FORUM:

(1) SEXUAL SELECTION IN AMPHIBIANS: A REPLY TO HALLIDAY AND VERRELL

RICHARD SHINE

Zoology Dept., The University of Sydney, New South Wales 2006, Australia.

The evolutionary interpretation of sexual dimorphism in amphibians has long been of interest to biologists. Charles Darwin (1874) noted of frogs that 'although cold-blooded, their passions are strong', and suggested that dimorphism should be common. However, he lacked the data to investigate further. Over one hundred years later, I reviewed available published literature to see whether any correlation was apparent between male-male combat and (i) large male body size relative to female size, and (2) the presence of enlarged spines or tusks in males. Such correlations were evident at the familial, subordinal and ordinal levels within the Amphibia and I interpreted these correlations as supporting the Darwinian hypothesis that male-male combat provided a selective advantage to large body size and weaponry in males (Shine, 1979). A recent review by Halliday and Verrell (1986), primarily a critique of my 1979 paper, concluded that both my specific results and my general approach were in error (e.g. 'attempts, such as that by Shine, to find correlations between behavioural and morphological characters are not useful', p. 90). I regret that I did not know of Halliday and Verrell's paper until after its publication, because most of their criticisms can easily be shown to be invalid.

The primary criticism levelled by Halliday and Verrell is that the data base and methodology for my 1979 paper are unreliable because (1) the information came from a wide variety of published sources, with highly variable samples sizes, techniques of measurement, and preparation of material; (2) placing any species in a single category introduces error because of possible intraspecific variation in sexual size dimorphism or reproductive behaviour; (3) analyses should have been done separately for various subgroups of amphibians (e.g. aquatic versus terrestrial species; prolonged versus 'explosive' breeders); (4) I compared dimorphism among amphibian species known to show combat, to dimorphism among species in which combat had not been recorded. Inevitably, future studies will show that many of these latter taxa also display combat behaviour.

I agree that all of these factors introduce potential error into my 1979 analysis; indeed, I pointed this out in the original paper (pp. 300, 302). Importantly, this error will introduce 1 andom 'noise' into the analysis rather than systematic bias. Thus, it will make it less likely for any statistically significant correlations between behaviour and morphology to be demonstrated. The existence of strong correlations between these variables in several amphibian taxa, despite such problems with the data, suggests that the underlying correlations must be very strong indeed. Thus, Halliday and Verrell's main criticism reinforces the conclusions of my 1979 paper, rather than casting doubt on them.

A second major criticism by Halliday and Verrell (1986) is to point out that there are several well-studied amphibian species which are clearly exceptions to the general correlation I found between large male size and male-male combat: that is, where males fight with each other, but are smaller than females. Halliday and Verrell are correct in viewing these cases as real exceptions rather than statistical 'noise', but the important point is that the general correlations exist (and are statistically significant) despite exceptions such as these. Neither are these cases directly contradictory to the Darwinian hypothesis. All that the hypothesis predicts is that large male body size is likely to evolve if combat is important in determining male reproductive success. Whether or not males grow larger than females will depend on other factors as well, including sexual differences in survivorship and selective pressures on female body size (see p. 302 of Shine 1979). The hypothesis makes no specific prediction about the size of males relative to females. The only basis for introducing sexual size dimorphism as a dependent variable in the analysis, rather than absolute male size, is essentially to use female size as a control. Hence, the prediction is that adding an extra selective pressure for larger male body size will tend to make it more likely (but certainly not inevitable) that males will grow larger than females, compared to a species where male body size is not under that pressure. Thus, many 'exceptions' (species with male combat, but with males smaller than females) would be expected *a priori*, and are completely consistent with the Darwinian hypothesis.

Halliday and Verrell (1986) also criticise my analysis on the grounds that it did not consider other behavioural strategies of males (e.g. mating interference), in which large body size may confer no advantage to males. Neither did I investigate other sexually dimorphic aspects of morphology (e.g. certain glands) or physiology (e.g. energetics of vocalisation). These criticisms misinterpret the intended scope of my paper. I set out to consider only those attributes of male amphibians (large body size and possession of 'weapons') which could readily be postulated to increase success in male-male combat, and to derive and test predictions from this hypothesis. Other sexually dimorphic attributes of amphibians also deserve attention, but were outside the scope of my 1979 paper. I specifically dealt only with the role of physical combat between males, not with any other form of male-male competition. This misunderstanding by Halliday and Verrell seems to be the basis for much of their discussion.

