Understanding Reversals in the Relative Strength of Sexual Selection on Males and Females: A Role for Sperm Competition?

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ABSTRACT: Sperm competition affects sexual selection intensity on males, but models suggest it cannot affect the relative intensity of sexual selection on males compared to females. However, if sperm competition depresses the payoff for male multiple mating, it could affect the relative intensity of sexual selection and even cause sexual selection to be more intense on females than males (reversal of typical pattern). To evaluate how sperm competition, energy availability, and parental investment affect the intensity of sexual selection on each sex, I constructed a simulation model using the relationship between fecundity and number of mates to estimate sexual selection gradients. Unlike earlier models, I include a trade-off between paternal investment and sperm competition ability. The amount of energy available for reproduction affects the sexual selection gradient for each sex. Reversals in the sex experiencing stronger sexual selection do occur when additional paternal investment reduces a male's ability to compete for fertilizations within females. The shape of the distribution of mates for each sex (determined by mate competition) is also important. Output from the model is qualitatively similar to empirical data from insects with paternal investment. This model challenges previous thinking about the role of sperm competition in sex-role reversal.

Keywords: sexual selection, Bateman curves, sex-role reversal.

Understanding which sex experiences stronger sexual selection is interesting for two reasons. First, it can help to explain rare reversals in typical sex roles, where females rather than males are more competitive for mates and males rather than females are more choosy among mates.

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Second, it can help to explain the evolution of sexual dimorphism that depends on the difference in the strength of sexual selection between males and females. To be able to predict which sex experiences sexual selection more strongly, several key factors affecting the strength of sexual selection on each sex must be evaluated. Parental investment affects the strength of sexual selection on males and females (Williams 1966; Trivers 1972; Emlen and Oring 1977), and both energy availability and parental investment play a role in determining which sex experiences sexual selection more strongly (Trivers 1972; Gwynne 1981, 1984; Arnold and Duvall 1994). Sperm competition, which can have strong effects on sexual selection acting on males (Parker 1970), is thought to have little influence on sex-role reversal (Simmons and Parker 1996). This last result is puzzling because, as sperm competition intensity increases, we expect the average fitness gains from each mating to drop for males (Simmons 1992, 1995), potentially decreasing sexual selection intensity on males. However, Simmons and Parker (1996) assume that there is no variation in male sperm competitive ability and that this ability is not correlated with mating frequency. If these assumptions are violated, for example, if preferred males reduce ejaculate volume (Simmons et al. 1999) to increase mating frequency, sex-role reversal may be more likely.

To evaluate the effects of factors such as those mentioned above on the potential for sex-role reversal, Arnold and Duvall (1994) suggest returning to Bateman's (1948) original point about the cause of sexual selection. A positive relationship between fitness and number of mates is the primary cause of sexual selection (fecundity is often used as a surrogate for fitness; see fig. 1; Bateman 1948). The rate of increase in this relationship can be estimated as a regression slope ("Bateman slope" estimates of sexual selection gradients; Arnold and Duvall 1994). If fitness does not increase with additional mates, Bateman slopes are flat, and no competition for mates is expected (either intrasexual competition or competition to be chosen by the opposite sex). Without competition, there will be no

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Figure 1: Bateman slopes. The relationship between fecundity (offspring number) and number of mates (represented by the slopes of the dashed regression lines, or Bateman slopes) for a hypothetical population with typical sex roles (i.e., males more competitive; females more choosy). The histograms show the frequency distribution of individuals with different numbers of mates. The lower regression slope for females shows that they do not gain as much fecundity by remating as males do. The Bateman slopes estimate the strength of sexual selection on mating success (the cause of sexual selection) not the strength of sexual selection on a trait.

sexual selection, and dimorphism between the sexes is not expected. Therefore, it makes sense to evaluate the effects of these three key factors on male and female Bateman slopes. Changes in the relative magnitude of male and female Bateman slopes (sex reversal of slopes) can be used to judge the importance of each factor in leading to sexrole reversal.

