Female copying increases the variance in male mating success

(evolution/sexual selection/female choice)

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ABSTRACT Theoretical models of sexual selection assume that females choose males independently of the actions and choice of other individual females. Variance in male mating success in promiscuous species is thus interpreted as a result of phenotypic differences among males which females perceive and to which they respond. Here we show that, if some females copy the behavior of other females in choosing mates, the variance in male mating success and therefore the opportunity for sexual selection is greatly increased. Copying behavior is most likely in non-resource-based harem and lek mating systems but may occur in polygynous, territorial systems as well. It can be shown that copying behavior by females is an adaptive alternative to random choice whenever there is a cost to mate choice. We develop a statistical means of estimating the degree of female copying in natural populations where it occurs.

A sex difference in variance in reproductive success often occurs owing to the variance among males in the number of mates (1–6). Both male–male competition and female choice can result in some males obtaining a disproportionate share of the matings (7). When the variance among males in mating success is associated with heritable variation in male phenotype, then selection can lead to sexual dimorphism through the exaggeration in males of characters selected against in females (4, 5, 8). For this reason, understanding the causes of variance in male reproductive success is central to an understanding of the process of sexual selection.

Consider lekking species, where large variances in the numbers of matings among males are commonly observed (9–14). The behaviors of females of lekking species suggest strongly that they visit and make an active choice of mates from among the males present on the lek. Nevertheless, the criteria influencing female choice remain obscure (15, 16). Although extensive studies (9–15, 17–19) of male position on leks, environmental correlates of male position, and direct measurement of male phenotype have yielded significant results, they have failed to explain all of the variance in male mating success in any species. The "excess" variance, whether small or large, is frequently attributed to either "noise" in the system, unmeasured variables, or interactions among variables.

We propose that "female copying" may be a significant factor contributing to the variance in male mating success. By female copying we mean that, when a female chooses a mate, she is influenced by the mate-choice behavior of other females (16, 20–24). Our concern is the situation where this influence is positive, such that a given female is more likely to mate with males that have mated previously. We will show that even a weak tendency by females to copy each other increases the variance in matings among males significantly. Whenever there is female copying, there are more males that

do not obtain mates and more males that obtain many mates relative to random mating. Thus, female copying increases the variance in male mating success by enhancing the relative mating success of some males and diminishing that of others. If it is difficult for females to distinguish adaptive differences among males or when there is a cost—e.g., time, energy, or risk of predation—to evaluating males (25), female copying may be an adaptive alternative to random choice. We show that the distribution of mates per male can be used to estimate the extent of female copying.

THE MODEL

Random Mating. Consider a population of c males and n females and let $R = n/c$ be the sex ratio. Assume that females choose males sequentially, and that each female chooses her mate from among the c males.

If mates are chosen randomly and independently by each female, then the probability that a given female will choose any one male is $1/c$: the likelihood that an individual male is chosen is inversely proportional to his representation in the population of males. The distribution of the numbers of mates per male will be binomial and defined by

$$f(x) = \binom{n}{x} p^x q^{n-x}, \qquad [1]$$

where $p = 1/c$, $q = 1 - p$, and n is the number of females choosing mates. The average number of mates per male is $n/c = R$, and the variance among males in the number of mates is defined as

$$\sigma^2 = \frac{n}{c}\left(1 - \frac{1}{c}\right)$$
$$= n(c - 1)/c^2. \qquad [2]$$

The expected variance in male mating success is approximately equal to the sex ratio when the number of males is large,

$$\lim_{c^2 \to \infty} \sigma^2 = n/c = R. \qquad [3]$$

The opportunity for selection, I (2, 4–6, 26), is the ratio of the variance in fitness to the square of the mean fitness, i.e., the variance in relative fitness. For selection to operate, I must be greater than zero and the value of I sets an upper limit on the amount of phenotypic change possible by selection. That is, $I > 0$ is a necessary but not sufficient condition for selection (4–6, 26). We are concerned here with the opportunity for sexual selection due to differences among males in mating success. In the case of random mating described above, $I = (c - 1)/n$, which is approximately 1 when the sex ratio is unity ($c = n$) and the number of males is large.

