge of two equally important aspects of mating patterns: the mating differential, which requires a focus on mechanisms generating covariance between trait values and mating success, and the Bateman gradient, which requires knowledge of the genetic mating system. An upper limit on the magnitude of the selection differential on any sexually selected trait is given by the product of the standard deviation in relative mating success and the Bateman gradient. This latter view of the maximum selection differential provides a clearer focus on the important aspects of precopulatory sexual selection than other methods and therefore should be an important part of future studies of sexual selection.

KEY WORDS: Mating differential, mating success, polygyny, polyandry, reproductive success, selection differential.

Sexual selection often is defined as selection arising as a consequence of competition for access to mates (Andersson 1994). This definition retains the essence of Darwin's (1871) original description of sexual selection and refers primarily to precopulatory sexual selection. With respect to precopulatory sexual selection, it is noncontroversial to suggest that the mating system is related to the intensity of sexual selection (Emlen and Oring 1977; Andersson 1994). For example, polygynous species are expected to experience stronger sexual selection on males than are monogamous species (Clutton-Brock et al. 1977; Payne 1984; Wade and Shuster 2004). This realization dates back to Darwin (1871) and has been supported by a number of comparative studies (Clutton-Brock et al. 1980; Møller 1997; Bro-Jørgensen 2007). Despite the lack of controversy associated with the qualitative idea of the

existence of a relationship between the mating system and the intensity of sexual selection, the development of methods for the quantification of mating patterns has been surprisingly difficult and contentious. The debate partly stems from misunderstanding and vagueness with respect to the meaning of mating system variables and their connections to selection theory, so the goal of this report is to provide an accessible treatment of the most widely used measures of mating systems and to consider the relationships between them.

The late 1970s and early 1980s witnessed the beginning of a new era of quantitative theory regarding sexual selection. The rediscovery of A. J. Bateman's (1948) classic paper (Trivers 1972), developments in mating system theory (Emlen and Oring 1977), and advances in quantitative genetics (Lande 1979) set the stage

for a more quantitative view of mating patterns with links to formal selection theory. Early developments along these lines were highly influenced both by Bateman's (1948) paper and by James Crow's "opportunity for selection" (Crow 1958). In a simple derivation, Michael Wade (1979) showed that, under a model of strict polygyny, the opportunity for selection is directly related to the variance in relative mating success, which came to be known as the "opportunity for sexual selection" (Wade and Arnold 1980; Arnold and Wade 1984a,b; Arnold 1986; Arnold and Duvall 1994). This initial progress relating mating systems to the potential for selection was rapidly greeted by severe criticism (Clutton-Brock 1983; Sutherland 1985a,b; Koenig and Albano 1986; Grafen 1987; Sutherland 1987; Hubbell and Johnson 1987; Grafen 1988). Rather than summarize the debate, which includes numerous valid points from both sides, I will attempt to describe our current state of understanding in a straightforward way.

The other major development in mating system theory related to Bateman's (1948) study concerned the introduction of the "Bateman gradient" (Arnold and Duvall 1994). While Bateman saw the higher variances in mating success and reproductive success in males relative to females as signs of sexual selection, he saw the stronger correlation between mating success and reproductive success in males as the cause of sexual selection (Bateman 1948; Arnold and Duvall 1994). Arnold and Duvall (1994) showed that this relationship between number of mates and number of offspring, which they called the sexual selection gradient, was the final path to fitness for all sexually selected traits in a path analysis treatment of the problem. In other words, they showed that differential mating success results in differential fitness only if the sexual selection gradient is nonzero. Arnold and Duvall (1994) also proposed that the sexual selection gradient is best estimated as a least-squares regression of reproductive success on mating success. This gradient came to be known as the "Bateman gradient" (Andersson and Iwasa 1996) to distinguish it from selection gradients on phenotypic traits (Lande and Arnold 1983). A steep Bateman gradient thus indicates a direct fitness benefit to multiple mating in terms of number of offspring, resulting in precopulatory sexual selection on traits correlated with mating success. A very shallow slope, however, implies that very little fitness will be gained per mating event, such that traits correlated with mating success will experience weak or no selection. Empirical and theoretical results seem to show that the Bateman gradient has utility in the study of sexual selection (Jones et al. 2000, 2002; Lorch 2002; Becher and Magurran 2004; Lorch 2005; Rios-Cardenas 2005; Mills et al. 2007; Webster et al. 2007; Lorch et al. 2008).

Over the last decade, several other ways of quantifying mating patterns with respect to sexual selection have been proposed and tested in various theoretical and empirical ways. For example, authors have suggested the use of Morisita's index (Morisita 1962), the index of resource monopolization (Ruzzante et al.

1996), or Nonacs' B-index (Nonacs 2000) as measures of mate monopolization (Kokko et al. 1999; Fairbairn and Wilby 2001). Well over a dozen other possible methods are summarized by Kokko et al. (1999). For some purposes, some of these other methods may be preferable to the ones based on Bateman's observations. I am here concerned with selection in particular, however, and these other methods possess no clear connections to formal selection theory. Such connections could be developed in principle, but little progress has been made on this front for metrics other than those inspired by Bateman (1948). Consequently, I focus on variables related to Bateman's principles here.

It is clear that precopulatory sexual selection will operate only if a sex exhibits variance in mating success, variance in reproductive success, and a nonzero Bateman gradient, but how are these variables related to one another? Here, I review theory related to the opportunity for selection, the opportunity for sexual selection and the Bateman gradient. In an attempt to cultivate an intuitive understanding of these variables, I keep the mathematics simple but as complete as possible. Finally, I consider the relationships between these measures and suggest a slightly improved way of thinking about precopulatory sexual selection. These considerations lead to a new metric of the maximum intensity of precopulatory sexual selection, which may be more intuitively appealing than current ways of quantifying mating patterns.

Mating Success and Reproductive Success

If precopulatory sexual selection arises as a consequence of competition for access to mates, then the currency of sexual selection should be the number of mates or the number of offspring produced during a selection episode. For example, a selection episode could be a particular breeding season. Individuals that compete successfully for access to mates will have greater mating success, where mating success is defined as the number of individuals with which successful mating takes place. A successful mating event would typically be one in which gametes are exchanged in some way, although the exact definition may be debatable. In species with large clutches, such as most fish and amphibians, virtually every successful mating event results in the production of some zygotes, so mating success can be inferred from the number of individuals of the opposite sex with which an individual produces biological offspring (Arnold and Duvall 1994; Jones et al. 2004, 2005). In species with very small families, such as birds and mammals, some males may transfer sperm that never fertilize an egg, and the measurement of mating success in these organisms may be more difficult (Dewsbury 2005; Parker and Tang-Martinez 2005).

