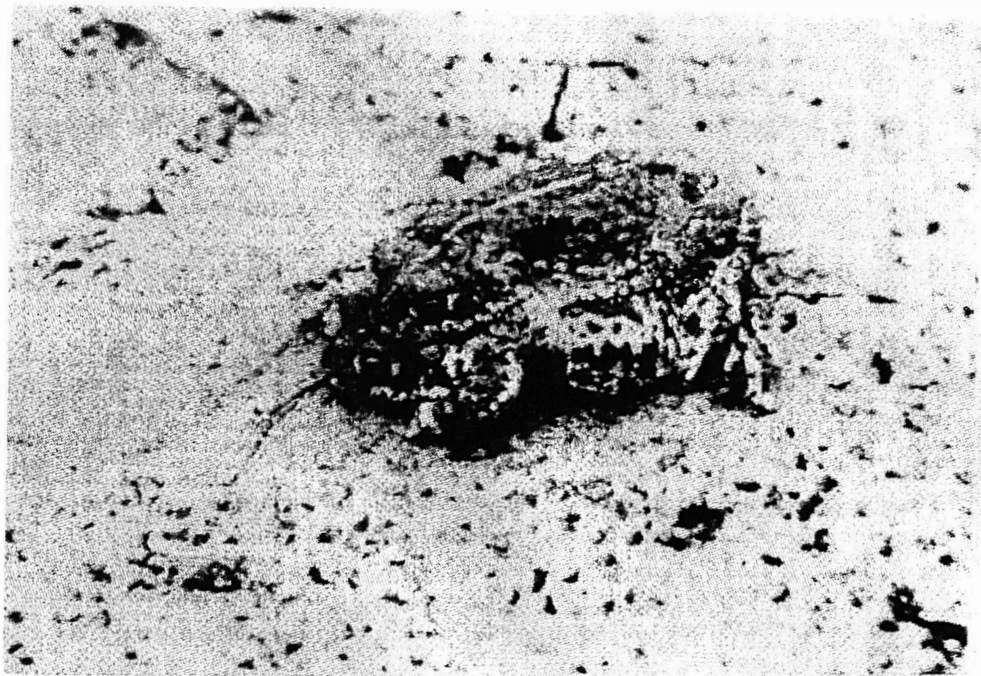


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REVIEW: SEXUAL SELECTION AND BODY SIZE IN AMPHIBIANS

T. R. HALLIDAY AND P. A. VERRELL

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

ABSTRACT

Sexual behaviour in amphibians is very diverse and variable. We examine Shine's (1979) conclusion that large male body-size is associated with combat and suggest that such a simplistic analysis is inadequate. We review briefly the recent literature and conclude that a full understanding of the role of sexual selection in amphibians requires a greater knowledge of variability in mating behaviour, alternative mating strategies, life history patterns, particularly growth, and physiological constraints on sexual behaviour.

INTRODUCTION

Sexual selection is that component of natural selection that favours characters giving individuals an advantage in competition with members of the same sex in terms of greater reproductive success. Evidence for the action and consequences of sexual selection is of two kinds, behavioural data on the dynamics of competitive and sexual behaviour in living animals, and comparison of the morphology of living species, with particular emphasis on sexual dimorphism.

Many amphibians are very suitable subjects for collecting data on the dynamics of mating behaviour since many of them form large, localised mating aggregations. In terms of morphology, several species provide an example of sexual dimorphism that is particularly challenging to sexual selection theory. It is widely assumed that, where males fight for access to females and larger males are at an advantage in fights, males will tend to be larger than females. In many anurans, fighting occurs in which there is a strong large-male advantage, but males are considerably smaller than females.

This topic has previously been reviewed by Shine (1979). In this paper we provide an alternative approach to Shine's, which we find flawed in several respects, as well as a review that takes into account more recent data and developments in sexual selection theory.

CRITIQUE OF SHINE (1979)

In his review, Shine (1979) concluded that, in most amphibian species, females are larger than males but that, in those species in which males compete for females, male size may approach or exceed that of females. In support of this conclusion, Shine listed published data on the incidence of male combat and on body size for many anuran and urodele species. He clearly recognised some of the limitations of this approach, stating that while use of these data on sexual

size differences introduces some error it has the compensating advantage of enabling me to include data from a large number of species' (p. 300).

