Using Upper Limits of "Bateman Gradients" to Estimate the Opportunity for Sexual Selection¹

PATRICK D. LORCH²

Biology Department, University of Toronto at Mississauga, Mississauga, Ontario L5L 1C6, Canada

SYNOPSIS. The widespread use of molecular markers to estimate parentage makes possible a new index of the opportunity for sexual selection. After demonstrating the need for a new measure, I develop one based on the upper limit on sexual selection. I describe what sets the upper limit for each sex by showing how maximum fecundity increases with number of mates, accounting for the amount of energy (or critical resources) available for reproduction and levels of parental care. For females the upper limit on sexual selection is set by the value of paternal investment that comes with each mating. For males, the upper limit on sexual selection is set by the fecundity of their mates (including any boost to female fecundity from paternal investment). Sex-roles are most likely to reverse (making males choosy and females competitive) when the amount of reproductive energy investment made by each sex is low, irrespective of the level of paternal investment. Finally, I propose that we use the difference between male and female upper limits on sexual selection to quantify sex differences in the opportunity for sexual selection. Using upper limits to estimate the opportunity for sexual selection is more intuitive than older methods (*e.g.*, standardized variance in mating success), it is experimentally measurable, and it is valuable in understanding the evolution of mating systems.

INTRODUCTION

Recent theoretical and empirical demonstrations have shown how molecular parentage data can be used to estimate overall sexual selection intensity (Arnold and Duvall, 1994; Jones et al., 2000, 2002, 2004). This approach incorporates direct measures of what Bateman (1948) described as the primary cause of sexual selection—the positive relationship between fecundity (offspring number) and mating success (number of different mates; Fig. 1). Without a positive relationship between fecundity and number of mates (or interchangeably mate quality), there is no fitness advantage to competing for mates and therefore no potential for sexual selection (Arnold and Duvall, 1994). Hence, little difference is expected between the sexes in morphology or behaviour. Arnold and Duvall (1994) suggest using least squares regression estimates of this relationship, referred to as "Bateman gradients" to estimate the intensity of sexual selection. These selection gradients, calculated separately for each sex, estimate how success in mate competition translates into increased fitness. This is a crucial step in understanding the evolution of sex differences by sexual selection (Arnold and Duvall, 1994), and can be particularly useful for understanding how selection on other aspects of a life history affect the overall strength of sexual selection (Lorch, 2002). In at least one example, Bateman gradients seem to be the best indicator of which sex experiences the strongest sexual selection on sexually dimorphic traits (Jones et al., 2002).

Historically, because of difficulty in estimating both

components of Bateman's relationship, estimates of the "potential" for sexual selection were used to understand the role of sexual selection in shaping sexual dimorphism. Until recently it was difficult to link offspring with parents (particularly fathers). As a result, measures of the "opportunity for sexual selection" (Wade, 1979; Wade and Arnold, 1980; Arnold and Wade, 1984) were commonly used to estimate the potential strength of sexual selection on males and females, and to describe mating systems (Wade, 1979; Wade and Arnold, 1980; Arnold and Duvall, 1994; Shuster and Wade, 2003). These measures of opportunity are based on the variance in reproductive success or the variance in mating success. They do not estimate actual sexual selection intensity but instead describe the potential or maximum strength of sexual selection in a population based on the variance in one or the other component of Bateman's relationship, not the relationship itself. In fact, variance-based estimates of opportunity must assume that Bateman's relationship exists and that it is stronger in one sex than the other. Violating these assumptions can cause erroneous conclusions about the relative strength of sexual selection acting on males and females (see below).

The most commonly used estimates of the opportunity for sexual selection are based on variance in mating success standardized by the squared mean mating success (referred to as I_{mates} ; Wade, 1979; Shuster and Wade, 2003; Webster *et al.*, 1995), following Crow's opportunity for selection (*I*; Crow, 1958, 1962). These estimates continue to be used despite strong criticisms that fall into two categories (for a review see Jones *et al.*, 2002): (1) these estimates of opportunity can be influenced by factors other than sexual selection, and (2) variance in mating success is not the appropriate metric to describe non-random mating due to sexual selection. Recently, there have been suggestions that I_{mates} be replaced by measures

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² Current address: Department of Biological Sciences, Kent State University, 256 Cunningham Hall, Kent, Ohio 44240-0001; e-mail: plorch@kent.edu



Mating success (number of mates)

FIG. 1. Relationship between fecundity and mating success for female and male *Drosophila melanogaster*, redrawn from data in blocks 5 and 6 (from Bateman, 1948). Points are means of fecundity across replicates. Lines represent regressions through points weighted by number in that mating class (see histograms). Males are filled points and bars, and solid line. Females are open points and bars, and dotted line.

based on resource monopolization (Kokko *et al.*, 1999; Fairbairn and Wilby, 2001) to take into account the dependence of I_{mates} on both mean number of mates and sample size. Use of I_{mates} persists because it is easily measured, closely linked to selection theory (Arnold and Duvall, 1994), and because, in at least one well studied example, it matches expectations based on Bateman gradients and direct measures of sexual selection on traits (rough-skinned newts, *Taricha granulosa*; Jones *et al.*, 2002, 2004).

