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SEXUAL SELECTION IN TOADS: THE ROLES OF FEMALE CHOICE AND MALE BODY SIZE

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Darwin (1871, p. 568) wrote "sexual selection depends on the advantage which certain individuals have over others of the same sex and species solely in respect to reproduction." This selection may act in several ways. Two extremes are either the individuals of one sex, usually males (but see Trivers, 1972), compete amongst themselves, with the winners acquiring the most mates; or the members of one sex, usually females, discriminate among members of the other sex choosing to mate with the most "attractive" individuals.

The first extreme of sexual selection, competition among males, has been documented by field studies on baboons (De Vore, 1965), dungflies (Parker, 1970), elephant seals (Le Boeuff, 1974), lizards (Trivers, 1972, 1976), prairie chickens (Robel, 1966), and sage grouse (Scott, 1942). For example, Le Boeuff (1974) found that less than one third of the males in a breeding aggregation accounted for all of the matings and that copulation frequency was correlated with social rank. Competition among males may be incited in turn by the behavior of females (Cox and Le Boeuff, 1977).

The second extreme of sexual selection, female choice among alternate mates, has not been studied as vigorously, and some biologists (Huxley, 1938; Lack, 1968) have doubted its importance to evolution. However, Trivers (1972) has theoretically shown the adaptive advantage that a female can gain by choosing the best of alternative mates and O'Donald (1972, 1973) with computer simulations has dem-

onstrated that female mating preference can result in a major change in gene frequency.

Anurans are excellent subjects for studies of sexual selection. Frogs and toads have a wide diversity of breeding habits, but the following generalized pattern of courtship is approximated by many species. Typically adults are terrestrial but congregate near lakes or ponds, usually during or after rain, for breeding. Males establish calling stations, which may be defended (e.g., Emlen, 1968, *Rana catesbeiana*) or occupied sequentially by several males (e.g., Fellers, 1975, *Hyla versicolor*). Females approach the male chorus and move towards a specific mate. Sometimes males orient towards an approaching female but in most species the female initiates amplexus by physically contacting the male or by remaining nearly submerged until she is close to a certain male. Different species have different relative combinations of the two modes of sexual selection: male-male interactions (e.g., territoriality, dominance in occupation of calling sites, leadership in calling sequence) and female choice among alternative males.

Anuran breeding behavior and reproductive success can be more easily studied than that of most vertebrates because the breeding season is often short, populations are concentrated in small areas, with patience all males can be located, fertilization is external so parentage is unambiguous because sperm is not stored by the female, and there is no parental care in most temperate species. Observation in both undisturbed natural choruses and in controlled laboratory experiments is possible.

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In this paper we present some field observations of two taxonomic groups of toads, *Bufo quercicus* and three populations of the *Bufo americanus* complex, in which the relations between male body size and reproductive success are measured. Three questions are asked. (1) Is there sexual dimorphism in body size within amplexing pairs? (2) Is there assortative mating with respect to body size? (3) Within a chorus are successful males significantly larger than unsuccessful males?

MATERIALS AND METHODS

Calling males and amplexant pairs of toads were collected from six breeding aggregations in eastern North Carolina. *Bufo quercicus* were collected from the Green Swamp, Brunswick County on 26 June 1974, and from two ponds in the Sandhills Game Management Area, Scotland County on 17 June 1976. *Bufo americanus* were collected near Corinth, Chatham County on 3 March 1977. *Bufo terrestris* were collected near Glendon, Moore County on 19 April 1966. Apparent *Bufo americanus* × *terrestris* intergrades were also collected near Sanford, Lee County on 19 April 1966. First each pond was searched and all amplexant pairs were collected and put in separate plastic bags. Then a collection of unsuccessful males was made by moving about the pond and collecting a sample of unmated calling males. Because toads were collected early in the evening probably no eggs were laid before capture. Pairs were kept in the bags overnight and many laid eggs. All toads and a sample of each clutch of eggs were preserved the day after collection. Egg diameters were measured to 0.02-mm precision with an ocular micrometer. Body size was measured to 1-mm precision by the distance from the tip of the snout to the distal end of the ischium after pressing the preserved toads flat against a tabletop. Sexes were easily determined by the presence or absence of a vocal sac.