To assess the value of Shine's data, we have consulted the papers that he cites. We suggest that the data on body-size are too inconsistent to permit statistical analysis of the kind that he used. Some authors give body-size data as snout-vent length, others as total length. In some papers, data are given as mean with variance, either with (e.g. Brame, 1968) or without the sample size (e.g. Mecham, 1968). Where given, sample sizes vary greatly. Some authors give mean body-lengths only (e.g. Peacock and Nussbaum, 1973), others give only the ranges for each sex (e.g. Highton, 1962). Data derived from fresh specimens are compared with material in museum collections, taking no account of shrinkage due to preservation (Lee, 1983; Verrell, 1985a). In some cases, authors discuss the possibility that there is geographical variation in body size (e.g. Rubenstein, 1969). For one genus, *Oedipina*, Student's t-tests on the original data (where sample sizes permit) show there to be no significant size differences between the sexes, although Shine states that, in three of the seven species listed, the female is larger than the male (data from Brame, 1968).

In his analysis, Shine ostensibly compared species in which males fight with those in which fighting is absent. However, inspection of his Table I reveals that he compared species with fighting with those in which it may or may not occur ('not recorded in these species', p. 300). Nearly all the primary sources cited are concerned with ecology, few of the authors being specifically concerned with sexual behaviour. It is clearly important in an analysis like Shine's that species be categorised as being definitely with or without fighting.

Shine acknowledges that the species he considers have very diverse natural histories, but he does not allow for confounding variables that might arise from inter-taxon comparisons. For instance, he compares species that breed on land with aquatic-breeding

species and he takes no account of marked variations between species in the duration of the breeding season. He also compares territorial with non-territorial species. Among urodeles, true territoriality has, to date, been described only in the terrestrial plethodontid salamanders. Studies in both the field (e.g. Jaeger, 1971) and the laboratory (e.g. Thurow, 1976) suggest that, in these urodeles, there is both inter- and intra-specific aggression in which both sexes participate. Large body-size is advantageous to individuals, of either sex, in aggressive encounters. In one species, *Plethodon glutinosus*, the male defends a territory against other males but allows females to enter for mating (Wells, 1980). Shine states that combat does not occur in this species and that the female is larger than the male. In fact, fighting between males is likely, and authors differ as to whether the female (Highton, 1962; Peacock and Nussbaum, 1973) or the male (Rubenstein, 1969) is the larger sex, or whether they are of equal size (Pope and Pope, 1951).

There are several other uncomfortable exceptions to Shine's conclusions which cannot be dismissed as statistical 'noise'. In the European toad, *Bufo bufo*, the breeding season is short (about 14 days) and scramble competition between males for females is intense (Davies and Halliday, 1979). Fights are frequent, vigorous and prolonged and, as clearly shown by both laboratory experiments and field data, there is a clear advantage to larger males, because they can both displace smaller males from the backs of female and can defend females more effectively against rivals (Davies and Halliday, 1977, 1979). Despite this clear advantage to large male size, males are substantially smaller than females (Davies and Halliday, 1979). As discussed below, this example shows that sexual dimorphism in body size is the result of a variety of selective forces and cannot be attributed solely to sexual selection.

We also question Shine's emphasis on 'combat' as a behavioural manifestation of inter-male competition. In many urodeles, males severely reduce the mating success of rivals by various forms of sexual interference (e.g. Arnold, 1976; Verrell, 1984). There is no evidence that body size has an influence on the effectiveness, either of sexual interference, or of a male's ability to counter it (sexual defence). In anurans, there have been several recent studies of mating dynamics that have considered body-size as an important determinant of male mating success but which have found other factors to be more important (see below).

Explanations for the evolution of body-size must take into account the effects of life-history and age, because amphibians typically continue to grow throughout life. This could create a misleading impression of sexual dimorphism if, within a population, members of one sex are larger than the other simply because they are older. This possible explanation for sexual dimorphism in body-size was considered by Organ (1961) in his study of *Desmognathus*, but is not considered in Shine's analysis.