In this article, I develop a model that examines the roles of energy availability, parental investment, and sperm competition in controlling the strength of sexual selection on each sex. In particular, I examine the role of sperm competition in reducing the intensity of sexual selection on males. The model uses Bateman slopes to estimate the intensity of sexual selection on each sex. My goal is to explore some of the conditions under which sexual selection is more intense on females than on males. I use an individual-based simulation of mating in populations with different levels of energy available for reproduction and different relative amounts of parental investment. This simulation explicitly includes a trade-off between mating frequency and sperm competitive ability that turns out to be important in leading to sex-role reversal. This work is novel when compared to earlier models that showed no effect of sperm competition on sex-role reversal.

Arnold and Duvall (1994) constructed an analytical model of nuptial-gift mating systems (where males provide food gifts at mating) that bears mentioning. They concluded that sex reversal in Bateman slopes depends on the odds of a female mating at least once being less than the average number of mates among females. This is a difficult condition to meet. However, their conclusion assumes both a random distribution of numbers of mates among females and no cost to producing nuptial gifts. When females are competing for valuable nuptial gifts, we would not expect female mating distributions to be random, and nuptial gifts should be costly to make. Although it would be possible to include a cost to making nuptial gifts in the Arnold and Duvall (1994) model, an analytical solution for arbitrary distributions of female mates would be difficult to obtain. The simulation model I present here represents a way around these difficulties that uses realistic (empirical) distributions of female mates to take into account competition for mates among females. Using empirical data in the model also provides a qualitative check of the model since mating distributions are derived from populations for which the sex roles are known.

Background on Sex-Role Reversal

Typical sex roles (competitive males and choosy females) are thought to prevail in most animals because males that mate multiple times generally gain more fecundity than females that mate multiple times, resulting in a larger male Bateman slope for males than females (Bateman 1948; fig. 1). Sex roles may occasionally reverse because females gain more fecundity than males by mating multiple times, resulting in stronger sexual selection on females than on males (Bateman 1948; Arnold and Duvall 1994). In most examples of sex-role reversal, females are able to increase their fecundity because each additional male invests in offspring, either offering them substantial male parental care (of young or eggs: giant waterbugs [Smith 1979; Kruse 1990], pipefishes [Berglund et al. 1989; Vincent et al. 1992; Berglund 1995; Jones et al. 2000], and spotted sandpipers [Oring and Lank 1986]) or meals (nuptial gifts: preydonating dance flies [Svensson and Petersson 1987; Cumming 1994]; katydids that donate edible spermatophores [Vahed 1998]). In a compelling example, Jones et al. (2000)

	Male					Female ^a	
	1	2	3	4	5	Mates (no.)	Fecundity
Female:							
1	0	0	1	2	0	3	15
2	0	0	1	0	1	2	62
3	0	0	0	2	2	4	178
4	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0
Male: ^a							
Mates (no.)	0	0	2	4	3		
Fecundity	0	0	38	136	81		
Male trait	77	-1.08	44	.93	62		

Table 1: Example 5×5 mating matrix for simulated populations that represents how the individual-based model works

Note: Actual tables were 100×100 . Cells contain the number of matings between a pair (if any; based on the parental table of Arnold [1994, p. S143]).

^a Marginal row totals (for males) and column totals (for females) are used to estimate the selection gradients (regression of fecundity on number of mates).

recently used Bateman slopes to demonstrate that the strength of sexual selection was stronger on females than males in the sex-role reversed pipefish, *Sygnathus typhle*. Therefore, sex-role reversal can occur when the relative fecundity gains from remating reverse.

