

NOTES AND COMMENTS

ON THE MEASUREMENT OF SEXUAL SELECTION

The theory of sexual selection was formulated by Darwin (1871) to explain the origin of sexually dimorphic traits that are detrimental to survival. Darwin believed that sexual selection arises from either mate choice or intrasexual competition for mates, reasoning that such traits could evolve if they conferred a fitness advantage on their bearer.

In part because of the obvious difficulties in quantifying the evolutionary effects of mate choice or intrasexual competition for mates, Wade and Arnold (Wade 1979; Wade and Arnold 1980; Arnold 1983; Arnold and Wade 1984*a,b*) operationally defined sexual selection as selection arising from variance in mating success; the clear intention of these authors was to allow for the empirical measurement of sexual selection while retaining the sense of Darwin's original definition. This definition has subsequently been used in several important studies (Fincke 1982; McCauley 1983; Price 1984), as well as in a recent influential reference (Partridge and Halliday 1984).

Our purpose is to show that variance in mating success is not necessarily a valid measure of the opportunity for sexual selection as defined by Darwin. After presenting three criteria we believe are desirable in order to distinguish sexual selection, we use examples to detail some difficulties arising from Arnold and Wade's definition, and we conclude by pointing out the potential difficulty of separating "sexual" and "natural" selection at all. We feel that this discussion is needed because further understanding of sexual selection will be obscured unless terminology is concordant with Darwin's original conception and unless the ambiguities in distinguishing and measuring sexual selection are appreciated. For an excellent summary of some of the alternative approaches that have been used to measure sexual selection, see Clutton-Brock (1983).

We propose three criteria for identifying sexual selection. (1) One or both of Darwin's agents of sexual selection, intrasexual competition for mates or mate choice, must be occurring. (2) As a consequence of these agents, there must be a variance in fitness. Variance need not be in mating success per se, but only in some episode of fitness (*sensu* Arnold and Wade 1984*a*). Note also that this criterion does not follow automatically from criterion 1; female choice, for example, may be strong but will not constitute sexual selection if each female chooses a mate according to independent criteria, thus resulting in no variance in

male fitness. (3) Selection must act on a character conferring some advantage “over other individuals of the same sex and species, in exclusive relation to reproduction” (Darwin 1871). As we point out below, this last criterion may be particularly difficult to apply unambiguously, obscuring the distinction between sexual selection and natural selection.

A primary difficulty with Arnold and Wade’s definition of sexual selection is the meaning of “mating success.” Here we define *mating success* as the number of mates acquired or matings achieved during some relatively long interval of time such as a day (for an insect), season (for a vertebrate), or lifetime. In contrast, *mating efficiency* is the rate at which matings are achieved during some short time interval (McCauley 1983); mating efficiency thus equals the “instantaneous mating success” used by Clutton-Brock (1983). Mating success and efficiency as so defined are distinguished only by an arbitrary time scale. However, the conceptual difference in the latter is that the rate at which matings are achieved is more readily confined to a meaningful, homogeneous time period; for example, the time spent in the mating arena in a lek species. The importance of this feature will be brought out below.

Sexual selection does not correspond to the variance in mating success as defined above. This is obvious if we consider the variance in lifetime mating success, which includes variance that results from survivorship (hence natural selection) as well as variance that possibly results from sexual selection (McCauley 1983). This is a serious shortcoming, given that fitness can be realistically assessed only with lifetime data (Cavalli-Sforza and Bodmer 1961; Grafen 1982; Clutton-Brock 1983; Koenig and Albano, MS). However, mating success measured on a short-term time scale need not correspond to sexual selection either, for at least four reasons.

First, random variation in reproductive success may result in considerable individual differences not caused by selection; this possibility was discussed by Houck et al. (1985), who also presented some techniques for dealing with the problem. Second, as recognized by Wade and Arnold (1980) and recently stressed by Howard and Kluge (1985), a biased sex ratio may cause a high variance in reproductive success in the absence of intrasexual competition or mate choice; some statistical methods for dealing with this problem are given by Wade and Arnold (1980). Third, as with lifetime mating success, both sexual selection and natural selection can act on traits associated with daily or seasonal mating success. Fourth, because of trade-offs between selective events, sexual selection may act on a particular trait in the absence of variance in mating success among individuals. The following examples demonstrate these latter two difficulties. These examples are hypothetical, but a discussion based on real data illustrating their essential aspects is briefly presented below.