A fourth criticism by Halliday and Verrell is that I did not consider that sexual size dimorphism could result from survivorship differences between males and females, rather than resulting from natural selection for different body sizes. Their assertion is incorrect. I argued that differential survivorship may be an important proximate cause of observed patterns of sexual size dimorphism in amphibians (p. 302).

Finally, Halliday and Verrell correctly point out an omission in my data for *Plethodon glutinosus*, in which I had overlooked records of male-male combat. The direction of sexual size dimorphism in this taxon is uncertain (and perhaps geographically variable), because published accounts disagree with each other. More detailed data on this species would be of value.

I do not wish to imply that my 1979 analysis lacks flaws. For example, recent methodological suggestions for such comparative studies (e.g. Harvey and Mace 1982) convince me that there are real dangers in using species as the units in such analyses; a more detailed consideration of the extent of phylogenetic conservatism among the variables studied would add to the value of my 1979 work. The other obvious difficulty is my reliance on an essentially anecdotal data base. The problem is not one of random error, but of the possibility of systematic bias (if, for example, behavioural studies — and therefore records of male combat - had concentrated on some 'type' of amphibian which also, for some unrelated reason, tended to have males larger than females). Such systematic biases are unlikely to be a major problem, because (a) there is no a priori reason to expect them, (b) they cannot explain the observed correlations between large male size and presence of 'weapons', and (c) further studies, as they accumulate, will readily show whether these correlations are indeed valid.

Despite these reservations about methodology, I disagree strongly with Halliday and Verrell's cavalier

dismissal of the general approach of comparative analysis. I see nothing in their criticisms to make me doubt the basic results from my 1979 study: large male body size (relative to female size) and 'weapons' are more common in amphibians known to show malemale combat, than in amphibians where no such combat has been described. This correlation strongly suggests that these attributes have evolved because they increase male reproductive success by promoting success in combat. I agree with Halliday and Verrell (1986) that no single hypothesis can explain the phenomenon of sexual dimorphism in amphibians: the interplay of various ultimate and proximate influences is bound to be extremely complex. Nonetheless, I remain convinced that comparative analyses of correlations between behaviour and morphology offer a powerful technique for discovering some of the most important of these influences.

ACKNOWLEDGEMENTS

I thank G. C. Grigg and R. A. Bradley for comments on the manuscript.

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(2) SEXUAL SELECTION IN AMPHIBIANS: A REPLY TO SHINE

Our most important criticism of Shine's (1979) paper was of his comparison between two categories of species, those with male combat and those in which combat may or may not occur. In his reply, Shine suggests that this will involve random 'noise' rather than systematic bias; I disagree. The first category includes species where fighting has been observed and described and there is no reason to suppose that future research will show that it does not occur in any of these species. The second category, however, may include many species in which fighting does occur but for which it has not yet been described because they have been inadequately studied. If fighting is described for any species in this second category, those species would have to be reallocated to the first category. This inbalance in the status of the two categories is surely a systematic one. Only the accumulation of future

studies will determine how significant is this source of error in Shine's analysis.

On the point that Shine excluded dimorphic characters that are not related to combat because they were outside the scope of his 1979 paper, I can only observe that the title of that paper was highly misleading. Sexual selection theory, since its original development by Darwin, has generally been regarded as having two major components, male competition and female choice. Many recent studies of sexual behaviour have shown that these two components, intrasexual and intersexual selection, are often acting together within a mating system such that it is difficult if not impossible to differentiate their effects (Halliday, 1978; Partridge and Halliday, 1984).

Behind our critique of Shine and his reply to it lies a basic question: whether or not cross-species statistical tests are a valid test of evolutionary theory. Provided, as Shine acknowledges in his reply, such tests control for the confounding effect of phylogeny, they may reveal biologically significant patterns. They can, however, only reveal correlations between characters and cannot prove a causal relationship between those characters. Neither can they necessarily shed light on the situation in a particular species, such as *Bufo bufo*. The uncritical use of evolutionary generalisations about the relationship between body size and sexual selection has been attacked in a recent paper by Greenwood and Adams (1987). They discuss what they describe as two fallacious assumptions: first, that if large size is favoured by sexual selection, males will be larger than females and, second, that if males are larger than females, this must be evidence of intrasexual selection among males. Our contention is that there is now so much evidence that body size is the product of many selection pressures in amphibians, that further research should be directed towards estimating

accurately the strength of these pressures in individual species, not in seeking generalisations across species.

I thank Paul Harvey for discussions of these issues. T. R. Halliday,

Department of Biology, The Open University, Milton Keynes MK7 6AA, England

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