

Sexual Selection: Harem Size and the Variance in Male Reproductive Success

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ABSTRACT: Sexual selection is potentially stronger than natural selection when the variance in male reproductive fitness exceeds all other components of fitness variance combined. However, measuring the variance in male reproductive fitness is difficult when nonmating males are absent, inconspicuous, or otherwise difficult to find. Omitting the nonmating males inflates estimates of average male reproductive success and diminishes the variance, leading to underestimates of the potential strength of sexual selection. We show that, in theory, the proportion of the total variance in male fitness owing to sexual selection is approximately equal to H , the mean harem size, as long as H is large and females are randomly distributed across mating males (i.e., $V_{\text{harem}} = H$). In this case, mean harem size not only provides an easy way to estimate the potential strength of sexual selection but also equals the opportunity for sexual selection, I_{mates} . In nature, however, females may be overdispersed with $V_{\text{harem}} < H$ or more aggregated than random with $V_{\text{harem}} > H$. We show that $H + (k - 1)$ is a good measure of the opportunity for sexual selection, where k is the ratio V_{harem}/H . A review of mating system data reveals that in nature the median ratio for V_{harem}/H is 1.04, but as H increases, females tend to become more aggregated across mating males with V_{harem} two to three times larger than H .

Keywords: sex ratio, sexual selection, male reproductive success, reproductive competition, harem size.

Measuring the opportunity for sexual selection is important for addressing many questions in behavioral evolution. In particular, it has been argued that strong sexual

selection favors female-biased sex ratios (Trivers and Willard 1973; Clutton-Brock 1991; Wade et al. 2003), testes size in primates (Harcourt et al. 1995), and maternal rather than paternal care in birds (e.g., Krebs and Davies 1993) and mammals (e.g., Clutton-Brock 1991). When the opportunity for sexual selection is strong, a few males are highly successful at mating while many other males go unmated, leading to a general expectation of an association between polygyny and strong sexual selection. However, because nonmating males are absent from nesting aggregations, inconspicuous, or otherwise difficult to find, they are often not counted in estimates of male reproductive success. Their omission tends to inflate estimates of average male reproductive success because the zeros are omitted from the average. At the same time, the variance is also diminished because each nonmating male contributes a value equal to the square of the mean reproductive success to the variance in male fitness. Both effects lead to underestimates of the opportunity for sexual selection relative to natural selection. Shuster and Wade (2003) discuss but do not provide a solution to these problems.

In this article, we demonstrate that under strong sexual selection, the variance in male reproductive fitness is determined in large part by the fitness difference between mating and nonmating males, with little contribution from the variation in mate numbers among mating males, that is, the males usually available for enumeration. When the primary sex ratio, R , is unity, we show that the variance in male reproductive fitness is approximately equal to $(H - 1)$, where H is the mean number of mates per mating males or the harem size. Since in many species H can be estimated from field observations or paternity analysis of offspring, it can be a useful surrogate for the opportunity for sexual selection, regardless of whether nonmating males can be observed and censused. (Indeed, without paternity analysis, it is difficult to determine whether an apparently nonmating male is nevertheless successful in extrapair copulations.) In a survey of the literature, we find that in most species, females are not randomly distributed across mating males. In these cases, the value of