Example 1. Variance in lifetime and daily mating success but no sexual selection.—Consider a species in which males aggregate at a mating site but do not defend territories, are not aggressive, and do not compete for mates in any way. (The interpretation of selective effects becomes more complex if this unlikely stipulation is violated; however, the point of the example remains.) Assume that females choose mates in a completely random fashion. Except for stochastic

variation, mating efficiency (measured while males are in the mating arena) is the same for all males, and there can be no sexual selection, inasmuch as both female choice and intrasexual competition for mates have been ruled out (criterion 1). Now assume that foraging skill varies among males and that foraging ability determines the survival of males as well as the proportion of time a male can energetically afford to spend in the mating arena. Variance in both lifetime and daily mating success might then be great, but it is appropriately viewed as potential for natural selection rather than sexual selection. Selection, in this case, would act primarily on foraging efficiency and would tend to favor high survival and longer lengths of time at the mating site.

Example 2. Trade-offs between natural and sexual selection resulting in no variance in fitness.—Consider a lek species dimorphic in abdominal coloration. Males with bright abdomens attract more mates than males with dull abdomens, but, because of their inconspicuousness, dull males are better foragers than bright males. Assume, as in the preceding example, that the amount of time males can afford to spend in the mating arena depends on their foraging success. Bright males can spend only one hour a day in the breeding arena and average four matings per hour; dull males can afford to spend four hours per day in the arena but average only one mating per hour. Given equal survival of the two morphs, both daily and lifetime mating success are equal for all males. Nonetheless, sexual selection occurs because females show strong preferences for males with brightly colored abdomens. This preference results in variance in an episode of fitness (mating efficiency), and the character in question (abdominal color) confers an advantage to males exclusively with respect to reproduction. This selection is completely cancelled, however, by natural selection for dull abdominal color and good foraging ability.

An example of the partitioning of the opportunity for selection acting on daily reproductive success in a small population of this hypothetical animal, following the methods of Arnold and Wade (1984a), is presented in table 1. Note that the trade-off between female choice (sexual selection) and foraging efficiency (natural selection) could just as easily be between female choice and survival if we hypothesize that bright males suffer higher predation rates rather than decreased foraging success. Similar kinds of trade-offs between natural and sexual selection have been documented in the calls of crickets (Bell 1979) and the neotropical frog *Physalaemus pustulosus* (Ryan et al. 1982). These examples represent exactly the kind of conflict that originally prompted Darwin to consider these selective forces independently.

In contrast to mating success, mating efficiency may often represent opportunity for sexual selection, as it does in example 2. However, this measure has its shortcomings as well. First, it is critical that the time period during which matings are measured be carefully chosen. In example 2, for instance, the critical period is while males are present at the mating site, since it is only then that female choice, if it exists, can be expressed. Second, sexual selection resulting from intrasexual competition for mates is potentially ignored. Reconsider example 2 and imagine that the time males spend at the lek, rather than depending directly on foraging ability, is determined by male-male interactions at the lek itself. For example,

TABLE 1

PARTITIONING OF THE OPPORTUNITY FOR SELECTION IN A HYPOTHETICAL LEK SPECIES
WITH A TRADE-OFF BETWEEN NATURAL AND SEXUAL SELECTION

SOURCE OF VARIATION IN RELATIVE FITNESS	CONTRIBUTION TO TOTAL OPPORTUNITY FOR SELECTION	
	Symbol	Value
Time at lek (w_1)	I_1	.43
Mating efficiency (w_2)	I_2	.68
Covariance between time at lek (w_1) and mating efficiency (w_2)		
Unweighted	$COI(1,2)$	-.68
Weighted by time at lek	$COI(1,2 1)$	-.43
Change in covariance between matings (w_1w_2) and mating efficiency (w_2) caused by time at lek	$COI(12,2 1)-COI(12,2)$.00
Total selection (matings, W)	I	.00

NOTE.—Six individuals are used: half are at the lek for 1 h and obtain four matings per hour; half are at the lek for 4 h and obtain one mating per hour.

because of their higher foraging success, dull males might be physically stronger, behaviorally dominant, and therefore able to exclude males with bright abdomens. With this modification, “time at the lek” represents sexual selection through male-male interactions, whereas “mating efficiency,” measured while males are at the lek, represents sexual selection through female choice. Clearly, the overall opportunity for sexual selection in this example is not appropriately measured by mating efficiency. In fact, because the two forms of sexual selection oppose each other, there is again no variance in daily or lifetime mating success despite the strength of both agents. Of course, we could also hypothesize that the two forms reinforce each other, such that the total opportunity for sexual selection is split equally between time at the lek and mating efficiency.