Simulation Model

I constructed an individual-based model to simulate mating within a population where the parents of each offspring are known (details and justification are in the appendix). I assumed reproductive output of females depended on total energy available for reproduction (basic level plus any acquired from mates). For a given round of simulations, the basic amount of energy females had to devote to reproduction was fixed. For each simulation round, I varied the basic amount of reproductive energy available to mimic a situation where either there is a change in food availability or there is a change in how energy is allocated to reproduction. Male reproduction depended on the energy available for both reproduction and paternal investment as well as on how male reproductive effort translated into offspring (e.g., whether males were successful in competition for mates and/or eggs, see "Sperm Competition and Multiple Mating"). Male reproductive energy was either fixed (at the basic energy level) for all males in a given round of simulation, or it increased linearly with an arbitrary trait value. The latter simulated variation in male condition correlated with a trait on which mate competition could be based. I also varied the value of paternal investment between simulations while holding female investment constant as a way of varying relative parental effort by each sex. I treated paternal investment as discrete donations of energy, which could represent either nuptial gifts, directly converted into additional eggs by females, or packets of paternal care, allowing females to produce more offspring by reducing her investment per egg. The output of the simulations allowed me to examine how male and female Bateman slopes (and the sexual selection gradients they represent) changed relative to each other due to changes in energy availability and relative parental investment. In particular, I was interested in which combinations of reproductive energy and paternal investment resulted in female Bateman slopes that were greater than the male slopes.

Sexual Selection Gradients

After simulating mating according to the rules described in the appendix, I used a "mating matrix" (see table 1) to find the actual fecundity and numbers of mates for each male and female. Then, for each simulated population, I calculated the regression of fecundity on numbers of mates for each sex. I used these Bateman slope estimates of the sexual selection gradients to calculate a mean slope for the 100 populations in each round of simulations. Estimates for simulated populations where males had identical traits differed due to random mating. To decide whether sexual selection was more intense on females than males, I looked at whether the population mean Bateman slope was greater for females than for males for a particular combination of average reproductive energy and value of paternal investment.

Sperm Competition and Multiple Mating

In this model, when females mate more than once, paternity is determined by the outcome of sperm competition. I assumed sperm mixed in a fair lottery (a male's fertilization success is proportional to the relative abundance of his sperm in a female). The number of sperm inseminated into each female increased with male reproductive energy level and decreased with his number of mates, resulting in a trade-off between mating frequency and sperm competitive ability. This trade-off simulates a system where males pay part of the cost of the paternal investment that comes with additional mating by reducing sperm production. I did two things to demonstrate the effects of this built-in trade-off on reducing male Bateman slopes. First, for comparison to the simulation output, I calculated the average male Bateman slope that would occur if there was no trade-off. With a fair sperm lottery, the average male Bateman slope (i.e., average fecundity gain with each additional mating) is simply the average female fecundity divided by the average number of mates. Second, to demonstrate that the trade-off was occurring, I measured the correlation between male relative fertilization success and number of matings in the simulated populations (see appendix). This correlation should decrease as gift size increases and be negative when sex reversal in Bateman slopes occurs.

Mate Competition

Mate competition will cause the distribution of number of matings for each sex to deviate from random. These distributions both influence and are themselves influenced by Bateman slopes. Females were assigned a number of mates from either a Poisson distribution or from one of six empirically derived mating distributions (fig. 2). Two of these are samples from the same population taken 2 wk apart, which allowed me to examine the effects of within-season changes in the mating distributions on the Bateman slopes. Male mating distributions were determined by whether or not they competed for mates based on male trait value.

Results

The simulation results shown connected by lines in figures 3, 4, and 5 represent the average of 100 estimates of three sexual selection gradients (one for females, one for males with no trait value variation, and one where male reproductive energy and mating success depended on variable trait values) for populations with 100 males and 100 females. Points representing average male Bateman slopes calculated assuming no trade-off between number of mates and sperm competitive ability are shown to indicate the effect of this trade-off. By comparing simulations with males that have identical amounts of reproductive energy to simulations with males whose energy and mating suc-

cess depend on a trait value, I have bracketed the range of possible male sexual selection gradients for a given set of parameters (male sexual selection estimates are highest when males compete and lowest when they do not compete).