Female Copying: Case 1. Again consider a population of c males and n females and let the first female choose her mate at random, where the probability that a given male is chosen is $1/c$ as above. We model female copying by increasing the probability that the next female will choose this same male relative to other males. Therefore, when the second female chooses her mate, we let the probability of her choosing the same male be increased and defined as $(1 + s)/(c + s)$, where s is a constant. (Note that in our model, $s > 0$; negative values of s could be used to evaluate the case where females avoid previously mated males.) The probability that an unmated male will be chosen by the second female is decreased from $1/c$ to $1/(c + s)$. For the third female, the probability of choosing a previously mated male depends upon how many females have already chosen him as a mate. If both the first and second females chose the same male, then the probability that he is chosen again by the third female is $(1 + 2s)/(c + 2s)$ and the probability that any of the remaining unmated males is chosen is $1/(c + 2s)$.

In general, for the ith female, the probability that a male is chosen is given by $(1 + hs)/\{c + (i - 1)s\}$, where $0 < h < (i - 1)$ is the number of females already choosing that male. (The denominator in these mating probabilities is always the number of males, c, plus s times the total number of matings so far). In this model, the probability that a male is chosen by a given female is an increasing function of the number of times he has been chosen before and a decreasing function of the number of times any other male has been chosen. The degree of female copying is s; the larger the value of s, the greater is the propensity of a female to "mimic" the behavior of other females when she chooses a mate.

One way to view this model is to imagine that each female assigns a score to sequentially examined males and chooses her mate based on the score of a male relative to the sum of all the males' scores. The scores of each male in the case of random mating would equal 1.0. With no copying, the sum of scores for all males would be $c \times 1 = c$ and the relative score for any one male would be $1/c$. When the first male mates, he would get a new score of $1 + s$. The sum of scores would be $c + s$, and thus the relative score for this first male at the time the second female chose her mate would be $1 + s/c + s$. As each female mates, the sum of scores increases by s. This is the same result as above.

The form of our model is analogous to that of a Polya Urn model (27–29) in which there is an urn with b black balls and w white balls. A ball is chosen at random, its color is noted, and then it is put back in the urn together with s additional balls of the same color. The Polya Urn model can be extended to the multivariate case (28) where there are initially a total of c balls, each of a different color, in the urn. Assuming that the urn initially contains 1 ball of each of c colors and that the value of s is a constant real number, the multivariate case is equivalent to our model of female copying. This permits us to use the equations for the mean and variance of the Polya–Eggenberger distribution to describe the distribution of mates per male for any degree of female copying, s.

Given that all males begin with the same probability of being chosen by the first female $(1/c)$, the cumulative distribution of matings per male can be obtained from the marginal distribution for any one male, which from the Polya–Eggenberger distribution (28) is

$$\Pr(x = r) = \frac{\binom{r - 1 + (1/s)}{r}\binom{n - r - 1 + (c - 1)/s}{n - r}}{\binom{n - 1 + c/s}{n}}. \quad [4]$$

The mean number of mates per male remains the same as in the case of random mating, $R = n/c$. The variance in

number of times a ball of a given color is drawn on repeated trials of n draws each (28) is

$$\sigma^2 = \frac{n(c - 1)\left(\dfrac{c}{s} + n\right)}{c^2\left(\dfrac{c}{s} + 1\right)}. \quad [5]$$

The variance among trials of n draws for one color (i.e., male) is the same as the average variance across colors within a trial as long as the initial probability of being chosen is the same $(1/c)$ at the start of each trial. Thus, with respect to our model of female copying, Eq. 5 is the equation for the variance in number of mates across males. The opportunity for selection is the ratio of this variance to the square of the mean, or

$$I = \frac{(c - 1)(c + ns)}{n(c + s)}. \quad [6]$$

Note that this equation for I is equal to that for I in the random mating case multiplied by the factor $(c + ns)/(c + s)$, which is always greater than 1 for all $s > 0$. Thus, female copying behavior always increases the opportunity for sexual selection.

We can rewrite Eq. 6 and show that as the number of males and females becomes large, I can be approximated by $(1/R) + s$. This result allows us to estimate s from empirical studies (see below).

Female Copying: Case 2. In case 1, it was assumed that females chose mates sequentially and that the mating decisions of individuals who selected previously were perceptible to each new female. In case 2, we imagine that the population of n females visits the lek (or male territories) in k groups of size n_i, where $i = 1, 2, \ldots k$, such that

$$n = \sum_{i=1}^{k} n_i. \quad [7]$$

Each group of females is considered to be independent, such that the matings that take place in one group are not influenced by the matings of females in any other group. Each group visits the lek, and within each group the dynamics are those described above for case 1.