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Table 1: Survey of values

Species	H	V_{harem}	k	V_B/V_M	V_H/H^2	N	Reference
Crustaceans:							
Sponge isopods (<i>Paracerceis sculpta</i>)	2.63	3.73	1.42	.53	.539	154	Shuster 1987
Insects:							
Australian lycaenid butterfly (<i>Jalmenus evagoras</i>)	2.27	3.40	1.50	.46	.660	15	Elgar and Pierce 1988
Alpine weta (<i>Hemideina maori</i>)	1.96	1.56	.80	.55	.406	49	Gwynne and Jamieson 1998
San Francisco forktail damselfly (<i>Ischnura gemina</i>)	4.39	9.78	2.23	.60	.507	57	Hafernik and Garrison 1986
Bamboo bugs (<i>Notobitus meleagris</i>)	1.92	1.07	.56	.62	.290	26	Miyatake 2002
Amphibians:							
Reed frogs (<i>Hyperolius marmoratus</i>)	1.95	2.04	1.05	.48	.535	22	Dyson et al. 1998
Strawberry poison dart frogs (<i>Dendrobates pumilio</i>)	4.89	16.54	3.38	.53	.692	9	Prohl and Hodl 1999
Reptiles:							
Prairie rattlesnakes (<i>Crotalus viridis viridis</i>)	1.42	.41	.29	.59	.204	12	Duvall and Schuett 1997
European grass snakes (<i>Natrix natrix</i>)	1.75	.52	.30	.72	.170	12	Madsen and Shine 1993
Birds:							
Brown-headed cowbirds (<i>Molothrus ater</i>)	1.36	.34	.25	.59	.184	89	Woolfenden et al. 2002
Sharp-tailed grouse (<i>Tympanuchus phasianellus</i>) A	1.5	.75	.5	.50	.330	4	Gratson et al. 1991
Sharp-tailed grouse (<i>T. phasianellus</i>) B	2.75	1.69	.61	.74	.230	4	
Sharp-tailed grouse (<i>T. phasianellus</i>) E	2.75	5.19	1.89	.48	.690	8	
Sharp-tailed grouse (<i>T. phasianellus</i>) A'	6	17.2	2.87	.64	.480	5	
<i>T. phasianellus</i> weighted average				.57	.483		
Indian peafowl (<i>Pava cristatus</i>)	3.88	7.61	1.96	.60	.506	8	Yasmin and Yahya 1996
Domestic peafowl (<i>P. cristatus</i>)	4.13	14.61	3.54	.47	.857	8	Petrie et al. 1991
<i>P. cristatus</i> average				.53	.682		
Cetti's warblers (<i>Cetti cetti</i>)	1.56	.47	.3	.65	.193	9	Bibby 1982
Mammals:							
Kipsigis men (<i>Homo sapiens</i>)							Mulder 1988
Nyongi (circumcised before 1921)	1.42	.47	.331	.56	.233	29	
Maina (circumcised between 1922 and 1930)	1.59	1.8	1.13	.34	.712	25	
Chuma (circumcised between 1931 and 1938)	1.14	.25	.22	.39	.192	38	
<i>H. sapiens</i> average				.43	.346		
Sac-winged bat (<i>Saccopteryx bilineata</i>)	2.17	1.97	.91	.56	.420	12	Voigt et al. 2001
Indian fruit bat (<i>Cynopterus sphinx</i>) 1997	4.47	24.65	5.52	.39	1.235	15	Storz et al. 2001
Indian fruit bat (<i>Cynopterus sphinx</i>) 1998	2.19	3.48	1.59	.43	.730	54	
<i>C. sphinx</i> average				.44	.840		
Humpback whales (<i>Megaptera novaeangliae</i>)	1.22	.29	.238	.48	.195	51	Cerchio et. al. 2002
Misaki feral horses	3.73	4.10	1.10	.71	.294	60	Kaseda and Khalil 1996
African lion (<i>Pantera leo</i>)	6.75	15.4	2.281	.72	.338	76	Packer et al. 1988
Red deer (<i>Cervus elaphus</i>)	4.31	4.5	1.04	.76	.242	35	Clutton-Brock et al. 1988

Note: A survey of the values for average harem size (H), variance in harem size ($V_{\text{harem}} = V_H$), the ratio of the variance in harem size to average harem size ($V_H/H = k$), the ratio of the variance in fitness between mating and nonmating males ($V_{\text{between}} = V_B$) to the total variance in male fitness ($V_{\text{males}} = V_M$), and the opportunity for sexual selection on harem-holding males ($V_H/H^2 = I_{\text{harem}}$); N = number of harem holding males in each data set; when more than one estimate was possible for a species, we calculated the weighted average for V_B/V_M . In column 5, roman type indicates estimates for values from a single study or article; bold type indicates the species value, which is sometimes a weighted average (as for *H. sapiens*) and sometimes the only estimate available for a species (as for *J. evagoras*).

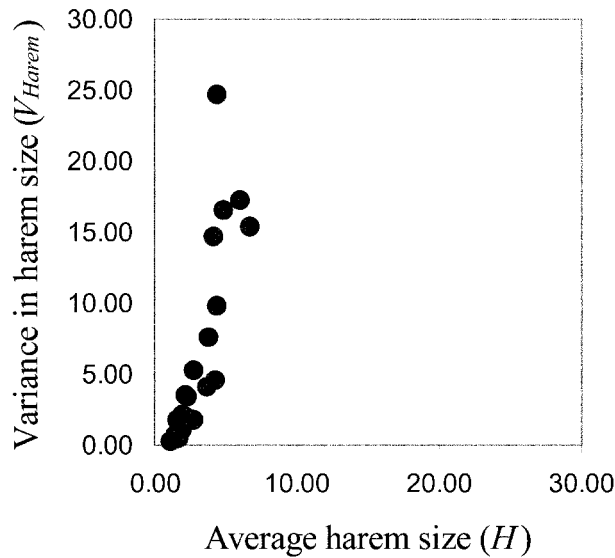


Figure 1: Relationship between H , the mean harem size, and V_{harem} , the variance in harem size, for 27 species belonging to six major animal taxa. This relationship ($F = 66.5$, $df = 1, 26$, $P < .001$; $Y = -5.02 + 3.66X$) indicates that V_{harem} is, in general, much larger than H in nature and that females tend to be more clumped around mating males than expected by chance.