The results shown in figure 3, in which the distribution of mates among females is random, are typical of the results for other female mating distributions. These results indicate that the trade-off between number of mates and sperm competitive ability is an important determinant of whether sex reversal in Bateman slopes will occur. When there is no trade-off, average male Bateman slopes are expected to increase with paternal investment level. They do so at a rate that makes sex reversal in Bateman slopes unlikely. To see this, since average female Bateman slope estimates are not affected by whether or not there is a trade-off, we can compare the female Bateman slope estimates to the calculated average for males and see that sex reversal in Bateman slopes never occurs. When there is a trade-off, the results in this figure also show that, for a given level of paternal investment, the difference in sexual selection gradients between males and females was lower when the basic amount of reproductive energy was halved. This is in agreement with conclusions based on upper limits of sexual selection (Lorch 1999). In addition, when sex reversal in Bateman slopes occurred in the simulation, it only occurred when males were not competing for mates based on male trait value. Sex reversal in Bateman slopes also occurred at lower paternal investment levels when mean reproductive energy was lower (fig. 3). Since these results are generally true for all female mating distributions, in what follows, I focus on new insights generated by the other female mating distributions.

Figure 4 shows that, in addition to the effects of the levels of both reproductive energy and paternal investment, the distribution of female mating is important. When the distribution from the sex-role reversed Mormon cricket population was used to constrain female mating (fig. 4A), sex reversal in Bateman slopes only occurred at low reproductive energy levels and then only when males had identical amounts of reproductive energy. A sex reversal in Bateman slopes did not occur when data from the "typical roles" or nonreversed Mormon cricket population were used to constrain female mating (although the gradients were close for low average reproductive energy with a large paternal investment; fig. 4B). Sex reversal in Bateman slopes occurred at both reproductive energy levels in simulations based on the unknown sex-role distribution for Mormon crickets (fig. 4C). At low energy levels (and high paternal investment level), reversals almost occurred even when male reproductive energy and mating success depended on trait value. Interestingly, the differences between male and female gradients were dra-



Figure 2: Comparison of the six empirical distributions (Mormon crickets on the left and *Metaballus litus* on the right) for numbers of mates among females used in the mating simulations represented in figures 4 and 5. Lines represent the Poisson expectation with the same mean (2.95 for *A*, 1.61 for *B*, 3.71 for *C*, 2.29 for *D*, 2.39 for *E*, and 3.25 for *F*). N = 21 (*A*), 31 (*B*), 79 (*C*), 24 (*D*), 67 (*E*), and 12 (*F*). Names and dates indicate population descriptor used in original papers (see "Mating Distributions").

matically lower with the unknown distribution that contained fairly large proportions of females who had not mated (fig. 2). Presumably because of this large zero class, in figure 4*C*, female gradients are >15 points higher than in figure 4*A* and 4*B*.

When the female mating distribution was constrained



Figure 3: Sexual selection gradient estimates when females are assigned a number of mates randomly from a Poisson distribution (mean = 4). Points represent the average of 100 Bateman slope estimates (regressions of fecundity on number of mates). Four sets of gradients are shown: female gradients, male gradients calculated based on no trade-off between number of mates and sperm competitive ability, male gradients from simulations for identical males, and male gradients from simulations when the probability of mating with a randomly encountered male depends on his random normal trait value. The figure shows that the difference in sexual selection gradients between males and females is smaller and that role reversal occurs at smaller gift values when mating energy is lower. For this and the next two figures, standard errors were <1.2 for all means and are not shown. All three figures show simulations of mean reproductive energy levels of 100 units on the left and 200 units on the right. The only difference between figures 3, 4, and 5 is the distribution of mates among females used in the simulations.

using the field data on *Metaballus litus*, sex reversal in Bateman slopes did not occur (fig. 5). However, when the distribution of the behaviorally role-reversed population was used to constrain female mating, the male and female gradients were very close (5 Bateman slope units apart) for relatively high levels of paternal investment at low reproductive energy levels. The two time-staggered samples (almost 2 wk apart) from the same population at Dunsborough (fig. 2*B*, 2*D*) give us some insight into how changes in the average female mating success can affect the relative strength of sexual selection on males and females. As the modal number of mates for females shifted from one to two, the difference in the strength of sexual selection on the two sexes shrank (cf. fig. 5*A*, 5*B*).

