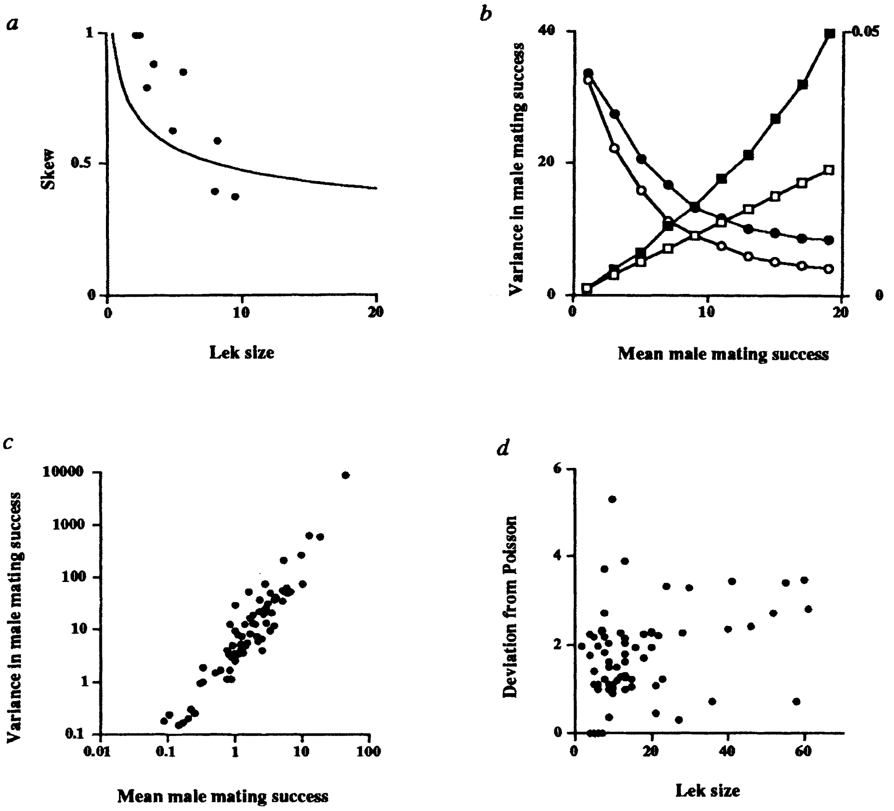
Measuring sexual selection

SIR — Many researchers have measured sexual selection on mating arenas (leks) in a wide variety of species. These studies have influenced our understanding of sexual selection because of the extreme variation in mating success among lekking males. One measure of this variation, used recently by Widemo and Owens[1], is the degree of skew. We will show that this measure has drawbacks.

Widemo and Owens examined mating skew on leks of different sizes to understand the decisions made by individuals of different rank. They suggested that for a species of wading bird, the ruff (*Philomachus pugnax*), mating skews decrease in larger leks because of increased aggression. This interesting approach illustrates the difficulties of using skew to measure variation in mating success. A null version of their model in which matings occur entirely at random shows that the measure of skew should decrease exponentially with lek size (*a* in the figure). Biological explanations for the drop in skew in larger leks are therefore unnecessary, as the drop can occur as an artefact of any formula for skewness.

This raises the more general issue of how to quantify sexual selection. One reason for the popularity of skew is that data are often depicted in histograms of mating success for individuals that have been ranked along the *x*-axis according to their success. These are not frequency distributions, but perhaps because of their apparent similarity it is tempting to quantify their asymmetry using measures of skewness from frequency distributions. The measure that best expresses the dispersion of a distribution is the variance, which is independent of sample size and has the considerable advantage of using classical evolutionary genetics to quantify intensity of selection[2].



a, Relationship between lek size and 'skew index'[1]. The points are ruff data[1] and the line is the expected relationship when females select males randomly (the null model). The expected distribution assumes that mean male mating success remains constant at unity throughout and hence the variance in male mating success is unity, although the relationship is not strongly affected by deviations from this assumption. *b*, Relationship between variance in male mating success and the skew index with respect to the mean male mating success (squares, variance; circles, skew; open symbols, random mating; solid symbols, aggregated matings; coefficient of variation^2 of aptitude for an encounter = 0.1). Lek size is 10. *c*, Relationship between mean male mating success and variance in male mating success for 74 leks of 19 species. All leks show greater variance in male mating success than expected from random mating. A linear regression with a slope significantly greater than unity (P<0.001) explains 88.0% of the variance in the variance of male mating success. *d*, Relationship between lek size and the variance in male mating success above that expected from random mate choice for 74 leks of 19 species, given by: $\log_e$(variance in male mating success) – $\log_e$(mean male mating success). Details of the model, references and species are given in ref. 3.

Comparison of male mating distributions involves two important variables: the number of males and the number of matings. Although variance is unaffected by the number of males, both skew and variance are affected by the number of matings. If the mean male mating success changes in a lek of fixed size, there is a negative correlation between the variance in mating success and the skew index, whether mating is random or aggregated (*b* in the figure).

Under random mate choice, the variance should equal the mean. The extra component of variance, beyond that due to random processes, can thus be determined simply by subtracting the mean from the variance. It is not readily possible to disentangle the skew statistic from its interdependence on both the number of males and the number of matings.

Does variance in mating success generally decline with lek size? Elsewhere[3], we have discussed a range of factors contributing to variance, including male quality and female copying. A survey of 74 leks from 19 species shows that across all leks mean male mating success accounts for 88% of the variance (*c* in the figure). The residual variance is not negatively correlated with lek size (*d* in the figure). Comparison of multiple leks within species still shows no pattern. In four species the trend was towards higher variance in larger leks, while in one species there was less.

Although we disagree over the measure of skew, we agree with Widemo and Owens that the sensible approach is to look at the costs and benefits to different males of displaying on different-sized leks. Unattractive males may indeed benefit from associating with attractive individuals. In explaining the colonial behaviour of fish, an equivalent approach has been useful[4].

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WIDEMO AND OWENS REPLY — We agree with Mackenzie *et al.* that variance has several convenient properties as a measure of the opportunity for sexual selection, even though Sutherland[5] has pointed out several serious problems with this approach. We maintain, however, that the skew index used by us handles some situations better than does variance since it takes the relative rather than the absolute differences between males into account.

We did not set out to measure the intensity of sexual selection, however. Our main point[1] was that it is necessary to focus on the success of individual, rather than