Reproductive success, on the other hand, is defined as the total number of progeny produced during the selection episode.

Hence, reproductive success is the quantity most closely associated with Darwinian fitness. If an individual's life is divided into a series of selective episodes, some of which are driven by sexual selection and some of which are dominated by natural selection, then reproductive success provides the most direct measurement of fitness during one of these sexual selection episodes. However, the interpretation is not entirely straightforward, as even during a particular breeding season, some of the variation in reproductive success may be caused by factors other than competition for access to mates, such as fecundity selection or chance events. Regardless, reproductive success, as a measure of fitness, must take center stage in the study of sexual selection.

The introduction of molecular markers to behavioral ecology over the last several decades permits the measurement of mating and reproductive success in unprecedented detail (Hughes 1998; Avise et al. 2002; Jones and Ardren 2003). Most studies aimed at understanding the intensity of sexual selection will benefit from some sort of molecular assessment of paternity or maternity, possibly augmented by behavioral observations. One clear advantage to such studies is that they allow the quantification of realized paternity and maternity, thus measuring the true currency of Darwinian selection. Fortunately, advances in high-throughput genotyping and data analysis techniques make such studies feasible.

Selection

Many sexually selected characters are quantitative traits, so their evolution under selection is described by the univariate breeder's equation

$$R = h^2 s, \quad (1)$$

where R is the response to selection, s is the selection differential, and h^2 is the heritability of the trait (Falconer and Mackay 1989). For the purposes of the study of selection, these three variables can be treated separately. Selection is not the same thing as a response to selection. Rather, selection refers to a nonrandom association between trait values and survival or reproduction, so selection can be measured in principle even when a response to selection is impossible (i.e., when $h^2 = 0$). This realization allows us to separate the study of selection differentials from the study of heritability, potentially simplifying the empirical assault on these issues. It also allows us to focus on the selection differential as the actual measure of the intensity of selection.

The selection differential is often defined as the difference in trait mean before and after selection (Lande 1979), or equivalently, as the mean trait value of the breeders minus the mean of the entire population of adults (Lynch and Walsh 1998). The selection differential is also equivalent to the covariance between trait values and relative fitness (Robertson 1966; Price 1970). This latter

definition will be more convenient for the current treatment. With respect to particular sexual selection episodes, absolute fitness will typically be measured as reproductive success by counting the number of offspring produced by each individual as Bateman (1948) did. Each individual's relative fitness is calculated by dividing the reproductive success of that individual by the mean reproductive success for all individuals of the appropriate sex.

In the analysis of selection, it is often desirable to measure selection differentials in terms of phenotypic standard deviations (Lande and Arnold 1983). One way to accomplish this goal is to standardize traits to have a mean of zero and a standard deviation of unity before the calculation of the selection differential by subtracting the mean trait value from each individual's value and then dividing each value by the trait standard deviation. The standardized selection differential (s') is then the covariance between the standardized trait values and relative fitness (i.e., relative reproductive success; Lande and Arnold 1983)

$$s' = \text{cov}(\text{standardized trait}, \text{relative fitness}). \quad (2)$$

The other way to calculate a standardized selection differential is to calculate the covariance between absolute trait values and relative fitness, which gives a selection differential (s), and then divide it by the trait phenotypic standard deviation to obtain s' . It is also worth noting that in the univariate case, the standardized selection differential (s') is equal to the standardized selection gradient, β' (Lande and Arnold 1983).

An estimate of the heritability of a sexually selected trait will not be accessible from a typical study of sexual selection within a breeding season, so it makes sense to focus on the selection differential rather than the response to selection. In other words, a central issue in sexual selection concerns how various aspects of reproductive ecology and environmental factors result in particular selection differentials on sexually selected traits. Thus, the selection differential is interesting in its own right and is a valid focus of studies of sexual selection. However, it is necessary to keep in mind that a complete understanding of the evolutionary trajectory of a trait will require separate studies of the heritabilities and genetic correlations of sexually selected traits (Lande and Arnold 1983).

The Opportunity for Selection

What is the opportunity for selection and why is it important? Here, I review Crow's original derivation (Crow 1958). The opportunity for selection is closely related to Fisher's fundamental theorem of natural selection (Fisher 1930; Crow 2002), which states that the rate of increase in fitness in a population is equal to the additive genetic variance in fitness. The opportunity for selection, originally called the "index of total selection" (Crow 1958), is a quantification of the rate at which absolute fitness

will increase in the population relative to the standing variance in absolute fitness, assuming that all variance in fitness is due to additive genetic effects (i.e., the heritability of fitness is one).

The derivation of the opportunity for selection assumes a Darwinian definition of fitness, measured as the expected number of progeny produced, and the fitnesses are assumed to be constant. Assuming that the population consists of n classes of individuals (i.e., genotypes or phenotypes), and that the frequency of each class is p_i with fitness w_i , then it is easy to see that the average fitness in the population is a weighted average

$$\bar{w} = \frac{\sum_{i=1}^n p_i w_i}{\sum_{i=1}^n p_i} = \sum_{i=1}^n p_i w_i. \quad (3)$$

The frequency of p_i after one generation of selection will then be $p_i w_i$, so the average fitness after one generation of selection will be

$$\bar{w}^* = \frac{\sum_{i=1}^n (p_i w_i) w_i}{\sum_{i=1}^n p_i w_i} = \frac{\sum_{i=1}^n p_i w_i^2}{\bar{w}}, \quad (4)$$

and the change in fitness from one generation to the next is $\Delta \bar{w} = \bar{w}^* - \bar{w}$. Hence, the relative change in fitness is

$$\frac{\Delta \bar{w}}{\bar{w}} = \frac{\sum_{i=1}^n p_i w_i^2 - \bar{w}^2}{\bar{w}^2} = \frac{V}{\bar{w}^2} = I, \quad (5)$$

where V is the variance in fitness. Thus, I measures the single-generation increase in absolute fitness in the population divided by mean fitness in the original population when variance in fitness is entirely due to additive genetic effects (Crow 1958).

The intuitive interpretation of I is not entirely obvious to everyone from Crow's (1958) derivation, so consideration of several aspects of I may help to clarify some of the underlying logic. With respect to sexual selection, reproductive success is the key measure of fitness. The opportunity for selection often is described as the variance in reproductive success divided by the square of mean reproductive success. This definition is correct, of course, but also is equivalent to the variance in relative reproductive success, calculated by dividing each individual's absolute reproductive success by the mean reproductive success for the sex under consideration.