H must be adjusted to provide an indicator of sexual selection's potential strength, and we derive a method for that adjustment.

Sexual Selection and the Variance in Male Reproductive Fitness

Fisher noted that because every offspring has one mother and one father, mean male fitness, W_{male} , equals the product of mean female fitness, W_{female} , times the mean number of mates per male, that is, the population sex ratio, R , expressed as the ratio of the number of females, N_{female} , to males, N_{male} (Wade 1979, 1995; Shuster and Wade 2003). When $R < 1$ and investment costs are equal for both sexes, females producing more daughters than sons have a fitness advantage, and the converse is true when $R > 1$ (cf. Hardy 2002; Jacobs and Wade 2003; Wade et al. 2003). Differential mortality may occur prior to sexual maturity between the sexes.

When males fight for and defend groups of females or when females exert a choice of mates, sexual selection creates two classes of males, mating and nonmating. The mean male mating success equals $p_s H$, the fraction of successful males, p_s , times the average number of mates per successful male, H . The total variance in male reproductive success has two components (Wade 1979, 1995; Shuster and Wade 2003): first, the variance in mating success

within the class of males that mate successfully because of variation among successful males in numbers of mates. Second, the variance in mating success between the class means of mating and nonmating males, H versus 0 , respectively. To see this, let p_0 be the fraction of nonmating males that are unsuccessful at reproductive competition and have zero mates, and let $p_s (= 1 - p_0)$ be the fraction of successfully mating males, which have one or more mates. By definition, the average number of mates per mating male, the harem size, H , equals

$$H = R/p_s. \quad (1)$$

When $R = 1$, H and p_0 are related by

$$p_0 = 1 - (1/H). \quad (2)$$

For example, when $H = 4$, $p_0 = 0.75$, and fully three-fourths of males are unmated. When $H = 20$, as it can for the northern elephant seal *Mirounga angustirostris* (LeBoeuf and Reiter 1988), $p_0 = 0.95$.

Because the average number of mates of nonmating males is uniformly 0 (Wade 1979, 1995), the average variance in mate number within each of the two male categories, mating and nonmating, is

$$V_{\text{within}} = (p_0)(0) + (p_s)V_{\text{harem}} = (R/H)V_{\text{harem}}, \quad (3)$$

where V_{harem} is the variance in mate numbers among mating males. Empirical observations from 27 studies of a variety of organisms (table 1) indicate that ratios of (V_{harem}/H) lie in the range of 0.22 for Kipsigis men, circumcised between 1931 and 1938 (Mulder 1988), to 5.52 for the Indian fruit bat *Cynopterus sphinx* (Storz et al. 2001), with a median value of 1.04.

The second component of the variance in male reproductive success is the variance between the classes of successful and unsuccessful males. It equals the square of the difference in mean success, that is, $(H - 0)^2$, multiplied by the variance between the mating categories, or

$$V_{\text{between}} = H^2(p_0)(p_s). \quad (4)$$

Again, using the relationship between H and p_s , V_{between} can be rewritten as

$$V_{\text{between}} = H^2[1 - (R/H)](R/H) = R(H - R). \quad (5)$$

If $R = 1$, $V_{\text{between}} = H - 1$. Thus, as H becomes large, V_{between} also becomes large, while V_{within} diminishes (see eq. [3]).