The overall mean number of matings remains equal to $R = n/c$. Eq. 5 now represents the variance in matings among males due to a visit by a single group of females,

$$\sigma_i^2 = \frac{n_i(c - 1)\left(\dfrac{c}{s} + n_i\right)}{c^2\left(\dfrac{c}{s} + 1\right)}. \quad [8]$$

Because the mating behavior within each group of females is independent of other groups, the matings obtained by males are independent across groups of females. That is, the covariances in numbers of matings by males across groups will, on average (i.e., over repeated samples), be zero. This permits us to write the expected variance in matings among males due to all n females as

$$E(\sigma^2) = \sum_{i=1}^{k} \sigma_i^2 = \frac{(c - 1)}{c^2(c + s)} \sum_{i=1}^{k} n_i(c + n_i s). \quad [9]$$

The size of a group of females can range from 1 to n, the total number of females. For simplicity, we imagine that each

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group is of the same size and vary the number of groups, k. The equation for the variance becomes

$$\sigma^2 = \frac{(c-1)n[c + (n/k)s]}{c^2(c+s)} \qquad [10]$$

and the opportunity for sexual selection, I, after simplifying,

$$I = \frac{(c-1)[c + (n/k)s]}{n(c+s)}. \qquad [11]$$

If we set $k = 1$, Eq. 11 reduces to Eq. 6. When we set $s = 0$, $I = (c - 1)/n$, which approaches the inverse of the sex ratio, $1/R$, when the number of males is large. The opportunity for selection in Eq. 11 exceeds that of the random case by the factor $[c + (n/k)s]/(c + s)$. This factor is always greater than 1 for $s > 0$ but is always less than or equal to $(c + ns)/(c + s)$, the factor describing the increase in I when all females visit the lek together (i.e., in one group). The effect of female copying on the opportunity for sexual selection increases as group size increases, or, conversely, decreases as the number of groups of females increases.

It is informative to investigate the effects of perfect copying within groups because it illustrates the maximum effect that female copying can have on the variance in male mating success. Imagine that within groups, the first female chooses her mate randomly, and then all other females in the group mate with that same male. Letting s approach infinity, the equation for I changes to

$$\lim_{s \to \infty} I = \frac{(c-1)}{k}. \qquad [12]$$

Thus, if there is perfect copying by females within groups, the opportunity for selection is increased over the case of random mating $[I = (c - 1)/n]$ by the factor $(n - k)/k$.

RESULTS

The opportunity for sexual selection owing to variation among males in mating success depends on population size $(n + c)$, the female/male sex ratio (R), and the parameter s (Table 1). I increases as the sex ratio decreases; i.e., when females are scarce relative to males, the opportunity for selection is the greatest. For a given sex ratio and value of s, the index I increases with increasing population size but not proportionately. For example, with a sex ratio of 1.0 and a value of s of 2.0, I increases from 2.25 to 2.91 as population size increases an order of magnitude (10 to 100; Table 1). It is clear from Table 1 that the sex ratio affects the opportunity for selection more than population size for all degrees of copying. Note also that, for large n and c, I converges to the value $s + (1/R)$.

In Fig. 1, we illustrate the frequency distribution of mates per male, assuming random mating and for two levels of female copying, $s = 1$ and 2. The population was assumed to consist of 50 males and 50 females; thus the mean mating success, 1.0 mate per male, is the same for both distributions. Female copying increases the frequency of extreme values in the mating distribution. Whenever there is female copying, there are more males that do not mate and more males that obtain large numbers of matings relative to random matings (Fig. 1).

In each case illustrated in Fig. 1, the majority of males obtain either 0 or 1 mating. We suggest that one can estimate the magnitude of s that could account for the observed distribution of mates by examining the ratio of the proportion of males that fail to mate, $\Pr\{x = 0\}$, to the proportion

obtaining exactly one mate, $\Pr\{x = 1\}$. Setting r in Eq. 4 equal to 0 and 1, respectively, the ratio of these two proportions is

$$s\left(1 - \frac{1}{n} + \frac{c-1}{ns}\right),$$

which is approximately

$$s + \frac{1}{R}$$

for large n. Thus, knowledge of the sex ratio of breeding adults (R) and the observed proportion of males in the two categories, 0 mates and 1 mate, information that is available in most empirical studies, permits us to estimate s. The ratio of these two proportions in the case of random mating can be obtained from Eq. 1 and is $(1/R)(c - 1)/c$, or approximately $(1/R)$ for large c.