To demonstrate how variance in mating success has been used and to highlight one weakness of the approach, I consider part of Bateman's (1948) data based on crosses in *Drosophila melanogaster* (Fig. 1, Table 1). The variance in mating success for one part of Bateman's data is 0.76 for males and 0.37 for females. Converting these raw variances to the standardized

 I_{mates} gives 0.28 for males and 0.14 for females. The sex with the larger I_{mates} (males in this example) is said to have a greater opportunity for sexual selection. This conclusion explicitly assumes that mating success covaries positively with fecundity (Wade, 1979, p. 744). For the data in Figure 1 this assumption seems to be valid for males but not for females. When there is no covariance between mating success and fecundity, I_{mates} tells us nothing about the opportunity for sexual selection. For this reason I_{mates} is not generally reported for females. Assuming that the relationship between fecundity and mating success is stronger in males than female when it is strong in both sexes, can lead one to interpret large I_{mates} as evidence for large opportunity for sexual selection (for a related point see Sutherland, 1985). These sorts of assumptions are no longer necessary when we can estimate the mating success and fecundity of all parents directly using Bateman gradients.

While Bateman gradients appear to be the best way to quantify overall levels of sexual selection (Jones et al., 2002, 2004), a measure of the potential or opportunity for sexual selection is still useful for comparisons between environments or taxa. In this paper I propose such an measure by examining what sets the upper limit on Bateman gradients. I first demonstrate the need for a new measure by reviewing recent literature. Here I show that in most studies where both I_{mates} and Bateman gradients are reported, conclusions about which sex has a higher opportunity for sexual selection conflict with conclusions based on Bateman gradients. I then use Bateman gradient estimates of sexual selection intensity to develop a bivariate analogue to older univariate estimates of opportunity for sexual selection. This work extends that of Arnold and Duvall (1994) and is in line with their use of Bateman gradients as an index of actual sexual selection intensities. These authors do not consider what sets the upper limit on sexual selection. With this new index, it is possible to estimate the opportunity for sexual selection without assumptions about the fecundity by mating success relationship. To demonstrate how this new measure of opportunity can be used, I apply it to the problem of how sex-role reversal can arise. In rare

TABLE 1. Comparison of variance-based measures of opportunity for sexual selection and actual Bateman gradient estimates.*

			Male	Gradient		Gradient	
Species	V_{male}	V_{female}	I _{mates}	Male	Female	ratio	Source
D. melanogaster (1–4) ^a	1.18	0.65	0.65	23.3	14.6	1.6	Bateman, 1948
D. melanogaster (5–6) ^a	0.76	0.37	0.28	39.5	2.4	16.5	Bateman, 1948
Dark-eyed Junco	0.67	0.50	0.65	2.6	2.9	0.90	Ketterson et al., 1997
Brown-headed cowbird	0.62	0.50	1.51	1.9	1.9	0.99	Woolfenden et al., 2002
Chipmunk T. amoenus	1.54	1.69	1.24	$\sim \! 1.67^{b}$	$\sim 0.8^{\rm b}$	~ 1.25	Schulte-Hostedde et al., 2004
Pipefish S. typhle	1.28	0.83	0.34	12.1	24.1	0.50	Jones et al., 2000
Newt T. granulosa	0.58	0.95	3.06	74.6	22.2	3.36	Jones et al., 2002

* V_{sex} is the variance in mating success for each sex, I_{mates} is the male variance standardized by the squared mean mating success, *Gradient* (*larger*) is the Bateman gradient of the sex with the larger gradient, and *Gradient ratio* is the ratio of male to female Bateman gradients. ^a Numbers in parentheses indicate range of replicates from Bateman's experiment.

^b Gradients and ratio estimated from Figure 2 in Schulte-Hostedde et al., 2004.