The total variance in male reproductive success, V_{mate} ,

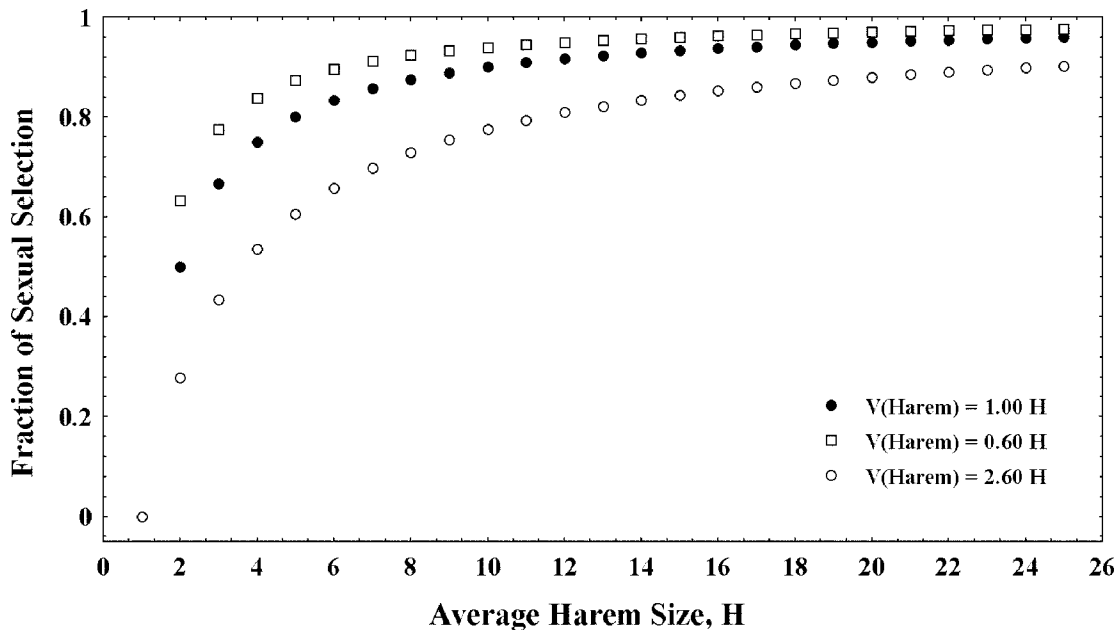


Figure 2: Ratio, $V_{\text{between}}/V_{\text{mate}}$, for three values of k , 0.60 (open squares), 1.0 (solid circles), and 2.60 (open circles). When $k < 1$, females are overdispersed across mating males, and more of the variance in male reproductive success stems from the difference between males winning and losing in reproductive competition (V_{between}) than it does when $k > 1$; that is, females are aggregated around certain males. However, in all cases, as H increases, the difference between mating and nonmating males becomes a larger fraction of sexual selection, V_{mate} .

is the sum of these two variance components, V_{within} and V_{between} :

$$V_{\text{mate}} = R(H - R) + (RV_{\text{harem}}/H). \quad (6)$$

When $R = 1$ and harem size is Poisson distributed (i.e., $V_{\text{harem}} = H$, as in the median value of 1.04 from table 1), then $V_{\text{mate}} = H$, and the opportunity for sexual selection, I_{mates} (see below), which equals V_{mate}/R^2 , is also H . The ratio $V_{\text{between}}/V_{\text{mate}}$ approaches unity with increasing H .

When harem sizes are not randomly distributed, we set $V_{\text{harem}} = kH$, where k is a constant of proportionality. When $k < 1$, then females are overdispersed across mating males, and when $k > 1$, they are underdispersed or clustered around certain mating males. For $R = 1$, $V_{\text{mate}} = I_{\text{mates}}$, which is $H + (k - 1)$. Empirical observations (table 1; fig. 1) indicate that mates are sometimes more evenly dispersed across mating males than random (i.e., $k < 1$) so V_{harem} tends to be less than H . Conversely, when mates are more clustered across mating males than random, $k > 1$, so V_{harem} tends to be greater than H (fig. 1). Using values for the ratio $V_{\text{between}}/V_{\text{mate}}$ of 0.60 and 2.60 to indicate overdispersion and clustering, respectively, we see in figure 2 that with increasing H , V_{between} represents most of the opportunity for sexual selection for $0.60 < k < 2.60$. However, when $k < 1$, more of the variance in male reproduc-

tive success stems from the difference between males winning and losing in reproductive competition than it does when $k > 1$. Thus, knowledge of the distribution of mates among mating males alone can be a very good indicator of the total opportunity for sexual selection acting on males.

The Opportunity for Sexual Selection and the Variance in Male Reproductive Fitness

Crow (1958, 1962) defined the opportunity for selection, I , as the variance in relative fitness, that is, the variance in fitness divided by the square of the average fitness, and he argued that it is a true measure of selection opportunity. The magnitude of change in phenotype (z) depends on the covariance with relative fitness, $\text{Cov}(z, w(z))$, which is usually less than perfect. In addition, because not all of the variation in fitness is heritable, not all of this variance can lead to changes in the distribution of phenotypes in a population by natural selection. Thus, I sets an upper bound not only on the change in mean fitness itself but also on the standardized change in the mean of all other traits. As Crow (1962) noted, whenever random or chance deaths occur, the effectiveness of selective deaths must be diminished. By chance, bad things happen to good genes and vice versa (Shuster and Wade 2003). If one eliminates

the random variation in mortality and reproduction, one overestimates rather than underestimates the potential strength of selection. In a survey of the strength of phenotypic selection in natural populations, Kingsolver et al. (2001, p. 251) found a pattern that “suggests that sexual selection is stronger than viability selection.” However, the absolute value of the median linear selection gradient on morphologies involved in mating success was 0.16, indicating that the opportunity for selection is often much greater than the strength of directional selection on a particular trait.