Although mating efficiency may often ignore sexual selection via intrasexual competition, in some cases it may do the opposite and fail to measure female choice.

Example 3. Variance in mating efficiency but no mate choice.—Consider a species in which males fly around searching for females, who are themselves randomly distributed in an appropriate habitat. Females do not discriminate in selecting mating partners, and males do not come into contact with one another. All males live for one day, forage in the morning, and spend the remaining daylight hours pursuing mates. Individuals vary in their foraging skills, and the amount of food eaten determines the speed with which males can search for females. In this case there is high variance in mating success and in mating efficiency (measured while males are searching for mates). Nonetheless, sexual selection through mate choice is absent. Variance in mating efficiency is due to sexual selection, however, if we accept the random mating flights of males as male-male competition for mates. If so, however, sexual selection then acts to increase foraging ability.

The opportunity for sexual selection through female choice in this example can be clarified by dividing mating efficiency into two components: the "encounter rate" that males have with females and an index of "mate selectivity" by females. The former variable, the rate at which males encounter females during their mating forays, varies according to their earlier foraging efficiency. The latter variable represents the probability that, having encountered a male, a female mates with him. It is this variable that does not vary among males and that best represents, in this example, the opportunity for sexual selection by female choice.

Is there a straightforward operational definition of sexual selection that applies to all species? We believe not; both the interpretation of the critical components of fitness, as well as the episodes themselves, vary from species to species. Furthermore, realistic situations are easily envisioned in which virtually any distinction between "natural" selection and "sexual" selection is obscure. For example, we have thus far considered variance in adult survival as unambiguously representing natural selection. But what if females choose older males as mates? (This could occur either by females discriminating some morphological character directly correlated with male age or by their choosing only males with whom they are familiar from prior days or seasons.) Then selection for males to increase survival and live longer is analogous to selection for the plumage or vocal characters more frequently assumed to be features chosen by females, and thus might reasonably be considered sexual selection.

This example illustrates well the ambiguity of criterion 3: it may often not be feasible to distinguish characters having multiple fitness effects from those conferring advantages related only to reproduction. Consequently, we caution against assuming, a priori, that any episode of fitness represents sexual selection. Only by careful examination of each component can it be decided whether mate choice or intrasexual competition for mates leading to variance in fitness is occurring, and whether the characters on which selection is acting might reasonably be construed to be in exclusive relation to reproduction.

An example of such a partitioning of fitness is presented in table 2. It is based in part on the life history of a short-lived, polygynous invertebrate (Koenig and Albano, unpubl. data); although easily modifiable to fit long-lived vertebrates, only a subset of the episodes listed would be applicable to most species. Lifetime fitness, in column 1, is the product of juvenile survivorship, lifetime reproductive success, and fertility of eggs. Lifetime reproductive success, in column 2, is the product of lifetime mating success, the proportion of matings resulting in oviposition, and the number of eggs laid per successful oviposition. Finer subdivisions are listed in subsequent columns. Mating success, in column 3, is the product of adult survival, the proportion of time devoted to reproduction, and mating efficiency. Finally, mating efficiency is the product of mate encounter rate and mate selectivity.

Many of the episodes listed in table 2 represent natural selection, although, as discussed above, situations in which virtually any episode of fitness might at least arguably fit our criteria for sexual selection can be envisioned. As discussed in example 2, the time devoted to reproduction may represent either natural selection or sexual selection through intrasexual competition. Mate selectivity and the

TABLE 2
PARTITIONING OF THE EPISODES OF SELECTION

Fitness Components	Components of Reproductive Success	Components of Mating Success	Components of Mating Efficiency
Juvenile survival			
Lifetime reproductive success	Lifetime mating success Proportion of matings that result in ovipositions Eggs laid per successful oviposition	Adult survival Proportion of time devoted to reproduction Mating efficiency	Mate encounter rate Mate selectivity
Fertility of eggs			