Role of Sperm Competition

If males pay the cost of additional mating by reducing sperm production (as I have assumed in these simulations), they will transfer fewer sperm to each mate, making males with high mating success less competitive for fertilizations than a similar-sized male with fewer mates. The effects of this trade-off can be seen by comparing male Bateman slope results with and without the trade-off in figures 3, 4, and 5. In addition, figure 6 shows that sperm competition ability decreased with paternal investment levels in these simulations. The correlation between relative fertilization success and numbers of mates went from significantly positive at low paternal investment levels to significantly negative at high paternal investment. The other female mating distributions gave comparable results (P. D. Lorch, unpublished data). What this means is that sperm competitive ability increased with multiple mating when paternal investment was cheap (relative to female investment) and decreased when paternal investment was expensive and that the largest decrease in sperm competitive ability (i.e., the smallest correlations) coincided with paternal investment levels that led to sex reversal in Bateman slopes. This was a direct result of paying the cost of additional mating (at a given level of paternal investment) by reducing the number of sperm transferred at each mating. This role of sperm competition in producing a sex reversal in the strength of sexual selection has not been previously recognized.



Figure 4: Sexual selection gradient estimates from simulations based on empirical Mormon cricket female mate distributions. Females are assigned numbers of mates from (A) a population that was role reversed (RR; fig. 2C); (B) a population that was not role reversed (NRR; fig. 2A); and (C) a population whose mating system was not known (UNK; fig. 2E). Points are as in figure 3. The distribution used in C (UNK; fig. 2E) is dominated by a large number of females who had not mated. In B, reversal only occurs at low reproductive energy levels when there is no variation between males.

Discussion

These simulation results demonstrate the importance of the three key factors identified in the introduction. Having less energy available for reproduction reduces the difference between male and female Bateman slopes. This makes sex reversal in these slopes more likely because males invest relatively more in offspring. Therefore, these two key factors, reproductive energy and relative parental investment, behave as we would expect based on previous empirical work. Role reversal occurs in species with costly nuptial gifts in environments where food is relatively scarce (Gwynne and Simmons 1990; Simmons 1992; Gwynne 1993; Simmons et al. 1993). Sperm competition alone does not make sex reversal in Bateman slopes more likely. However, if males pay the cost



Figure 5: Sexual selection gradient estimates from simulations based on empirical *Metaballus litus* female mate distributions. Females are assigned numbers of mates from a distribution based on (A) a population that was not role reversed (*NRR*; fig. 2B); (B) the same population 12–13 d later (fig. 2D); and (C) a role-reversed population (*RR*; fig. 2F). Points are as in figure 3. Sex-role reversal does not occur in the simulations based on *M. litus* distributions, although male and female gradient estimates are closest when they are behaviorally sex-role reversed.

of additional mating (and the attendant paternal investment) by reducing sperm competitive ability (e.g., by slowing sperm production), sperm competition clearly can play a role in producing sex reversal in Bateman slopes.

The claim that sperm competition is important in determining whether sex-role reversal occurs seems to contradict the results of Simmons and Parker (1996). These authors found that sperm competition cannot affect male potential reproductive rate (PRR) and therefore cannot affect the likelihood of role reversal. However, their model depends on the two assumptions mentioned earlier: that there is no variation in male sperm competitive ability and that this ability is not correlated with mating frequency. In my simulations, both of these assumptions are violated



Figure 6: Sperm competition and sex-role reversal. The index represents the Spearman rank correlation between relative fertilization success and number of mates (see appendix). Points above and below the two solid horizontal lines are significantly different from zero ($\alpha = 0.05$). Data shown are for two example female mating distributions (Poisson [mean = 4] and Polson Mormon crickets [*MCUnk*]) split by basic reproductive energy level.