The first set of statistical tests deter-

mined if there was a consistent relative size difference between mates in a population. This sexual dimorphism was measured by a Student's *t*-test for paired observations (Steel and Torrie, 1960, p. 78) after testing for homogeneity of variance within sexes by an *F* test.

The second set of tests determined if within a population of amplexing pairs the large females tended to pair with large males (positive assortative mating) or with small males (negative assortative mating), independent of any sexual dimorphism in body size. This assortative mating was tested by a product moment correlation coefficient between the size of the male and female in each pair.

The third set of tests determined if females mated at random with the available males. Nonrandom mating choice of females with respect to male body size was tested by comparing the sizes of successful males (those in amplexus) to unsuccessful males (those calling in the same chorus) with *t*-tests or analyses of variance following *F* tests for homogeneity of variance between the two groups of males.

The selective advantage of female body size was studied by regression analysis of clutch size (number of eggs deposited) on body size and mean egg size (five eggs per clutch) on body size.

RESULTS

Bufo quercicus.—In the Scotland County populations (Table 1, Fig. 1) sexual dimorphism within pairs was significant (Scotland-1, $t = 4.36$, 23 d.f., $P < 0.01$; Scotland-2, $t = 5.69$, 11 d.f., $P < 0.01$) with males being 2.2 and 2.7 mm smaller, respectively than their mates. There was no assortative mating in either population (Scotland-1, $r = -0.23$, 23 d.f.; Scotland-2, $r = 0.32$, 11 d.f.). Mating was significantly nonrandom ($t = 2.82$, 47 d.f., $P < 0.01$), Scotland-1 successful males were 1.3 mm larger than unsuccessful males (no test for Scotland-2 population).

The regression of clutch size on female

TABLE 1. Summary of sample sizes and body sizes (snout-ischium length in mm).

	Green Swamp	<i>Bufo quercicus</i> Scotland-1	Scotland-2	<i>Bufo americanus</i>	<i>Bufo</i> intergrades	<i>Bufo</i> <i>terrestris</i>
Number of pairs	20	25	13	7	4	4
Males—mean	25.7	28.0	29.3	53.1	55.2	55.5
variance	3.7	2.9	1.1	3.8	10.0	6.3
Females—mean	25.2	30.2	32.0	64.1	65.0	58.4
variance	1.9	2.1	3.1	6.6	19.1	27.7
Calling males						
number	14	24	none	11	30	12
mean	23.6	26.7		57.1	53.3	52.7
variance	1.6	2.3		28.0	9.9	20.1

snout-ischium length does not account for a significant amount of variation ($F_{1,14} = 0.83$, coefficient of determination = 0.057). The regression of the mean egg diameter of five eggs per female on her snout-ischium length is also not significant ($F_{1,36} = 0.59$, coefficient of determination = 0.016). These analyses are based on the 38 females from the two Scotland County collections that laid at least five eggs.

In the collection from the Green Swamp (Table 1, Fig. 1) there was no significant sexual dimorphism within pairs ($t = 0.988$, 19 d.f.) and there was no assortative mating ($r = 0.11$, 18 d.f.). Mating was significantly non-random ($t = 3.57$, 32 d.f., $P < 0.05$) because successful males average 2.3 mm larger than unsuccessful males.

Bufo americanus.—Sexual dimorphism was highly significant ($t = 8.644$, 6 d.f., $P < 0.01$); males average 11 mm smaller than their mate (Table 1). There was no assortative mating among pairs ($r = -0.098$, 5 d.f.) and mating was random with respect to male body size ($t = 0.542$, 16 d.f., $P < 0.05$).