The data in Fig. 1 provide an example of estimating s. With 50 males and 50 females randomly mating, we expect 18.21 (36.4%) males to fail to mate and 18.58 males (37.2%) to obtain one mate (Fig. 1). With s equal to 1.0 (i.e., the probability that a male who already has one mate will mate with another female is increased from 0.020 to 0.039), we expect 24.75 males will fail to obtain mates and 12.63 to each mate once. The ratio of the proportions is equal to 1.96, which is approximated by $s + 1/R$ (see above). The estimate of s is thus 0.96, very close to the actual value of 1.0.

Differently put, when the number of males is large and the sex ratio is approximately unity, there is a simple and sensitive test for the possible existence of female copying. First, testing the observed distribution of matings among males with that expected under random mating (from the binomial distribution) will test for nonrandom mating. Second, calculating the ratio of the observed proportions of males that do not mate with those that mate once estimates s. This estimates the degree of female copying that could account for the observed deviation from random expectation, assuming that female copying is the only factor responsible for nonrandom mating. Of course, female copying would seldom be the only process resulting in a deviation from

Table 1. Opportunity for selection, I, in relation to the number of males and females, the female/male sex ratio, R, and the degree of female copying s (see text for description of model)

R	s	I for various numbers of females*		
		10	50	100
2.0	0	0.40	0.48	0.49
	1	1.00	1.38	1.44
	2	1.43	2.22	2.36
	3	1.75	3.00	3.24
	4	2.00	3.72	4.08
	5	2.20	4.40	4.90
1.0	0	0.90	0.98	0.99
	1	1.64	1.92	1.96
	2	2.25	2.83	2.91
	3	2.77	3.70	3.84
	4	3.21	4.54	4.76
	5	3.60	5.35	5.66
0.5	0	1.80	1.96	1.98
	1	2.45	2.88	2.94
	2	3.00	3.77	3.88
	3	3.46	4.62	4.81
	4	3.86	5.44	5.71
	5	4.20	6.24	6.60

*Maximum number of females. For example, in the case where the sex ratio is 0.5, if there is a maximum of 10 females, the number of males used in the analysis was 5.
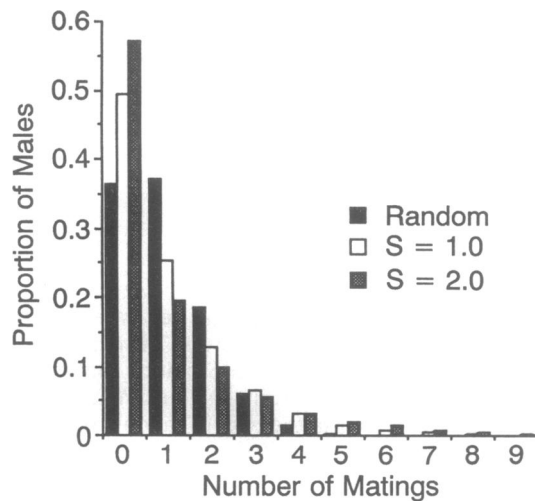
FIG. 1.   Frequency distribution of matings among males under random mating and assuming copying behavior in females. The population size is 50 males and 50 females. The distributions with female copying were generated from Eq. 4 under case 1 (see text) by assuming values of s of 1.0 and 2.0. For $s = 1.0$, $I = 1.96$ and for $s = 2.0$, $I = 2.83$.

random expectation or the appearance of contagion in the choice of mates by females. The estimation of s by the method suggested provides a means of making a preliminary assessment of the maximum possible influence of copying behavior on male mating success. Negative estimates of s would indicate that females avoid choosing mated males as mates.

When n females visit males in small groups (case 2), copying behavior by females within groups again increases the overall variance in mating success among males and the opportunity for selection, but the effect is diminished. The largest effects of copying occur when there are a small number of groups, each with many females, or when the tendency to copy (s) is high (Table 2). With perfect copying within each small group of females, I increases multiplicatively over the random mating case by the size of the group of females. Thus, if group size is 2 females, I is doubled over that expected under random mating; if group size is 3 females, I is tripled, etc.