Of course, a selection differential is the covariance between a trait and relative fitness, so I can be interpreted as the covariance between relative fitness and itself, which makes I a selection differential on relative fitness. This interpretation of I allows a separation of the issue of heritability of fitness and the opportu-

nity for selection. One important criticism of I as a measure of the intensity of selection is that the actual change in fitness from one generation to the next will almost certainly be less than that predicted by I , because not all of the variance in fitness in a population is due to additive genetic variance. However, in some sense the issue of the amount of standing variance in relative fitness and the amount of this variance attributable to additive genetic effects should remain separate in the same way that a selection differential can be calculated separately from the response to selection.

The final point to consider with respect to I is that it measures a quantity that may not be especially interesting to sexual selection researchers. Usually, we are not focused on the increase in fitness over time in populations—indeed, the use of relative fitness in most evolutionary analyses eliminates any consideration of generation-to-generation changes in mean fitness. Rather, we are interested in changes in trait values over time. The opportunity for selection often is described as the maximum rate at which trait values can increase in a population as well, but this assertion, which is made without reference to units, also is difficult to interpret.

Although I does measure the maximum rate at which fitness will increase in the population, it may be useful to consider the maximum rate at which the value of a trait can increase in a population, in units of phenotypic standard deviations, due to selection. As noted above, the standardized selection differential determines the maximum rate of change of a trait due to selection. What is the maximum absolute value of the standardized selection differential in terms of I ? The answer is clear from the definition of the correlation coefficient, which is constrained to have values between -1 and 1 . The correlation between a standardized trait (z) and fitness (w) is

$$r = \frac{\text{cov}(z, w)}{\sigma_z \sigma_w}, \quad (6)$$

where σ_z is the standard deviation of the trait, which for a standardized trait is 1, and σ_w is the standard deviation of relative fitness. Thus, if we set r equal to 1 (the maximum value) and rearrange equation (6), we see that the absolute value of $\text{cov}(z, w)$ must be at most $\sigma_z \sigma_w = (1) \sigma_w$. In other words, the maximum magnitude of a selection differential for a trait, in units of phenotypic standard deviations, is equal to the standard deviation in relative fitness (Fig. 1), a point that was appreciated by Arnold and Wade (1984a). In some ways, the square root of I may consequently be a more intuitively satisfying metric of the maximum intensity of sexual selection than I . Regardless, the connection to selection theory is obvious: variation in fitness is necessary for selection to operate and any study of natural or sexual selection should report this variable (Hersch and Phillips 2004).

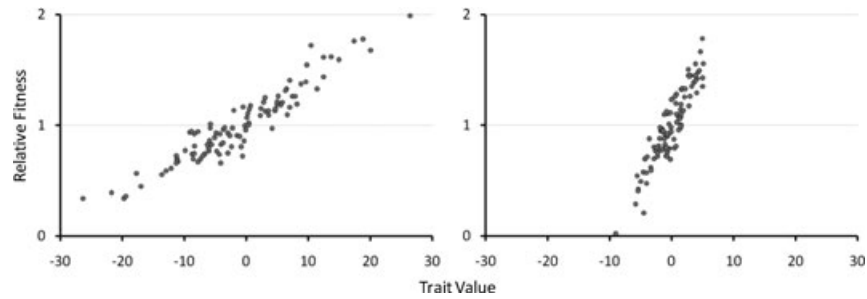


Figure 1. Hypothetical data illustrating two possible relationships between trait values (on an arbitrary scale) and relative fitness. Both panels have a correlation of 0.95 between trait values and fitness and the same variance in relative fitness. Assuming equal heritabilities, a population characterized by the relationship on the left would experience a larger absolute change in trait values due to selection than a population like the one shown on the right. However, the populations would experience the same increase in fitness and the same increase in trait values in units of phenotypic standard deviations. In the left panel, $l = 0.11$, $\sqrt{l} = 0.33$, s (the absolute selection differential) = 2.89, and $s' = 0.31$. In the right panel, $l = 0.11$, $\sqrt{l} = 0.33$, $s = 0.87$, and $s' = 0.30$. Thus, the standardized selection differential can be larger than l , but is always smaller than the square root of l .

The Opportunity for Sexual Selection

The opportunity for sexual selection differs from the opportunity for selection in that the former focuses on mating success and the latter on reproductive success. Interest in precopulatory sexual selection demands consideration of differential mating success. The opportunity for sexual selection (I_s) was developed with such a focus in mind. The idea underlying I_s dates back to Bateman (1948), who noticed that male flies have greater variance in mating success than female flies, but the formalization of the idea is attributable to Wade (1979).

Wade (1979) considered the sources of variation in reproductive success for males under a strictly polygynous mating system, in which males can mate with multiple females but each female can mate only once. The derivation is clear and accessible in both Wade (1979) and Shuster and Wade (2003), so I do not reproduce it here. This analysis identified two main sources of variance in reproductive success of males under strict polygyny (i.e., the reproductive success of females is nested within that of males). One source of variance is due to differences in the number of mates among males, and the other source of variance arises from variation in brood size among females, such that

$$I_m = RI_f + I_s, \quad (7)$$

where R is the ratio of the number of males to the number of females in the population, I_m is the variance in relative reproductive success for males, I_f is the variance in relative reproductive success of females, and I_s is the variance in male mating success divided by the square of mean mating success.

Unfortunately, the interpretation of this equation by Wade (1979) and other scientists appears to have resulted in a bit of a logical misstep that has only been partially corrected by subsequent work. The problem seems to have occurred in generalizing

the opportunity for sexual selection to all types of mating systems. Assuming an equal sex ratio, equation (7) can be rewritten as $I_s = I_m - I_f$, implying that the sex difference in the opportunity for selection is a key variable with respect to the intensity of sexual selection on males. However, this relationship only holds for the polygynous mating system modeled by Wade (1979). To illustrate the problem (also see Wade 1987, Shuster and Wade 2003), we can define a brood as the total complement of progeny for a female during the selection episode of interest (e.g., the breeding season) and a clutch as a subset of the female's progeny that originated from a single mating event. Each female will have one brood. If females can mate only once, then each female also has a single clutch, but if females can mate more than once, a female may have multiple clutches with different fathers within a brood. In other words, the success of females is no longer nested within males. Regardless of the mating system, the variance in male relative reproductive success includes a term for variance in mating success among males and a term for variance in clutch size (which equals brood size only in the case of strict polygyny). Thus, equation (7) should be rewritten as

$$I_m = QI_c + I_s, \quad (8)$$

where I_c is the variance in clutch size divided by the square of the mean clutch size and Q is the reciprocal of mean male mating success. If each female mates only once, then equation (8) is the same as equation (7) because $I_f = I_c$ and Q is equal to the ratio of males to females. In principle, a mirror-image of this equation can be derived for females, and it would be equally applicable.