FIG. 2. Relationship between fecundity and mating success for female and male *Drosophila melanogaster*, redrawn from data in blocks 1–4; (from Bateman, 1948). Points are means of fecundity across replicates. Lines represent regressions through points weighted by number in that mating class (see histograms). Males are filled points and bars, and solid line. Females are open points and bars, and dotted line.

but interesting mating systems with reversals in typical sex roles, we would expect the Bateman gradient to be larger in females than males (this is seen in a pipe-fish; Jones *et al.*, 2000). To better understand when sex-role reversal may occur, I examine how the upper limits on sexual selection for each sex (*i.e.*, the *maximum* possible Bateman gradients) are affected by energy availability and parental investment. Finally, I suggest that we use the difference between the sexes in the upper limit on sexual selection to estimate the sex-difference in the opportunity for sexual selection (the potential strength of the force driving sexual differentiation; Arnold and Wade, 1984).

I_{mates} as a Measure of Opportunity

 I_{mates} can overestimate the opportunity for sexual selection if assumptions of fecundity-mate number covariance are not met. I_{mates} also has no upper bound, making it difficult to decide what value constitutes a "large" opportunity for sexual selection. Is the I_{mates} value of 0.28 considered above a high value indicating the large opportunity for sexual selection we expect based on the male Bateman gradient (see Table 1 and Fig. 1)? Based on the Bateman gradients, males gain roughly 39 offspring per additional mate, female gain only 2 (males gain 16 times more). To judge the size of the opportunity, we can compare this I_{mates} value to the value for the rest of Bateman's (1948) data (Fig. 2, Table 1). $I_{mates} = 0.65$ for males in this portion of the data (split by Bateman from the other part based on large mean female fecundity differences; Bateman, 1948). This value remains larger that the previous es-

timate even if we adjust for the large bias in operational sex ratio (OSR) caused by large numbers of unmated males, giving $I_{mates(adj)} = 0.53$ (Shuster and Wade, 2003). While I_{mates} is roughly twice as large as in the previous case, males only gain 23 offspring by remating; females gain a comparatively large 15 offspring (males gain 2 times more). Using I_{mates} to judge opportunity leaves us with the impression that sexual selection should be stronger in the second part of the data, while the Bateman gradients and intuition suggest the opposite. We are misled when we use I_{mates} alone to judge opportunity because the assumption that only males gain fecundity by remating is violated in the data presented in Figure 2. Jones et al. (2002) make a strong case for combining Bateman gradients and variance-based approaches to avoid being misled in this way, but I feel I_{mates} adds little to the Bateman gradients when describing the relative strength of sexual selection acting on males and females.

Several other examples from the literature lead to similarly misleading conclusions when I_{mates} is used to estimate the opportunity for sexual selection (Table 1). In dark-eyed juncos (*Junco hyemalis*), brown-headed cowbirds (*Molothrus ater*) and yellow-pine chipmunks (*Tamias amoenus*), the I_{mates} values are equal or higher than values the for both parts of the *D. melanogaster* data. In contrast, in all three of these examples, neither sex gains more than three offspring by remating, and male and female Bateman gradients are close to equal. Concluding that the opportunity for sexual selection is larger in cowbirds than in *D. melanogaster*, for example, would go against both conclusions based on the Bateman gradients and intuition.

In two cases the conclusion based on I_{mates} matches the conclusion drawn based on Bateman gradients. The pipefish, Sygnathus typhle, represents an interesting case because they experience sex-role reversal (males provide all parental care, females are competitive for mates). In this species, when males were limited, the male I_{mates} (0.34) was smaller than in females (1.02), as expected based on mating behavior and Bateman gradients. Females gain twice as many offspring by remating as males (Bateman gradients of 24.1 for females 12.1 for males). Also in the rough-skinned newt (Taricha granulosa), the conclusion drawn using I_{mates} agrees with the one based on Bateman gradients. In spite of these successes, the large number of discrepancies between the I_{mates} and Bateman gradients approaches suggests the need for a new measure of the opportunity for sexual selection.

UPPER LIMITS ON SEXUAL SELECTION

A new measure of the opportunity for sexual selection, that is closer to our expectation based on Bateman gradients, can be derived by considering what sets the upper limit on these gradients. We know that sexual selection intensity is affected by the amount of energy (or critical resources) available for reproduction and parental care patterns (Williams, 1966; Parker, 1970; Trivers, 1972; Emlen and Oring, 1977; Gwynne,



FIG. 3. The upper limit on sexual selection is represented by the slope of the lines where there is a large amount of reproductive energy (High; solid lines and circles) and a small amount (Low; dotted lines and squares). Lines for males (filled symbols) and females (open symbols) are shown separately. A represents the case for no nuptial gifts; B represents the case where nuptial gifts are represented as 10 arbitrary fecundity units. The difference in slope between male and female lines is greater with high than with low energy ($\Delta S_H > \Delta S_L$), but is not affected by nuptial gift value (ΔS in $A = \Delta S$ in B).