Finally, we are critical of the emphasis that Shine places on body-size and on weapons used by males

during fighting. There are many other morphological features in which the sexes are dimorphic, notably in the many and varied glands of male urodeles and, more specifically, the bright colours and elaborate crests of European nexts (*Triturus*) and the premaxillary teeth of certain plethodontids (Arnold, 1977). In anurans, males of many species have a highly-developed vocal apparatus and produce complex and energetically-expensive vocalisations.

The comparative method is a widely-used and potentially powerful means for testing hypotheses about the adaptive significance of specific characters, but is one that must be used with caution (Clutton-Brock and Harvey, 1984). We suggest that Shine's analysis violates at least two of the limitations of the method identified by Clutton-Brock and Harvey: that numerical estimates extracted from the literature be accurate, and that there be an awareness that body size is correlated with a large number of behavioural and ecological variables.

URODELES

Among urodeles, sexual dimorphism in body-size is generally slight or absent and it is usually the female that is the larger sex. In 35 genera listed by Shine (1979), the female is larger in 16, the male in 8 and males and females are of equal size in 11. Vigorous and prolonged fighting appears to be rare in urodeles, though good data are scarce, and there seem to be no species that have evolved specialised structures for fighting. It is noteworthy that in three species in which fighting between males has been described recently, *Notophthalmus viridescens* (Verrell, 1986a), *Parame-sotriton hongkongensis* (Sparreboom, 1984) and *Salamandra salamandra* (Kastle, pers. comm.), males are smaller than females, contrary to Shine's conclusion.

There are many other aspects of sexual dimorphism than body size, and many more ways of competing than by overt fighting. Sexual interactions in urodeles involve the transfer of secretions from male to female and males in many species develop very large glands in the breeding season, usually on the head, and perform elaborate movements by which the male applies his glands to the female's snout (Arnold, 1977; Arnold and Houck, 1982). In *Triturus*, male odour is water-borne and is transferred to the female by fanning, a rapid movement of the tail (Halliday, 1974). The male's courtship pheromone is produced by the dorsal gland (also referred to as the abdominal gland), one of a number of glands opening into the male's cloaca (Malacarne *et al.*, 1984). In the breeding season, the dorsal gland increases in size dramatically, in some males representing 10 per cent of their total body weight (Verrell *et al.*, 1986). *Triturus* courtship also involves visual displays and the genus is highly unusual among urodeles in that males develop elaborate decorations in the breeding season, including a large dorsal crest and conspicuous skin patterns (Halliday, 1975, 1977).

The most fully-described form of sexual competition between males is sexual interference, whereby males disrupt the courtship behaviour of rivals. This takes a

variety of forms, including moving between a courting male and a female and displaying to her, mimicking female behaviour so as to induce a male to deposit a spermatophore that will not be picked up, and depositing a spermatophore on top of that of a rival. Sexual interference has been described in two ambystomatids, *Ambystoma maculatum* and *A. tigrinum* (Arnold, 1977), a plethodontid, *Plethodon jordani* (Arnold, 1977), and two salamandrids, *Triturus vulgaris* (Verrell, 1984) and *Notophthalmus viridescens* (Verrell, 1982a, 1983). It may have evolved independently in each of these families, or may have arisen in a common ancestor, in which case it is an extremely ancient pattern of behaviour. Sexual interference is a form of mating competition in which large body-size does not confer any advantage. Small males can interfere as effectively as large males and the effectiveness of behaviour patterns by courting males that counteract its effects (sexual defence) is not dependent on body-size. Territoriality in plethodontids may be a form of sexual defence since it will exclude potential rivals from the mating area. In *Plethodon vehiculum* aggression is more strongly associated with mating activity than with the defence of food resources (Ovaska, in press). In this genus, however, males are smaller than or equal in size to females (Shine, 1979).