Hence, theory related to the opportunity for sexual selection shows that variance in reproductive success is partially due to variation in mating success and partially due to variation in the number of progeny produced per mating event. In the present analysis, we are concerned mainly with precopulatory sexual selection,

so it is appropriate to focus on the variation in fitness caused by variation in mating success. Equation (8) shows that variance in reproductive success can be caused by variance in mating success, and it is this cause of variance in reproductive success that is most interesting with respect to competition for access to mates in the sexually selected sex. Assuming that every mating event is equal in terms of the number of progeny produced, the opportunity for selection and the opportunity for sexual selection will be equal. In addition, an absence of variance in mating success implies an absence of competition for access to mates.

We can now draw several conclusions regarding the opportunity for sexual selection. First, I_s must be larger than zero for precopulatory sexual selection to occur (ignoring selection driven by mate quality or offspring quality). Second, I_s is appropriately calculated for males or females as the variance in relative mating success (i.e., the variance in absolute mating success divided by the mean absolute mating success squared). Third, the sex difference in variance in relative reproductive success is not a generally applicable method for quantifying the mating system. And fourth, a nonzero I_s for a sex does not guarantee that sexual selection is operating, because equations (7) and (8) ignore potential covariance between mating success and clutch size, and these covariances may sometimes be negative (Wade 1979; Arnold and Wade 1984a). In other words, it is possible to have a high variance in mating success but a low variance in reproductive success, especially in the sex limited by gamete production or parental care. Overall, I_s is an important variable with respect to sexual selection, but it provides less than a complete picture.

The Bateman Gradient

So far, we have seen that variance in mating success and variance in reproductive success are necessary for precopulatory sexual selection to operate, but how are these variances connected within the framework of selection theory? Bateman (1948) identified the crux of an answer to this question in his original paper, but his ideas were not fully appreciated until Arnold and Duvall (1994) treated them in a formal analysis.

Arnold and Duvall (1994) made several important contributions to thought regarding the relationship between mating success and reproductive success highlighted by Bateman (1948). They defined the Bateman gradient (β_{ss}), as the slope of the least-squares regression of reproductive success on mating success. If we are talking about sexual selection resulting from competition for access to mating opportunities, then the Bateman gradient is the final path to fitness for all sexually selected traits. In other words, success in mating competition results in an increase in mating success but an increase in mating success must result in an increase in Darwinian fitness, measured as reproductive success in this case, for selection to operate. Thus, a trait that increases mating success will have a positive selection differential only

if the Bateman gradient is positive. Finally, Arnold and Duvall (1994) provided another intuitive way of thinking about the Bateman gradient, which also justifies the logic behind the use of a least-squares regression approach. If we consider mating success to be a trait, then the Bateman gradient measures the selection gradient on this trait. In a population with a steep Bateman gradient, then, there will be persistent directional selection on mating success and any trait correlated with mating success will increase in frequency or experience directional selection.

With respect to the interpretation of mating patterns in natural populations, consideration of the Bateman gradient leads to the conclusion that a nonzero Bateman gradient is necessary for sexual selection to operate. The sex with a shallow Bateman gradient is likely to be limited in reproduction by intrinsic factors, such as the rate at which it can produce gametes or care for offspring, whereas the sex with a steep Bateman gradient is limited by access to mating opportunities (Bateman 1948; Arnold and Duvall 1994). As with other quantities based on Bateman's work, this viewpoint only applies to the precopulatory phase of sexual selection and ignores variation in mate or offspring quality. Hence, for precopulatory sexual selection to operate, in terms of strict numerical competition for mating opportunities, the Bateman gradient, the opportunity for selection, and the opportunity for sexual selection must all be positive. The remaining question concerns the meaning of the relative magnitudes of these quantities.

The Mating Differential and the Bateman Gradient

I propose here a slightly improved way of thinking about I , I_s , and β_{ss} , which combines these quantities in a single, intuitive framework that pinpoints the important issues regarding the quantification of mating systems and sexual selection. Clearly, these quantities are related, and any study that permits estimation of β_{ss} also has sufficient data to calculate I and I_s . The Bateman gradient is often thought of as a quantity that measures the conversion of meaningful variation in mating success into variation in Darwinian fitness, as measured by reproductive success.

With respect to precopulatory sexual selection, we are interested in traits that result in an increase in mating success. In other words, we are interested in the covariance between trait values and mating success. In this vein, I define the "standardized mating differential," m' , as the covariance between a phenotypic trait, standardized to have a mean of zero and a standard deviation of 1, and relative mating success (i.e., mating success divided by mean mating success):

$$m' = \text{cov}(\text{standardized trait value, relative mating success})(9)$$

The mating differential reflects directional sexual selection only if the covariance between the trait and mating success is

somehow accompanied by covariance between the trait and reproductive success (i.e., a nonzero selection differential). Of course, the Bateman gradient comes into play here, and it is easy to show how by examining the definitions of these covariances. Here, I assume that reproductive success is our measure of fitness and that it is standardized to have a mean of one (i.e., relative fitness), such that

$$w_i = \frac{W_i}{\bar{W}}, \tag{10}$$

where w_i is individual i 's relative reproductive success, W_i is individual i 's absolute reproductive success (i.e., the number of offspring produced during the selection episode of interest), and \bar{W} is the mean absolute fitness of the sex under consideration. The phenotypic trait is standardized differently from fitness, so

$$z_i = \frac{\zeta_i - \bar{\zeta}}{\sigma_\zeta}, \tag{11}$$

where z_i is the standardized trait value for individual i , ζ_i is the original trait value for individual i , $\bar{\zeta}$ is the mean trait value for the sex under consideration, and σ_ζ is the trait standard deviation in the sex of interest. This trait standardization results in selection and mating differentials that are in units of phenotypic standard deviations.

Recall that the standardized selection differential on a phenotypic trait is the covariance between the standardized trait and relative fitness. In other words, using the definition of a covariance

$$s' = \text{cov}(z, w) = \frac{\sum_{i=1}^n z_i w_i}{n} - \bar{z} \bar{w}. \tag{12}$$

It is instructive to consider this selection differential in terms of relative mating success, which is possible for a known Bateman gradient. Assuming that m_i is individual i 's relative mating success, obtained by dividing absolute mating success by the mean mating success for the sex in question in the same way relative fitness is calculated according to equation (10), then we wish to obtain equation (12) in terms of m_i rather than w_i . If the relationship between mating success and reproductive success is approximately linear, then $w_i = \beta_{ss} m_i + a + \varepsilon_i$, where a is the intercept of the regression line relating reproductive success to mating success and ε_i is an error term describing individual i 's deviation from the line. Recalling that \bar{z} is zero, and substituting this relationship into equation (12), we obtain

$$\begin{aligned} s' &= \frac{z_1(\beta_{ss} m_1 + a + \varepsilon_1) + z_2(\beta_{ss} m_2 + a + \varepsilon_2) + \dots + z_n(\beta_{ss} m_n + a + \varepsilon_n)}{n} \\ &= \frac{\beta_{ss} \sum_{i=1}^n z_i m_i + a \sum_{i=1}^n z_i + \sum_{i=1}^n z_i \varepsilon_i}{n}. \end{aligned} \tag{13}$$