1981, 1984). I now examine how these two factors affect the upper limit on sexual selection for each sex (*i.e.*, the upper limit on the Bateman gradients), describing the effect of different levels of reproductive energy independent of the effects of different levels of parental investment by each sex. It is important to keep in mind that I am talking about *upper limits*, not actual or average levels of sexual selection. It is unlikely that many individuals will reach these upper limits in nature, but the upper limits tell us about how strong sexual selection could be.

To examine what sets the upper limit on sexual selection for each sex, assume a hypothetical case, where all females have equal fecundity and matings are not costly. Next consider a group of females that mate in such a way as to maximize their fecundity: they all mate and get a full packet of paternal investment when available. If there is no paternal investment in offspring (solid lines in Fig. 3A), females do not gain fecundity by remating (beyond the sperm from their first mating), so the upper limit on sexual selection for females is zero (seen as the slope of the lines linking maximum fecundities in Fig. 3). If the males do provide paternal investment, maximum female fecundity can increase with additional mates (solid lines in Fig. 3B) at a rate equal to the effect of a unit of paternal investment on her fecundity. So the upper limit on sexual selection is set for females by the value of the paternal investment that comes with each mating.

Now consider a group of males that mate in a similarly "ideal" way: they all mate with virgin females who do not mate again (i.e., no sperm competition). When males do not invest in offspring, maximum male fecundity is expected to increase with each additional ideal mate at a rate equal to female fecundity. If males do invest in offspring, their maximum fecundity now increases at a rate equal to the female's fecundity plus the boost in fecundity that she receives from paternal investment. So the upper limit for males is set by the fecundity of their mates (including the boost from paternal investment, if any). This means that the upper limit for males always keeps pace with the upper limit for females. More importantly, it means that the difference between male and female upper limits (ΔS) does not depend on paternal investment levels but instead depends on average female fecundity (compare ΔS within and between parts of Fig. 3).

NEW MEASURE OF OPPORTUNITY

Arnold and Duvall (1994) contend that if all females mate once, there is no sexual selection on females and average male Bateman gradients will always be greater than females (as long as the number of male mates can vary). More interesting, from the point of view of understanding the opportunity for sexual selection on each sex, is to consider how the upper limit on sexual selection (*i.e.*, the upper limit on Bateman gradients) for each sex differs. Based on my earlier verbal arguments about ideal mates, the formal relationship between maximum fecundity (F^* , for females or males) and number of ideal mates ($x_{ideal} > 0$, for females or males) is:

$$F_f^* = \bar{A} + \bar{b}x_{ideal,f} \tag{1}$$

$$F_m^* = (\bar{A} + \bar{b}) x_{ideal,m} \tag{2}$$

where \bar{A} is the average potential fecundity of a female in the absence of paternal investment, \bar{b} is the average size of the paternal investment (either gifts or care of young, in units of eggs), and high and low reproductive energy levels are represented as high and low \bar{A} .

In a particular population, if \overline{A} and \overline{b} are assumed to be the means of random normal distributions that do not covary, the female upper limit is equal to the value of an average unit of paternal investment (\bar{b}) . With the same assumptions, the male upper limit is equal to the average fecundity of a female that mates once $(\bar{A} + \bar{b})$. The upper limit of sexual selection on males will be greater than for females whenever $\bar{A} >$ 0. The difference in these upper limits on males and females depends on \overline{A} alone and not on \overline{b} . Therefore, while paternal investment alone can cause substantial increases in the upper limit of sexual selection on females, it cannot cause a reversal in the relative strength of sexual selection unless it reduces a male's success at competing for fertilizations (Lorch, 2002). However, the difference between the sexes in the upper limit on sexual selection (ΔS) is reduced when \bar{A} is smaller, even when there is no paternal investment. This makes it more likely for sex-reversal in Bateman gradients to occur when matings are not ideal (e.g., when there is sperm competition) and some critical resource is rare (e.g., protein rich food for nuptial gift giving katydids; Gwynne and Simmons, 1990; Simmons, 1992; Gwynne, 1993; Simmons et al., 1993).

The upper limit on sexual selection for each sex can be used as an estimate of the opportunity for sexual selection in that sex. This estimate describes how strong the relationship between fecundity and number of mates *can be* for each sex, and tells us more about the potential for sexual selection than does the variance in either of its components. Based on this simple theory the upper limit for males will always equal or exceed female upper limits. The theory predicts that sex-reversal in Bateman gradients and sex-role reversal will only occur when \overline{A} is small relative to \overline{b} and when males are drawn further from their upper limit than females.