(as might be expected in animals with costly paternal investment). The number of sperm the simulated males transferred depended both positively on male trait value (z_m) and negatively on the numbers of mates he had (x_m) , so there was definitely variation in the number of sperm transferred by each male and consequently in sperm competitive ability. Additionally, if the number of sperm transferred depends on $z_{\rm m}$ and $x_{\rm m}$, sperm competitive ability can be correlated with mating frequency. Making x_m depend positively on z_m is equivalent to making male "timeout" negatively correlated to $z_{\rm m}$ and $x_{\rm m}$ (where time-out is time spent unable to mate and is inversely related to potential mating frequency). Simmons and Parker (1996) make the important caveat that adaptive changes in timeout may occur as a result of selection due to increased sperm competition intensity. This, in turn, can lead to reductions in male PRR and to sex-role reversals (Simmons and Parker 1996).

The distributions of mates for both sexes are also important determinants of whether sex reversals in Bateman slopes occur. If there are large numbers of females that have not mated (fig. 2E), the difference between females and males in the strength of sexual selection is smaller (fig. 4C). This is true primarily because having large numbers of females unmated (either because of intense mate competition or as might occur early in the mating season)

increases the average sexual selection gradient for females that do mate; there are relatively more males available for mating and paternal investment. It is possible that the female mate distribution from Polson, Montana (fig. 2E), represents a sample taken early in the reproductive season and that some females had not mated yet. When the season starts, and as females become sexually mature, many will be unmated. As the season progresses, the distribution will stretch out, and the relative number of unmated females will shrink. The difference in the strength of sexual selection on males as compared to females should shift as the season progresses. We see evidence for this in the two staggered samples for females of Metaballus litus from the Dunsborough site. As the modal number of mates for females increases, the difference in the strength of sexual selection on males versus females decreases (cf. fig. 5A, 5B). Temporal changes in the relative strength of sexual selection on males and females have important consequences for the evolution of mating behavior; however, this topic has been little studied (but see Kruse 1990). For males, the distribution of mates was varied by either allowing or not allowing male mate competition. Sex reversals in Bateman slopes only occurred when males were not allowed to compete based on male trait value. Competition among males generally increased male Bateman slope estimates (see figs. 3–5), making sex reversal in Bateman slopes less likely. This influence of competition on Bateman slope is interesting because the increasing Bateman curve is the presumed cause of mate competition, but the relationship is also influenced by competition. Part of this influence is undoubtedly due to competition leading to relatively more unmated individuals. In species with costly nuptial gifts, food scarcity may limit male competition a priori, increasing the likelihood of sex reversal in Bateman slopes by decreasing male Bateman slopes.

In these simulations, males transferred fewer sperm to each female to pay the cost of additional mating. Another reasonable way for males to pay this cost would be to allow marginal decreases in paternal investment levels with increased numbers of mates (Gwynne 1984, 1990). This effect alone (without coincident decreased sperm competitive ability) is unlikely to produce sex-role reversal. Based on what I have said elsewhere about the upper limits on sexual selection (upper limits on Bateman slopes; Lorch 1999), decreasing average paternal investment levels does not bring the upper limits on sexual selection for males and females any closer together. This should also be true for average Bateman slopes if the averages are dependent on the same thing as their upper limits. In other words, average female Bateman slopes should depend on average paternal investment level, and average male Bateman slopes should depend on average female fecundity, including paternal investment. If females have any eggs before they mate, so that the average male Bateman slope is not dependent solely on average paternal investment, reducing paternal investment with additional mating should decrease female Bateman slopes more than male slopes, making a sex reversal in Bateman slopes unlikely. Others have examined a negative effect of increased paternal investment on mating rate (i.e., larger time-out between mating; Arnold and Duvall 1994; Parker and Simmons 1996).

As I said before, Arnold and Duvall (1994) concluded that in order for sex reversal in Bateman slopes to occur, the odds that a female mates at least once must be less than the average number of mates among females. In most of the simulations presented here where there is a sex reversal in Bateman slopes, this condition is not met (results not shown), so based on the Arnold and Duvall (1994) result, sex reversal should not occur. The simulation results show that when we use realistic female mating distributions and when we allow males to trade additional mating for reduced sperm competitive abilities, we find that sex reversal in Bateman slopes is more likely.