DISCUSSION

Among the possible factors influencing mating decisions by females in natural populations, Clutton-Brock and his collaborators concluded for fallow deer that "The main criterion affecting the movements of does between bucks seemed to be the size of a buck's harem" (ref. 21, p. 464). It was our purpose in this paper to examine quantitatively how copying behavior by females could influence the variance in matings among males and therefore the opportunity for selection. It

Table 2. Opportunity for selection, I, as a function of group size in females

Number of female groups	Group size	I		
		$s = 1.0$	$s = 5.0$	$s = 10.0$
1	50	1.92	5.35	8.98
5	10	1.16	1.78	2.45
10	5	1.06	1.34	1.63
25	2	1.02	1.09	1.17
50	1*	0.98	0.98	0.98

The model assumed 50 males and 50 females.
*Where group size is 1 individual, the model is equivalent to random mating.

is clear that the effects of copying behavior on the opportunity for selection can be substantial (Table 1, Fig. 1).

The parameter s is not directly interpretable in terms of the number or proportion of females that might copy one another. The model does not assume that there are distinct "types" of females, e.g., choosing and copying females (20). The model assumes only that females are influenced by the decisions of other females. The parameter s reflects the degree of this influence.

Females could be influenced by the mating decisions of other females in one of two ways. If females visit males in groups, females could observe the actions and mating decisions of other females. Visits by groups of females, as well as solitary individuals, are common in lek-breeding bird species (9, 10, 14). A second mechanism by which females can be influenced by the mating decisions of others occurs when females remain on the territories of the males that they mate with, as, for example, in polygynous, territorial, and harem mating systems (20). In such situations, regardless of whether females visited males solitarily or in groups, they could assess the actions of previously mating females simply by noting the distributions of females among male territories.

Although we have emphasized the case in which females copy or behave similarly to one another, it is also possible, particularly in territorial, polygynous species, that the influence of other females could be negative. Here, females might avoid territories that are already occupied by females or males that are already mated. Females may exhibit such avoidance with or without aggressive behavior by the resident female. In our model, avoidance can be analyzed by letting s take on negative values. Complete avoidance by females of males already mated (s equals negative infinity) would yield a variance in mating success near 0 (all males would have the same number of mates), and variable degrees of avoidance would produce variance values between 1.0 (random mating) and 0.

Do females copy each other in natural situations? Several workers studying lek-mating birds have suggested (9, 10, 16) that copying behavior may be likely or possible in those species. Females in lek species frequently visit males in large groups, and in at least one species (the bird of paradise *Parotia lawesii*), females visit males over an extended period of time prior to mating (14). Clear evidence for copying behavior has been demonstrated in mammals (21), fish (21–23), and a marine isopod (30), and copying has been suggested in birds (references above). Conspecific queuing or association behavior has been modeled (31) and observed (32) in *Anolis* lizards and is not different in kind from the female mate-choice behavior that we are suggesting here. It is intriguing that species in which copying has been suggested or demonstrated are invariably promiscuous and thus candidates for strong sexual selection. The opportunity for a large variance in male mating success in promiscuous species due female choice could be greatly exaggerated through female copying.

Regardless of whether mate choice carries adaptive consequences, female copying may always be an adaptive alternative to random choice in the presence of choosing females when there is a cost to mate choice (20). In the case of adaptive choice, copying females would always do better, on average, then randomly choosing females because some fraction of the time they could copy adaptively choosing females and share in the benefits of mate choice. This same argument would apply if preferences in females evolved through runaway selection as correlated responses to male traits (8, 33) rather than as an adaptive means of identifying the fittest males (34): copying females always do better than randomly choosing females.

Whenever the cost to making a mating decision is large and the information necessary to make an informed decision is

difficult to gather, then "social learning," a form of copying, is more likely to lead to an individual's determining the most adaptive local behavior than is individual decision making (ref. 35, p. 116). We believe that choice of mates by females is a difficult decision-making process that shares several points of similarity with the arguments of Boyd and Richerson (35) favoring social learning. The work of Losey *et al.* (20) showed that under certain circumstances, copying females can also have higher a fitness than actively choosing females. For these reasons, we suggest that female copying is not only a possible cause of the variance in male mating success but also a plausible one.

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