This expression can be further simplified by making the reasonable assumption that there is no covariance between an individual's trait value (z_i) and the individual's deviation from the regression line (ε_i) and by recognizing that a is multiplied by \bar{z} , which is zero in this case. Thus equation (13) reduces to

$$s' = \frac{\beta_{ss} \sum_{i=1}^n z_i m_i}{n}. \tag{14}$$

Above, I defined the standardized mating differential as the covariance between trait values and mating success. Using the definition of the covariance, we see that

$$m' = \text{cov}(z, m) = \frac{\sum_{i=1}^n z_i m_i}{n} - \bar{z} \bar{m} = \frac{\sum_{i=1}^n z_i m_i}{n}, \tag{15}$$

so the standardized selection differential is simply the product of the standardized mating differential and the Bateman gradient

$$s' = \beta_{ss} m'. \tag{16}$$

If precopulatory sexual selection is operating in a system, then competition for access to mates will lead individuals with favorable trait values to obtain more mates than individuals with less favorable trait values. Of course, this process is characterized by covariance between mating success and trait values, resulting in a nonzero mating differential. The central role of the Bateman gradient in sexual selection is then to convert this mating differential into an actual selection differential on the trait. This result also reveals the standardization that should be employed to compare Bateman gradients between populations or sexes. The original description of the Bateman gradient (Arnold and Duvall 1994) used absolute mating success and absolute reproductive success. In the formulation here, however, mating success and reproductive success should be converted to relative values by dividing by their respective means.

The Maximum Standardized Sexual Selection Differential

One interesting result from the consideration of mating and selection differentials presented here is that it identifies a previously unappreciated upper limit on the intensity of selection in natural populations that may be more intuitively comprehensible than other such measures. As in the case of s' discussed above, the

maximum value that m' can take is constrained by the fact that the corresponding correlation must be between -1 and 1 . Recall that m' is the covariance between a standardized trait (which has a standard deviation of 1) and relative mating success, so m' cannot be larger than the standard deviation in relative mating success (see above for a more detailed explanation). The standard deviation in relative mating success is the square root of I_s , so the standardized selection differential, in units of phenotypic standard deviations, must be less than or equal to the product of the Bateman gradient and the square root of I_s

$$|s'| \leq s'_{max} = \beta_{ss} \sqrt{I_s} \quad (17)$$

This upper limit (i.e., $s'_{max} = \beta_{ss} \sqrt{I_s}$) may be more useful than I or I_s alone for several reasons. First, it makes use of information from both the variation in mating success and the Bateman gradient. Second, this measure is in units of phenotypic standard deviations, so it can be used in the breeder's equation to calculate the maximum rate of phenotypic evolution for a trait. Because s'_{max} is concerned only with the maximum selection differential, it makes no implicit assumptions about the heritability of traits or fitness. It simply places an upper bound on the strength of sexual selection during a sexual selection episode. Finally, the total opportunity for selection (I) is not part of this measure. This point is important, because variance in reproductive success is attributable partially to sexual selection and partially to natural selection on fecundity or fertility. Thus, s'_{max} is one step closer to the sexual selection process, because it only deals with selection generated by differential mating success.

The Two Parts of Precopulatory Sexual Selection

This view of selection and mating differentials results in a conceptual partitioning of the process of precopulatory sexual selection. On the one hand are mechanisms that generate covariance between trait values and mating success, and on the other hand are the mechanisms that convert this sort of covariance into selection differentials on traits. The results of these two types of mechanisms are the two terms in equation (16), i.e., the mating differential (m') and the Bateman gradient (β_{ss}). This way of viewing sexual selection provides a reformulation of the question of why some population experience stronger sexual selection than others. Such differences between populations result either from different genetic mating systems or from different covariances between trait values and mating success. Thus, studies of sexual selection should endeavor to investigate the factors shaping both of these equally important parts of the process.

Mating differentials can potentially be described using a number of different approaches. Indeed, these sorts of studies

are staples of research on sexual selection (Andersson 1994). The most relevant type of study for sexual selection in nature would involve direct observation of mating events or experimental manipulations in the field coupled with genetic verification of parentage (Pemberton et al. 1992; Coltman et al. 1999; Sheldon and Ellegren 1998, 1999; Say et al. 2003). These studies can be difficult for a variety of reasons, but they have the advantage that they describe the actual mating events and results of such events in a natural setting. Less complete studies in natural population also can result in important insights, provided that they offer some information regarding the covariance between trait values and mating success (Johnsen et al. 2001; Jones et al. 2001, 2002). For species in which natural mating aggregations are empirically inaccessible, it may be necessary to resort to artificial breeding populations in the field or laboratory. The most informative studies of this kind mimic natural conditions as closely as possible and use genetic techniques, possibly augmented by behavioral observations, to describe mating patterns (Jones et al. 2004, 2005; Mills et al. 2007). Even this type of study is not always possible, requiring some researchers to resort to laboratory-based mate preference trials, involving either real or simulated stimulus animals (Jennions and Petrie 1997; Rosenthal and Evans 1998; Candolin 2003). The problem with this latter type of study is that the conversion of a mate preference expressed in the laboratory to an expected mating differential in a natural setting requires knowledge of many parameters, such as mate searching patterns, the social setting of mate choice, and spatial dispersion of individuals, which are not easily obtained from most natural systems. Nevertheless, in all these contexts, the mating differential is a critical parameter in sexual selection and is a worthy focus of research.

The second key part of precopulatory sexual selection, i.e., the Bateman gradient, is obtainable from knowledge of the genetic mating system, which describes the patterns of biological parentage in a breeding population. In an ideal situation, the genetic mating system can be measured at the same time as the mating differential by conducting a parentage analysis on the breeding population. The challenge lies in obtaining complete enough samples to completely describe parentage (Jones and Ardren 2003). For cases in which complete or nearly complete sampling is impossible, it may be desirable to set up laboratory breeding populations from which the variables of interest can be calculated (Jones et al. 2004, 2005; Mills et al. 2007). From the parentage data, the Bateman gradient can be calculated easily, and the opportunity for sexual selection can also be determined, with no knowledge of the phenotypic values of the individuals in the population, thus permitting calculation of s'_{max} . In some cases, field studies of parentage may be prohibitively difficult, either because breeding aggregations are too large or because insufficient proportions of adults or progeny can be sampled. Under such circumstances, it may be possible to estimate upper limits on Bateman gradients

Table 1. Mating system and sexual selection statistics for male and female rough-skinned newts. These values were calculated from the pooled, 1:1 sex ratio treatments of Jones et al. (2004), which included parentage data for a total of 48 adult males and 45 adult females. Statistics are defined in the text. The last column represents the rightmost term from equation (13), which is the covariance between trait value and residual reproductive success (from the regression of relative reproductive success on relative mating success). Mating differentials and selection differentials are calculated for tail height.