The significance of sexual interference and other forms of male competition as a source of variance in male reproductive success is uncertain, because its frequency depends largely on the dynamics of natural breeding populations, about which little is known. In this context, what is important is not the overall sex ratio, but the operational sex ratio, defined by Emlen and Oring (1977) as the ratio of sexually active males to sexually responsive males. Our recent study of *Triturus vulgaris* in the field suggests that the operational sex ratio can change markedly during the breeding season, from an excess of females at the beginning to an excess of males later on when females start egg-laying and become unreceptive (Verrell and Halliday, 1985). Field observations by one of us (PAV) suggest that, as we predict, sexual interference is more frequent in the later part of the season when active males greatly outnumber receptive females. The only other study of changes in the operational sex ratio during the season is that of *Ambystoma jeffersonianum* by Douglas (1979), who found that sexually active males always outnumbered receptive females, but more so early in the season.

Body size is an important determinant of reproductive success in urodeles, in both sexes, because it is correlated with measures of fecundity, oocyte number in females, testis size in males (Verrell *et al.*, 1986). While body size is generally correlated with age, the relationship explains only a small proportion of the total variance in body size (Halliday and Verrell, in press). Much more important is the variation that exists within age-classes, suggesting that the major determinant of body size is growth before the age of first reproduction.

Another factor that will affect male reproductive success is the rate at which spermatophores can be produced. In *Triturus vulgaris*, males show a decline in

their daily spermatophore production over the course of a season (Halliday, 1976) and males require more than 24 hours to replenish their supply of available spermatophores (Verrell, in press). Spermatophore production rate will be an important determinant of male reproductive success for several seasons. First, if it is slow, males may frequently encounter females at times when they have little or no sperm with which to inseminate them. Secondly, male display rate is correlated with spermatophore supply (Halliday, 1976) and, because males must display at a high rate if they are to attract females (Teysedre and Halliday, 1986), their chances of inseminating females will be reduced while they are replenishing their spermatophore supply. Finally, because females store sperm and may mate with more than one male, sexual selection may take the form of sperm competition, though there is as yet little direct evidence that this is a significant factor in urodeles (Halliday and Verrell, 1984).

Evidence for mate choice in urodeles has been sought but has proved elusive, and there is clearer evidence for choice by males than by females. Males of both *Triturus vulgaris* (Verrell, 1986) and *Notophthalmus viridescens* (Verrell, 1982b, 1985b) show a preference for larger, more fecund females. Female choice is manifested in *T. vulgaris* by a greater tendency to pick up spermatophores deposited by males that produce several than from those that put down a few (Halliday, 1974, 1983), and by their being more responsive to males that display at a high rate (Teysedre and Halliday, 1986).

In conclusion, variance in the reproductive success of male urodeles is a product of several factors, including the operational sex ratio, the ability to produce spermatophores, mate choice and the development of epigamic characters. If body size is important, its significance lies not in fighting but in its relationship to fecundity. The complexity of the determinants of mating success in urodeles is illustrated by a recent, detailed study of *Desmognathus ochrophaeus* (Houck *et al.*, 1985). This showed that there is variance in the mating success of both sexes, more markedly among males, but did not reveal any morphological correlate of such variation.

ANURANS

Mating systems among frogs and toads are both diverse and, within species, highly variable, making it difficult to classify them into mutually exclusive categories (Wells, 1977a; Arak, 1983a). Interspecific differences are related largely to variation in the duration of the breeding season; species with a very short season (explosive breeders) tend to show scramble competition resulting in random mating, those with the longest seasons tend to have a territorial system in which males defend mating and/or spawning sites. Between these extremes there is a variety of patterns, perhaps the most common being a lek-like system in which males defend calling sites but not resources. Within species, variation can be considerable, both between populations and, within a

population, between years. Such variation is a function of variation, not only in breeding season duration, but also population density and operational sex ratio (Arak, 1983a).

Within-species variation in mating dynamics may have important consequences for the intensity with which sexual selection acts on males. For example, a switch in male behaviour, from calling to females from fixed positions to active searching and fighting for females, has been described for *Bufo canorus* (Kagarise-Sherman, 1980) and *B. calamita* (Arak, 1983a) and, in both cases, is associated with a high population density. Such a switch may mean that different male characters are favoured by sexual selection at different times and in different places: call characteristics when density is low, mobility and strength when it is high. Theoretical discussions of sexual selection typically envisage a powerful, sustained and one-directional selection pressure as being a necessary condition for the evolution of an elaborate or extreme male character. The behavioural plasticity observed in many anurans will tend to mitigate against such conditions.