NOTE.—Not all episodes are applicable to all species; see the text.

mate encounter rate, when they are distinguishable, may represent sexual selection in most or all cases. (They would not be distinguishable in a lek species in which females choose first among leks and then only secondarily among males present at the lek; clearly some degree of female choice may already have come into play before the females encounter any males whatsoever.) Variance in lifetime (or some other relatively long-term) mating success clearly is likely to overestimate sexual selection, since it combines variance from adult survival, proportion of time devoted to reproduction, and mating efficiency (example 1). These episodes can either reinforce or oppose each other (example 2), thereby further rendering mating success an inadequate measure of sexual selection.

Darwin (1871) anticipated many of the problems discussed here when he wrote that "in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection." As exemplified by the work of Endler (1980), Ryan et al. (1982), and Houck et al. (1985), the prospects for identifying and measuring sexual selection, at least by mate choice, may be more promising than Darwin feared. However, it is critical to try to associate selective episodes with specific agents of selection and only then to propose that they represent sexual selection or natural selection. Otherwise, the potential for misunderstanding will almost certainly exceed the potential for sexual selection, whatever it may be.

ACKNOWLEDGMENTS

We especially thank S. Arnold for commenting on the manuscript, M. Wade for helping us calculate opportunities for selection, and both of them for stimulating

our thoughts on sexual selection. P. Gowaty, T. Halliday, R. Howard, M. Ryan, N. Staub, K. Sullivan, P. Williams, and several reviewers aided the manuscript with their comments and diverse opinions.

LITERATURE CITED

- Arnold, S. J. 1983. Sexual selection: the interface of theory and empiricism. Pages 67–107 in P. Bateson, ed. *Mate choice*. Cambridge University Press, Cambridge.
- Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38:709–719.
- . 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38:720–734.
- Bell, P. D. 1979. Acoustic attraction of herons by crickets. *J. N.Y. Entomol. Soc.* 87:126–127.
- Cavalli-Sforza, L. L., and W. F. Bodmer. 1961. *The genetics of human populations*. Freeman, San Francisco.
- Clutton-Brock, T. H. 1983. Selection in relation to sex. Pages 457–481 in D. S. Bendell, ed. *Evolution from molecules to man*. Cambridge University Press, Cambridge.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. John Murray, London.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34:76–91.
- Fincke, O. M. 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10:293–302.
- Grafen, A. 1982. How not to measure inclusive fitness. *Nature (Lond.)* 298:425–426.
- Houck, L. D., S. J. Arnold, and R. A. Thisted. 1985. A statistical study of mate choice: sexual selection in a plethodontid salamander (*Desmognathus ochrophaeus*). *Evolution* 39:370–386.
- Howard, R. D., and A. G. Kluge. 1985. Proximate mechanisms of sexual selection in wood frogs. *Evolution* 39:260–277.
- McCauley, D. E. 1983. An estimate of the relative opportunities for natural and sexual selection in a population of milkweed beetles. *Evolution* 37:701–707.
- Partridge, L., and T. Halliday. 1984. Mating patterns and mate choice. Pages 222–250 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. 2d ed. Blackwell, Oxford.
- Price, T. D. 1984. Sexual selection of body size, territory and plumage variables in a population of Darwin's finches. *Evolution* 38:327–341.
- Ryan, M. J., M. D. Tuttle, and A. S. Rand. 1982. Bat predation and sexual advertisement in a neotropical anuran. *Am. Nat.* 119:136–139.
- Wade, M. J. 1979. Sexual selection and variance in reproductive success. *Am. Nat.* 114:742–747.
- Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice, and sperm precedence. *Anim. Behav.* 28:446–461.

WALTER D. KOENIG

HASTINGS RESERVATION
UNIVERSITY OF CALIFORNIA
STAR ROUTE BOX 80
CARMEL VALLEY, CALIFORNIA 93924

STEPHEN S. ALBANO*

MOORE LABORATORY OF ZOOLOGY
OCCIDENTAL COLLEGE
LOS ANGELES, CALIFORNIA 90041

Submitted April 25, 1985; Revised July 18, 1985; Accepted September 6, 1985

* Present address: Department of Zoology, University of California, Berkeley, California 94720.