Sex	I_s	I	β_{ss}	$\sqrt{I_s}$	\sqrt{I}	s'_{max}	m'	$m' \beta_{ss}$	s'	cov(z, ϵ)
Male	0.48	0.86	0.99	0.69	0.93	0.68	0.20	0.20	0.36	0.15
Female	0.32	0.30	0.20	0.55	0.56	0.11	0.03	0.01	-0.10	-0.10

through careful experimentation in a laboratory setting (Lorch 2002, 2005). Regardless, it appears that some assessment of patterns of mating and reproductive success will be necessary for a complete explanation of the factors determining the intensity of sexual selection.

An Empirical Example

Here, I illustrate the calculation of the variables discussed above using an empirical dataset. The dataset under consideration is an assessment of sexual selection in experimental populations of the rough-skinned newt (Jones et al. 2004), and it is available for download at <http://www.bio.tamu.edu/USERS/ajones/JonesLab.htm>. The experiment involved setting up artificial groups of breeding newts, allowing them to mate, and assessing parentage of the resultant offspring with microsatellite markers. The use of a closed system permitted complete determination of parentage, and measurement of phenotypic attributes of adults facilitated the estimation of selection differentials on male and female traits. Rough-skinned newts are sexually dimorphic, and males are characterized by a striking tail crest that appears to be a target of sexual selection (Janzen and Brodie 1989; Jones et al. 2002, 2004) so I focus on tail height as the trait of interest.

Upon completion of the parentage analysis, each individual adult in the dataset has values for mating success (total number of mates), reproductive success (total number of offspring), and the trait value (tail height). The first step is to standardize the trait values by subtracting the trait mean and dividing by the trait standard deviation for each individual. After this standardization, the trait mean will be zero and the standard deviation will be one, so any selection differentials will be in units of phenotypic standard deviations. Mating success and reproductive success are then standardized by dividing by mean mating success and mean reproductive success, respectively. The standardized values of mating success and reproductive success will have a mean of one, but the variances could take any nonnegative value.

Once the various values are standardized, the calculation of the variables of interest is straightforward. The opportunity for sexual selection (I_s) and the opportunity for selection (I) are

merely the variances in relative mating success and relative reproductive success, respectively. The Bateman gradient (β_{ss}) is the least-squares regression of relative reproductive success on relative mating success (i.e., the covariance between relative mating success and relative reproductive success divided by the variance in relative mating success). The standardized mating differential (m') is the covariance between the standardized trait values and relative mating success, and the standardized selection differential (s') is the covariance between the standardized trait values and relative reproductive success. Finally, the maximum standardized selection differential due to precopulatory sexual selection (s'_{max}) is the product of β_{ss} and the square root of I_s .

These values are presented for male and female newts in Table 1, and the Bateman gradients for the two sexes are shown in Figure 2. Several key points emerge from some of the new variables presented in this table. For instance, males experience stronger sexual selection than females. This pattern was implied by the analyses of I , I_s , and β_{ss} presented in previous papers (Jones et al. 2002, 2005), but a better understanding of the relationships among these variables leads to clearer insights. For example, not only are males experiencing stronger sexual selection on tail height, as evidenced by a much larger s' , but sexual selection on male tail height is stronger than precopulatory sexual selection on any trait in females. This latter conclusion must be true because s'_{max} is merely 0.11 in females, which is only about a third the magnitude of the actual selection gradient on tail height in males. Interestingly, the intensity of selection on tail height in males is about half of s'_{max} for males, so some of the variation among males with respect to reproductive success must be due to stochastic factors or selection on other traits.

One final interesting point with respect to the newt data concerns the expectation that s' should equal the product of m' and β_{ss} , which turns out not to be precisely true for either sex. The discrepancy is due to the right-most term in equation (13). This term is the covariance between trait values and residual reproductive success from the regression of reproductive success on mating success (Fig. 3). A positive value for this term indicates that individuals with larger trait values produce more offspring per mating event. Thus, postcopulatory sexual selection or fecundity selection could result in nonzero values for this term. This result leads

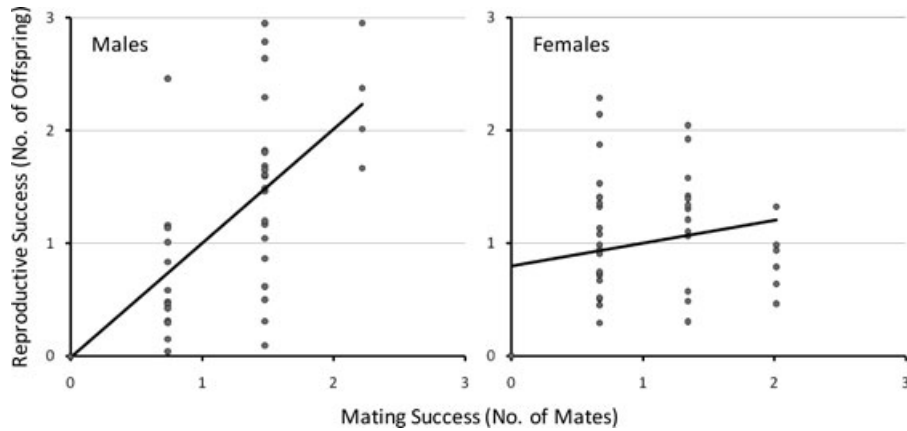


Figure 2. Bateman gradients for male and female rough-skinned newts. For comparison among sexes, populations, or species, the Bateman gradient should be calculated as the slope of the least squares regression of relative reproductive success on relative mating success. The male Bateman gradient is significantly steeper than zero ($N = 48$, $P < 0.001$), whereas the female Bateman gradient is not ($N = 45$, $P = 0.20$). See Table 1 for the values of the Bateman gradients (β_{SS}).

to the useful insight that the product of m' and β_{SS} is the portion of the selection gradient due to precopulatory sexual selection, such that any discrepancy between this product and the actual selection gradient (s') is due to postcopulatory sexual selection or