How to measure it

Obtaining these new estimates of the opportunity for sexual selection can be done easily in the lab by measuring the fecundity of females with one *versus* two mates. Such estimates require sexually mature virgin females and unmated males with an equivalent range of male and female body sizes in both groups. The male upper limit can be estimated as the fecundity of once-mated females. The female upper limit can be estimated from the difference in fecundity between once-mated and twice-mated females, each mating with a randomly chosen unmated male.

Field estimates of this new measure are also possible (though not ideal) using the same data used to estimate Bateman gradients. For males, the fecundity of females that mate once is an estimate of the new measure of opportunity for sexual selection. Female estimates are more of a problem from field data. When the effects of paternal investment are large, the simple difference between the fecundity of once- and twicemated females may provide a reasonable estimate of the upper limit on sexual selection for females. Female body size and fecundity are expected to covary, affecting both estimates of female Bateman gradients (Ketterson et al., 1998; Prosser et al., 2002) and upper limits on these gradients. Controlling for the effects of female body size on fecundity and comparing field to lab estimates will ultimately show whether estimating female upper limits from field data is reasonable.

Being able to estimate the opportunity for sexual selection in the lab is an advantage over variancebased estimates. In order to get a lab estimate of I_{mates} that tells you anything about natural opportunity for sexual selection, for example, you must attempt to mimic natural mate competition and operational sex ratios (OSR). Failing to do so will produce estimates that tell you little or nothing about the opportunity for sexual selection in natural populations. This is not to say that lab manipulations such as manipulating the OSR are not useful, since they can tell you about how changes in OSR affect the strength of sexual selection acting on each sex (*e.g.*, Jones *et al.*, 2000, 2004).

SEX-DIFFERENCES IN OPPORTUNITY

In the context of variance-based estimates, sex-differences in the opportunity for sexual selection, an important force driving differentiation of male and female morphology and mating behaviour, was expressed as the difference between the two sexes in the standardized variance in mating success (e.g., $I_{mates,males}$ $- I_{clutch, females}$; Shuster and Wade, 2003). This approach suffers from all of the criticisms discussed earlier, particularly when one sex lacks the assumed covariance between mating success and fecundity. In the context of upper limits, the sex difference in the opportunity for sexual selection is the difference between male and female upper limits on sexual selection (ΔS in previous section). This new measure has several desirable properties. First, it measures the maximal amount of force that can drive differences between the sexes. If Bateman is correct and the primary cause of sexual dimorphism is the sex-difference in the relationship between fecundity and mating success, the upper limit

on this sex-difference is estimated by ΔS . Second, the new estimate removes the need for assumptions about how fitness and mating success covary between the sexes. Finally, like the upper limits themselves, the difference between male and female upper limits is in units of offspring gained per additional mating. This makes it is easy to judge the importance of sexual selection as a force for generating sexual dimorphism.

CONCLUSION

I have proposed a new estimate of the opportunity for sexual selection based on the upper limit on "causal" sexual selection using the upper limit on Bateman gradients. The rate at which this upper limit increases with additional mates for males equals the average fecundity of females (including any increase in fecundity she gains by mating). For females, the upper limit equals the unit value of paternal investment given with each mating. Both of these upper limits can be estimated with laboratory matings. The male upper limit can be estimated as the average fecundity of a group of virgin females mated once to virgin males. Female upper limits can be estimated by taking the difference in average fecundity of once- and twice-mated females. The difference between male and female upper limits (the sex-difference in the opportunity for sexual selection) decreases when there is less energy available for reproduction and this difference does not depend on paternal investment level. Sex-reversal in Bateman gradients, therefore, is more likely to occur when there is less reproductive energy available, simply because the upper limit on the strength of sexual selection is more nearly equal for males and females. This is in agreement with empirical observations that show sexrole reversal can be induced by experimentally reducing the protein content of food, requiring males to invest relatively more in offspring (Gwynne and Simmons, 1990; Gwynne, 1993), or when the presence of gut parasites reduces nutrient uptake (Simmons and Zuk, 1992; Simmons et al., 1993). Paternal investment (either in the form of nuptial gifts or paternal care) allows females to gain fecundity by remating and is therefore necessary to cause sex-reversal in Bateman gradients, but it is not sufficient by itself. Without something like a tradeoff between paternal investment and sperm competition, sex-reversal in Bateman gradients will not occur (Lorch, 2002). Using upper limits on Bateman gradients to estimate the opportunity for sexual selection is more in line with our expectations based on existing Bateman gradient data. This new index is experimentally measurable. And it is useful for understanding the effect of energy allocation and paternal care on sexual selection.

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