Our estimates of I_{mates} and the opportunity for sexual selection measure the variance in relative male reproductive fitness. The I_{mates} estimate sets an upper limit on the response to sexual selection because not all male mating is differential with respect to male traits. By chance, some males obtain more mates than others just as, by chance, some individuals die before expressing their good or bad genes for viability. Furthermore, only the heritable fraction of the differences between selected and nonselected individuals can be transmitted across generations. However, because sexual selection is one of the strongest evolutionary forces, placing an upper bound on it is of interest.

Review of Harem Size Literature

If harem size is a quantitative estimate of the opportunity for sexual selection, we expect the relative magnitudes of H and V_{harem} not only to reveal the approximate distribution of females with males but also to predict the degree of sexual dimorphism in harem-forming species. Although variation in the form of male ornamentation as well as the confounding effects of selection in unknown contexts have hindered the establishment of a convincing general relationship (see Slatkin 1984), an evolutionary link between sexual dimorphism and harem size, both within and among taxa, has been recognized since Darwin ([1859] 1964; [1874] 1974). Among pinnipeds, ungulates, and primates, harem size has been shown to predict the degree of sexual dimorphism in body size (Alexander et al. 1979; pinnipeds corrected for phylogeny, Lindenfors et al. 2002). These and other comparative phylogenetic analyses have shown a relationship between large harem size and sexual dimorphism that may well be causal.

In our survey, we included only those studies for which we could calculate the distribution of females with males directly, that is, those studies reporting both the mean and the variance of the distribution of females with males ($N = 27$; table 1). Our results show considerable variation in the degree to which females may be evenly distributed or aggregated around mating males, and as noted above, when V_{harem} is smaller than or larger than H , estimates of H will either underestimate or overestimate the oppor-

tunity for sexual selection, respectively, with the magnitude of this error decreasing with increasing values of H (fig. 2).

Where possible, we ranked species within major taxa by the magnitude of the ratio $V_{\text{between}}/V_{\text{male}}$. For the taxa in table 1, the average value of this ratio (\pm SE) was 0.572 ± 0.025 , indicating that a majority of the variance in fitness among males arises from the difference in fitness between mating and nonmating males. In all species shown in table 1, sexual dimorphism exists to varying degrees, but most studies do not provide standardized estimates of degree of sexual dimorphism. Although we expect that sexual dimorphism will prove to be correlated with the potential strength of reproductive selection acting on males, we have shown (Shuster and Wade 2003) that the sex difference in the opportunity for selection should be a better predictor of sexual dimorphism. However, in the context of male-limited selection, it is important to have estimates of the opportunity for selection resulting from competition for mates.

Measurements of H within a single breeding season may either underestimate or overestimate the variance in fitness among males, depending on whether the covariance across breeding seasons between male age and his cumulative mating success is positive, negative, or 0. If older males tend to obtain larger harems as they age, then this positive covariance will cause single-season estimates of H to underestimate V_{between} . If older males tend to become less successful as they age, then single-season estimates of H will tend to overestimate V_{between} because total fitness variance will be ameliorated among years. If there is no covariance between male age and cumulative mating success, then estimates of H within a season will provide a reasonable estimate of V_{between} for any season, and no correction is likely to be necessary. Clearly, the degree to which these multiseason effects lead to errors in single season estimates of H will depend on the lifespan of the species considered, with greater deviations appearing in longer-lived species. Thus, in long-lived species, there may be good reason to integrate the effects of iteroparity into estimates of the opportunity for sexual selection, as we have discussed elsewhere (Shuster and Wade 2003).

In summary, we have shown that the distribution of females across mating males can be used to estimate the opportunity for sexual selection acting in species with harem-holding males. A survey of 27 studies across 17 taxa indicates that reproductive competition comprises 57.2% of selection on males. Furthermore, as H increases, it appears that females become more clustered across mating males (fig. 1), an interesting observation in its own right. However, if paternity analyses were available, the percentage of selection that is sexual selection on males would be diminished if nonharem-holding males were re-

sponsible for the majority of stolen copulations or augmented if stolen copulations accrued to males with the larger harems at the expense of males with smaller harems. Nevertheless, it is useful to have a formal relationship between harem size and the potential strength of reproductive competition among males that can be applied to data from natural populations.

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