Another factor tending to reduce the intensity and uni-directionality of sexual selection in anurans is the existence, in many species, of alternative male mating strategies. Arak (1983a) identifies two types of alternative strategy, depending on the type of mating system. In species in which males fight for females, the alternative strategy is to search for unpaired females. In those in which males attract females by calling or by defending resources, it is to adopt silent or non-territorial 'satellite' behaviour. In many cases, the alternative strategy is shown by males that are inherently less competitive, most commonly because of small body-size. In calling species, however, satellite behaviour may be adopted temporarily by males that have become exhausted after a period of sustained calling (Ryan, 1985; Robertson, 1986a). The relative frequency of individuals adopting an alternative strategy is largely dependent on total population density and may thus be very variable, in both time and space (Arak, 1983).

The intensity of sexual selection on males pursuing a primary mating strategy with partly depend on the relative mating success of individuals adopting an alternative strategy; the more successful the alternative strategy, the less strongly will the primary strategy be favoured. In *Hyla cinerea*, calling males and non-calling satellites experience approximately equal mating success (Perrill *et al.*, 1978); in *Bufo calamita* satellites are less successful than callers (Arak, 1983a).

In species in which males fight to obtain and defend females, it has commonly been found that larger males have higher mating success. Examples include: *Bufo americanus* (Gatz, 1981), *B. bufo* (Davies and Halliday, 1979), *B. woodhousei* (Woodward, 1982) and *Rana sylvatica* (Howard, 1980). In all these species, as in the majority of anurans, males are smaller than females (Woolbright, 1983). It seems clear, therefore, that whatever the strength of sexual selection favouring large body-size in males, it is not as strong as selection for large size in females. This conclusion was reached for *Rana sylvatica* by Howard and Kluge (1985). We

agree with Woolbright (1983) that the adaptive value of large size in females arises from its positive correlation with fecundity, but disagree with him that males are smaller than females because of energetic constraints (see also Sullivan, 1984). Skeletochronological data for *Bufo bufo* suggest that males reach sexual maturity at least one year before females (Gittins *et al.*, 1982; Hemelaar, 1983). Annual growth rate appears to be much faster in anurans before the onset of breeding than it is during adult life (Halliday and Verrell, in press), and this may well account for the larger body size of females in breeding populations.

It has been suggested that body size (usually measured as snout-vent or snout-urostyle length) is not the most significant correlate of male mating success. Howard and Kluge (1985) present evidence that male arm-length is more important in *Rana sylvatica* and suggest that males with longer arms can maintain a more secure grip on females.

While several studies of anuran mating patterns have sought evidence for a large-male advantage, many have found that the most significant correlate of male mating success is the amount of time for which males are present at a breeding site. This effect has been shown for *Bufo calamita* (Arak, 1983b), *B. woodhousei* (Woodward, 1982), *B. rangeri* (Cherry, pers. comm.), *Hyla chrysoscelis* (Godwin and Roble, 1983), *H. rosenbergi* (Kluge, 1981), *H. cinerea* (Gerhardt, pers. comm.), *Centrolenella fleischmanni* (Greer and Wells, 1980; Jacobson, 1985) and *C. prosoblopon* (Jacobson, 1985). In *Rana clamitans*, higher mating success falls to those males that spend the most time in good-quality territories, in terms of their suitability for oviposition (Wells, 1977b). A correlation between mating success and time spent in mating activity may be due to the latter being a function of variance in the ability of males to meet the physiological demands of mating activity. That sexual and competitive behaviour is energetically expensive for male anurans is suggested by data indicating substantial weight losses during the mating period (Arak, 1983a; Robertson, 1986a; Wells, 1978), and by studies of the energetics of mating behaviour (Bucher *et al.*, 1982; MacNally, 1981; Ryan *et al.*, 1983; Sullivan and Walsberg, 1985; Taigen and Wells, 1985; Wells and Taigen, 1984).