Conclusion

In addition to the effects of reproductive energy and relative parental investment on sexual selection, sperm competition appears to play an important role in leading to stronger sexual selection on females than males. Specifically, when males pay the cost of making additional paternal investment by reducing the number of sperm transferred to each female, sexual selection can become stronger on females. This is a new perspective that may help to explain the distribution of sex-role-reversed mating systems. For example, it might explain why so few insects with nuptial gifts exhibit sex-role reversal. Out of the many Orthoptera with nuptial gifts (>17 subfamilies), sex-role reversal is known in only three species (Gwynne 1995). It may be that only in these three species do males reduce the number of sperm they produce to pay for additional mating. Perhaps in these species, sperm are unusually costly to produce or are not stored in large numbers. The prediction is that species (or populations, in species where role reversal depends on environment) with sex-role reversal should exhibit a negative correlation between number of mates and number of sperm inseminated per mating, while sister species (or populations) without sex-role reversal should show no such trade-off.

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APPENDIX

Model Details

Mating

The model (implemented in a "C" program, available from author upon request) tracked individuals using a mating matrix (see example in table 1). The mating matrix was filled by following these steps (starting with step 2 if males were identical).

Step 1. The program randomly assigned each of 100 males a standard normal trait value (mean = 0, standard deviation = 1) that was used to determine exactly how much energy a male had for reproduction, his maximum number of mates, and the chances that he mated successfully when he encountered a potential mate. This sexually selected trait could represent a metric traitlike body size (Partridge and Farquhar 1983; Partridge et al. 1986) or a secondary sex character (Andersson 1994), or it could represent condition (defined as resources available for survival and reproduction; Rowe and Houle 1996).

Step 2. The program then randomly assigned each female a number of mates based on either a Poisson distribution (with mean of 4; see "Mating Distributions" for justification) or an empirical distribution (see "Mating Distributions"; fig. 2).

Step 3. Mating encounters: For each female, a male was randomly chosen from a pool of eligible males. Males were removed from the pool when they had mated more than a maximum number of times. This maximum was determined by dividing the amount of reproductive energy a male had by the sum of the value of paternal investment plus one arbitrary energy unit set aside for sperm costs for each mating (see "Parental Investment and Sperm Allocation"). Actual numbers of sperm per mate were determined based on actual numbers of mates (see "Parental Investment and Sperm Allocation").

Step 4. Mate choice: In simulations in which males did not differ, females mated with each randomly encountered male. When males did differ, the program then decided whether a pair mated based on the following rule: mate with a probability that is a linear function of the male trait value (as in the open-ended preference of Lande 1981). A rule like this would be expected to act when the outcome of male-male competition or female choice depends on some trait of males that is correlated to the amount of energy he devotes to reproduction. Such a rule will also act in nuptial-gift systems when there is a positive correlation between the speed at which a male produces gifts and his trait value. I determined male mating success this way because male mating distributions are not known for any species for which female mating distributions are known.

Step 5. The program then repeated steps 3 and 4 until all females had mated their predetermined number of times.