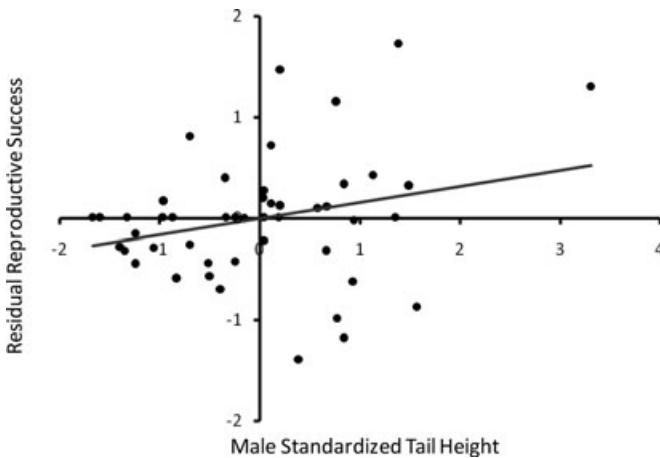


Figure 3. Residual reproductive success (from the regression of relative reproductive success on relative mating success, i.e., Fig. 2) as a function of tail height in males. This figure illustrates that the rightmost term in equation (13), $\frac{\sum_{i=1}^n z_i \epsilon_i}{n}$, is positive for male newts, explaining why s' is not exactly equal to $m'\beta_{SS}$. The interpretation of this observation is interesting, because it indicates that males with larger tail height values may fertilize more eggs per mating event (although the relationship is not quite significant, with $N = 48$ and $P = 0.08$, indicating a need for additional work on this topic). Thus, the portion of s' due to precopulatory sexual selection is $m'\beta_{SS}$, and the discrepancy between s' and $m'\beta_{SS}$ is due to the fact that mating events appear to be more successful for males with larger trait values. Such a discrepancy indicates that postcopulatory sexual selection or fertility selection could be at work.

some type of natural selection. The exact cause of the discrepancy would have to be diagnosed by additional experiments. In the case of newts, both m' and s' are significantly positive, indicating significant precopulatory sexual selection on male tail height, and the source of the discrepancy between s' and m' is not statistically significant (Fig. 3), suggesting that more work will be necessary to determine whether or not post-copulatory sexual selection is also at work in rough-skinned newts.

Conclusions

In this report, I have tried to clear up some misconceptions regarding the quantification of mating systems and sexual selection. A focus on measures related to Bateman's principles is a natural extension of selection theory, and the relationships between Bateman's principles and selection differentials are clear. My goal is a quantification of mating systems that both facilitates comparative work and is intuitively understandable. With this goal in mind, it seems clear that the key parts of precopulatory sexual selection involve the mating differential on the one hand and the Bateman gradient on the other. A variety of behavioral experiments and parentage analyses will be necessary to quantify all of the meaningful parameters in any particular system. If an understanding of sexual selection is a goal, however, the aim of behavioral experiments should be to ascertain the mechanisms generating covariance between trait values and mating success in natural populations. Hence, some effort should be made to relate observations in the laboratory to behavior in the field, especially in terms of the mating differential. These studies should be complemented by parentage studies, which should strive to quantify the Bateman gradient. A secondary role of these studies will be to provide a measure of s'_{max} , an upper limit on standardized selection gradients that makes much better use of the data than any

of the measures currently in use. Although there is still much theoretical and empirical work to be done on these issues, especially concerning topics such as age structure, alternative reproductive tactics, and sexual selection on the multivariate phenotype, my hope is that this treatment will stimulate a continuing effort to implement standard approaches to the quantification of mating systems and sexual selection.

Correction statement: Equation 3 and 4 have been corrected since online publication.

ACKNOWLEDGMENTS

I am grateful to C. Small, K. Paczolt, N. Ratterman, and two anonymous referees for helpful comments on this manuscript. I especially would like to thank S. Arnold for providing feedback on this article and for his generosity in discussing selection and related issues with me over the last decade.

LITERATURE CITED

- Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.
- Andersson, M., and Y. Iwasa. 1996. Sexual selection. *Trends Ecol. Evol.* 11:53–58.
- Arnold, S. J. 1986. Limits on stabilizing, disruptive, and correlational selection set by the opportunity for selection. *Am. Nat.* 128:143–146.
- Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection—theory. *Evolution* 38:709–719.
- . 1984b. On the measurement of natural and sexual selection—applications. *Evolution* 38:720–734.
- Arnold, S. J., and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. *Am. Nat.* 143:317–348.
- Awise, J. C., A. G. Jones, D. Walker, J. A. DeWoody, and Collaborators. 2002. Genetic mating systems and reproductive natural histories of fishes: lessons for ecology and evolution. *Ann. Rev. Genet.* 36:19–45.
- Becher, S. A., and A. E. Magurran. 2004. Multiple mating and reproductive skew in Trinidadian guppies. *Proc. R. Soc. Lond. B* 271:1009–1014.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- Bro-Jørgensen, J. 2007. The intensity of sexual selection predicts weapon size in male bovines. *Evolution* 61:1316–1326.
- Candolin, U. 2003. The use of multiple cues in mate choice. *Biol. Rev.* 78:575–595.
- Clutton-Brock, T. H. 1983. Selection in relation to sex. Pp. 457–481 in D. S. Bendall, ed. *Evolution from molecules to men*. Cambridge Univ. Press, Cambridge.
- Clutton-Brock, T. H., P. H. Harvey, and B. Rudder. 1977. Sexual dimorphism, sociometric sex ratio and body weight in primates. *Nature* 269:797–800.
- Clutton-Brock, T. H., S. D. Albon, and P. H. Harvey. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature* 285:565–566.
- Coltman, D. W., D. R. Bancroft, J. A. Smith, T. H. Clutton-Brock, and J. M. Pemberton. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Mol. Ecol.* 8:1199–1209.
- Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. *Human Biol.* 30:1–13.
- . 2002. Perspective: here's to Fisher, additive genetic variance, and the fundamental theorem of natural selection. *Evolution* 56:1313–1316.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. J. Murray, London.
- Dewsbury, D. A. 2005. The Darwin-Bateman paradigm in historical context. *Integr. Comp. Biol.* 45:831–837.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- Fairbairn, D. J., and A. E. Wilby. 2001. Inequality of opportunity: measuring the potential for sexual selection. *Evol. Ecol. Res.* 3:667–686.
- Falconer, D. S., and T. F. C. Mackay. 1989. *Introduction to quantitative genetics*. Longman Group, Harlow, UK.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford.
- Grafen, A. 1987. Measuring sexual selection: why bother? Pp. 221–233 in J. W. Bradbury and M. B. Andersson, eds. *Sexual selection: testing the alternatives*. Wiley, Chichester.
- . 1988. On the uses of data on lifetime reproductive success. Pp. 454–471 in T. H. Clutton-Brock, ed. *Reproductive success*. Univ. of Chicago Press, Chicago.
- Hersch, E. I., and P. C. Phillips. 2004. Power and potential bias in field studies of natural selection. *Evolution* 58:479–485.
- Hubbell, S. P., and L. K. Johnson. 1987. Environmental variance in lifetime mating success, mate choice, and sexual selection. *Am. Nat.* 130:91–112.
- Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology* 79:383–399.
- Janzen, F. J., and E. D. Brodie. 1989. Tall tails and sexy males—sexual behavior of rough-skinned newts (*Taricha granulosa*) in a natural breeding pond. *Copeia* 1989:1068–1071.
- Jennions, M. D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev. Camb. Phil. Soc.* 75:21–64.
- Johnsen, A., J. T. Lifjeld, A. Andersson, J. Örnborg, and T. Amundsen. 2001. Male characteristics and fertilisation success in bluethroats. *Behaviour* 138:1371–1390.
- Jones, A. G., and W. R. Ardren. 2003. Methods of parentage analysis in natural populations. *Mol. Ecol.* 12:2511–2523.
- Jones, A. G., G. Rosenqvist, A. Berglund, S. J. Arnold, and J. C. Awise. 2000. The Bateman gradient and the cause of sexual selection in a sex-role-reversed pipefish. *Proc. R. Soc. Lond. B* 267:677–680.
- Jones, A. G., D. Walker, and J. C. Awise. 2001. Genetic evidence for extreme polyandry and extraordinary sex-role reversal in a pipefish. *Proc. R. Soc. Lond. B* 268:2531–2535.
- Jones, A. G., J. R. Arguello, and S. J. Arnold. 2002. Validation of Bateman's principles: a genetic study of mating patterns and sexual selection in newts. *Proc. R. Soc. Lond. B* 269:2533–2539.
- . 2004. Molecular parentage analysis in experimental newt populations: the response of mating system measures to variation in the operational sex ratio. *Am. Nat.* 164:444–456.
- Jones, A. G., G. Rosenqvist, A. Berglund, and J. C. Awise. 2005. The measurement of sexual selection using Bateman's principles: an experimental test in the sex-role-reversed pipefish *Syngnathus typhle*. *Integr. Comp. Biol.* 45:874–884.
- Koenig, W. D., and S. S. Albano. 1986. On the measurement of sexual selection. *Am. Nat.* 127:403–409.
- Kokko, H., A. Mackenzie, J. D. Reynolds, J. Lindstrom, and W. J. Sutherland. 1999. Measures of inequality are not equal. *Am. Nat.* 72:358–382.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402–416.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lorch, P. D. 2002. Understanding reversals in the relative strength of sexual selection on males and females: a role for sperm competition? *Am. Nat.* 159:645–657.