An alternative way by which larger males could gain a mating advantage is if they are preferred as mates by females (Halliday, 1983b). Female choice for larger males has been reported for *Bufo americanus* (Fairchild, 1984), *B. quercicus* (Wilbur *et al.*, 1978), *B. woodhousei fowleri* (Fairchild, 1981), *Hyla crucifer* (Gatz, 1981b; Forester and Czarnowsky, 1985), *H. marmorata* (Lee and Crump, 1981), *H. versicolor* (Gatz, 1981b), *Physalaemus pustulosus* (Ryan, 1980), *Rana catesbeiana* (Emlen, 1976; Howard, 1978) and *R. clamitans* (Ramer *et al.*, 1983). In many of these cases, it is suggested that the adaptive advantage of female choice for larger males is that they will tend to mate with males that are older and, therefore, of proven survival capacity. We suggest that, because age and size are generally only weakly correlated in anurans, the adaptive value of larger males is more likely to lie in their rapid early growth (Halliday and Verrell, in press).

Several studies have obtained evidence for females choice on the basis of individual variation in the male advertisement call. In some species, the fundamental frequency of the call is inversely correlated with body-size, providing a cue by which females could potentially mate preferentially with males of a specific size. Such a preference, for larger males, has been reported in *Physalaemus pustulosus* by Ryan (1985) and Robertson (1986b) has found that female *Uperoleia rugosa* use call frequency to identify and mate preferentially with males whose weight is approximately 75 per cent of their own. Several other studies have found a tendency by females to approach calls with features that indicate high energy expenditure by the males that produce them. Females prefer high intensity (louder) calls in *Bufo calamita* (Arak, 1983a) and *Hyla versicolor* (Fellers, 1979), calls with a high repetition rate in *Bufo woodhousei* (Sullivan, 1983), calls of long duration in *Hyla regilla* (Whitney and Krebs, 1975), and calls that contain extra components in *Physalaemus pustulosus* (Ryan, 1985). Whether or not such preferences are adaptive for females is uncertain (Halliday, 1983b). Males that produce more energetically expensive calls may be fitter than other males, in terms of their ability to survive, and such fitness may be heritable, but this has yet to be demonstrated. At present, a more parsimonious explanation is that females are attracted to those calls that provide the most powerful stimulus or which are easiest to locate.

CONCLUSIONS

Amphibian mating systems are not as simple as they might appear to the casual observer; this is arguably the only generalisation it is safe to make about them. Attempts, such as that by Shine, to find correlations between behavioural and morphological characters are not useful, because they fail to take into account the diversity and variability of amphibian behaviour, or the variety of factors that have influenced their evolution. In particular, it is becoming increasingly apparent that body-size in amphibians cannot be explained solely in terms of sexual selection; because body-size is related to fecundity and age, its evolutionary basis must be sought through an understanding of life history. Recent studies have also shown that it can be misleading to categorise the sexual behaviour of any given species. Amphibian behaviour is very variable and is highly influenced by the dynamics of a breeding population which, in turn, vary in both time and space. The situation is further complicated by the existence in many species of alternative male mating strategies, the effect of which is to diminish the extent to which any one category of male achieves higher mating success. These are often rather subtle forms of behaviour that are revealed only by intensive observation.

We suggest that studies of amphibian sexual behaviour, if they are fully to reveal the effects of sexual selection, must address three aspects. First, many amphibians are long-lived and breed more than once. Natural selection acts on lifetime reproductive success which may or may not be accurately estimated from observations made in a single season. There is a

need for more studies that measure male reproductive success over several seasons. Secondly, body-size is an important determinant of reproductive success in many species, but the factors that are important in its evolution are poorly understood. Sexual selection may play some part, but more needs to be known about the factors that regulate growth in amphibia. Finally, there is increasing evidence that amphibian sexual behaviour is subject to physiological constraints and that these may be what limits male mating success. Such constraints include respiratory limits on display in urodeles and calling in frogs and the rate at which spermatophores are produced in urodeles. To understand the role of sexual selection in amphibians, behavioural biologists will need to turn to the considerable knowledge being gathered by physiologists.

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