Reproductive Energy and Fecundity

For simplicity, I chose to focus on reproductive energy rather than the broader reproductive effort (which includes energy, time, and risk). Before females began mating, I assigned each one the basic amount of reproductive energy (E_0) . In simulations in which all males were identical, I did the same for males. There are no data to suggest what the relationship between trait value and reproductive energy available to each male (E) should be, so where males differed in trait value, I arbitrarily assumed each male's E to be in linear proportion to their trait value (slope = 0.25). Males with a trait value of 0 had E = E_0 . Those with a positive trait had proportionally more than E_0 , and those with negative values had proportionately less. The assumption had the effect of producing equal variance in E regardless of E_0 . The value of E_0 was fixed at either 100 or 200 arbitrary energy units for both males and females in a given round of simulations. I set an energy unit to equal the cost of producing one egg. Males used reproductive energy for both paternal investment and sperm; females used it only for eggs. Each time a female mated with a given male, she gained s_m sperm (see "Parental Investment and Sperm Allocation") that subsequently mixed with all other sperm stored in her reproductive tract. Females gained energy with each mating in proportion to b (paternal investment, in energy units) and produced a total of $E + bx_f$ eggs (where $x_f =$ number of mates for females). Her fecundity was then equal to the number of eggs she produced. Male fecundity by each female was proportional to his share in her stored sperm (sperm lottery, see "Parental Investment and Sperm Allocation"), and his total fecundity was the sum of the number of offspring he gained with each female.

Paternal Investment and Sperm Allocation

Paternal investment could not be so large that males gave all their reproductive energy as investment in offspring and none as sperm. To ensure this, males with too little energy to mate successfully once were not allowed to mate, and the maximum number of mates was determined as described earlier. Thus, one of the costs of multiple mating and giving away multiple packets of paternal investment is a limit on the number of mates for a given male. I varied paternal investment value (b) in units of five, from five up to the largest value that did not result in fewer male mates than female mates (15 for $E_0 = 100$ and 25 for $E_0 = 200$). I arbitrarily assumed that sperm cost 0.001 energy units to make. The number of sperm males ejaculated into each mate at each mating was calculated as $s_{\rm m} = (E - bx_{\rm m})/0.001\bar{x}_{\rm m}$ (where E and b are as above, $x_{\rm m}$ = number of mates for males, and $\bar{x}_{\rm m}$ = mean number of mates for males in a simulated population). With this model for sperm partitioning, I assumed that the cost of additional paternal investment was also paid in part by reducing the number of sperm ejaculated into each female, which reduced a male's ability to compete for fertilizations within each of his mates. This is a realistic way of paying the cost of additional mating if the average value of paternal investment with each mating is fixed in a population (e.g., fixed nuptial-gift value) and there is a fixed mating period so that males that mate more times have less time between mating to produce sperm (Heller and von Helverson 1989). (See "Discussion" for another way of paying for additional mating.) I assumed that no first- or lastmale sperm precedence occurred and that sperm competition was by lottery (a male's fertilization success is proportional to the relative abundance of his sperm in a female). Lotteries appear to occur in several nuptial-gift giving insects, including in three cricket genera (Allonemobius [Howard and Gregory 1993], Teliogryllus [Simmons 2001], and Grylloides [Sakaluk 1986]) and in the katydid genus Decticus (Wedell 1991). To demonstrate the effects of the built-in trade-off between mate number and sperm competitive ability, I measured the correlation between relative fertilization success and number of matings in the simulated populations. I derived these data using simulation runs in which males competed for mates based on a variable trait value, calculated the average relative fertilization success of each male (the proportion of each mate's eggs that he fertilized averaged over all mates), and then examined how the Spearman rank correlation between a male's relative fertilization success and his number of mates changed as gift value increased.

Mating Distributions

Although mating frequency has been studied in a number of animals, the distributions are rarely published. In all simulations, I constrained the mating distribution of females to fit either a Poisson distribution (mean = 4) or one of six unpublished distributions for field-caught females of two katydid species (Mormon crickets *Anabrus simplex* and *Metaballus litus*; D. T. Gwynne, personal communication; see fig. 2). The Poisson was used to simulate a random distribution of female mates. A mean of four was used because it is the upper limit of field estimates from the katydid female mating distributions (see fig. 2 legend for means and sample sizes). Smaller mean numbers of mates would make sex reversal in the strength of sexual selection less likely. Collection localities and the methods used to determine the empirical mating distributions have been described elsewhere for sex-role reversed and nonreversed Mormon cricket populations (Gwynne 1984), for a Mormon cricket population whose mating system was unknown (Gwynne 1993), and for both role-reversed and nonreversed populations of *M. litus* (Gwynne 1985).

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