- . 2005. Using upper limits of “Bateman gradients” to estimate the opportunity for sexual selection. *Integr. Comp. Biol.* 45:924–930.
- Lorch, P. D., L. F. Bussiere, and D. T. Gwynne. 2008. Quantifying the potential for sexual dimorphism using upper limits on Bateman gradients. *Behaviour* 145:1–24.
- Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer, Sunderland, MA.
- Mills, S. C., A. Grapputo, E. Koskela, and T. Mappes. 2007. Quantitative measures of sexual selection with respect to the operational sex ratio: a comparison of selection indices. *Proc. R. Soc. Lond. B* 274:143–150.
- Møller, A. P. 1997. Immune defence, extra-pair paternity, and sexual selection in birds. *Proc. R. Soc. Lond. B* 264:561–566.
- Morisita, M. 1962. I_{δ} , a measure of dispersion of individuals. *Res. Pop. Ecol.* 4:1–7.
- Nonacs, P. 2000. Measuring and using skew in the study of social behavior and evolution. *Am. Nat.* 156:577–589.
- Parker, P. G., and Z. Tang-Martinez. 2005. Bateman gradients in field and laboratory studies: a cautionary tale. *Integr. Comp. Biol.* 45:895–902.
- Payne, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.* 33:1–53.
- Pemberton, J. M., S. D. Albon, F. E. Guinness, T. H. Clutton-Brock, and G. A. Glover. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* 3:66–75.
- Price, G. R. 1970. Selection and covariance. *Nature* 227:520–521.
- Rios-Cardenas, O. 2005. Patterns of parental investment and sexual selection in teleost fishes: do they support Bateman’s principles? *Integr. Comp. Biol.* 45:885–894.
- Robertson, A. 1966. A mathematical model of the culling process in dairy cattle. *Anim. Prod.* 8:93–108.
- Rosenthal, G. G., and C. S. Evans. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proc. Natl. Acad. Sci. USA* 95:4431–4436.
- Ruzzante, D., D. C. Hamilton, D. L. Kramer, and J. W. A. Grant. 1996. Scaling of the variance and the quantification of resource monopolization. *Behav. Ecol.* 7:199–207.
- Say, L., F. Naulty, and T. J. Heyden. 2003. Genetic and behavioural estimates of reproductive skew in male fallow deer. *Mol. Ecol.* 12:2793–2800.
- Sheldon, B. C., and H. Ellegren. 1998. Paternal effort related to experimentally manipulated paternity of male collared flycatchers. *Proc. R. Soc. Lond. B* 265:1737–1742.
- . 1999. Sexual selection resulting from extrapair paternity in collared flycatchers. *Anim. Behav.* 57:285–298.
- Shuster, S. M., and M. J. Wade. 2003. *Mating systems and strategies*. Princeton Univ. Press, Princeton, NJ.
- Sutherland, W. J. 1985a. Chance can produce a sex difference in variance in mating success and explain Bateman’s data. *Anim. Behav.* 33:1349–1352.
- Sutherland, W. J. 1985b. Measures of sexual selection. *Oxf. Surv. Evol. Biol.* 1:90–101.
- . 1987. Random and deterministic components of variance in mating success. Pp. 209–219 in J. W. Bradbury and M. B. Andersson, eds. *Sexual selection: testing the alternatives*. Wiley, Chichester.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Heinemann, London.
- Wade, M. J. 1979. Sexual selection and variance in reproductive success. *Am. Nat.* 114:742–747.
- . 1987. Measuring sexual selection. Pp. 197–207 in J. W. Bradbury and M. B. Andersson, eds. *Sexual selection: testing the alternatives*. Wiley, Chichester.
- Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. *Anim. Behav.* 28:446–461.
- Wade, M. J., and S. M. Shuster. 2004. Sexual selection: Harem size and the variance in male reproductive success. *Am. Nat.* 164:E83–E89.
- Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2007. Promiscuity drives sexual selection in a socially monogamous bird. *Evolution* 61:2205–2211.

Associate Editor: M. Rausher