Bufo terrestris × *americanus* (intergrade population).—Sexual dimorphism was highly significant ($t = 5.455$, 3 d.f., $P < 0.01$); males were nearly 10 mm smaller than females (Table 1). No significant amount of assortative mating was present ($r = 0.58$, 2 d.f.) and mating was random ($t = -0.244$, 32 d.f., $P > 0.05$).

Bufo terrestris.—There was no sexual

dimorphism within the four amplexed pairs ($t = 0.860$, 2 d.f., $P > 0.05$) (Table 1). No significant amount of assortative mating was present ($r = -0.46$, 2 d.f.) and mating was random ($t = 0.382$, 16 d.f., $P > 0.05$).

These last three collections were made by the senior author 10 yr ago and egg sizes and clutch sizes were not determined. Collins (1975), however, found a highly

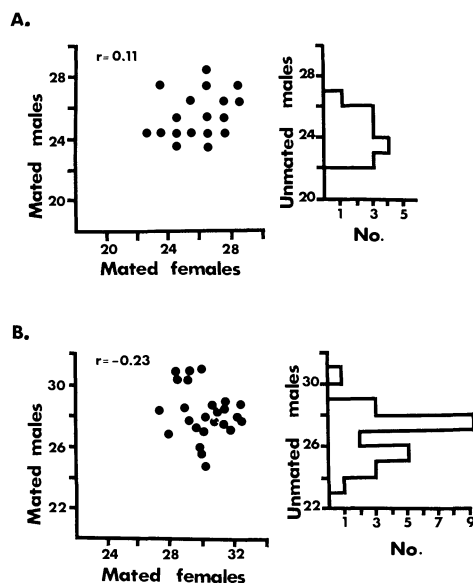


FIG. 1. Relationship between the snout-ischium lengths (in mm) of male and female pairs and calling but unmated males in the same aggregation: A. *Bufo quercicus*, Green Swamp; B. *Bufo quercicus*, Scotland-1.

TABLE 2. Summary of tests for: (1) sexual dimorphism, (2) assortative mating with respect to body size, (3) correlation between body size and mating success of males.

Population	Test 1 ♀ ♀-larger ♂♂?	Test 2 Size-assortative mating?	Test 3 Successful ♂♂ larger than unsuccessful ♂♂?
<i>Bufo quercicus</i>			
Green Swamp	no	no	2.1 mm
Scotland-1	2.2 mm	no	1.3 mm
Scotland-2	2.7 mm	no	no test
<i>B. americanus</i>	11 mm	no	no
<i>B. terrestris</i> × <i>B. americanus</i>	10 mm	no	no
<i>B. terrestris</i>	no	no	no

significant correlation between egg size and female body length ($r = 0.422$, 47 d.f., $P < 0.01$) and between clutch size and female body length ($r = 0.848$, 12 d.f., $P < 0.01$) for a population of *Bufo americanus* in Michigan.

In summary, for all species mating is not assortative (Table 2). That is, there is no correlation between the body sizes of mates. Because our sample sizes were small, however, the null hypothesis was easily accepted. Within pairs, males are significantly smaller than females in two of three comparisons in each taxonomic group. Larger males had a clear mating advantage in all populations of *Bufo quercicus* but not in any populations of the *Bufo americanus* complex.

DISCUSSION

Licht (1976) has just published some carefully taken field observations of sexual selection in Ontario populations of *Bufo americanus*. His hypothesis is "that the mating call of the male toad indicates his fitness, both as being the right species (Blair, 1964) and the right body size." He interprets his data in terms of the optimal size difference between a male and a female that is the most efficient for amplexus. If the male is too large, he restricts the female's swimming movements and her respiration. If the male is too small, he is easily dislodged from amplexus by rival

males and his cloaca is not properly juxtaposed to the female's cloaca to effect efficient fertilization.

Our hypothesis is that females choose the largest males available because there is a selective advantage in large body size per se. We have demonstrated that large *Bufo quercicus* males have a mating advantage. Large males may be more attractive to females because they are either older than the average male in the chorus or have had faster growth rates. Both are a sign of vigor and, perhaps, of a good genotype. Old age is a *post facto* demonstration of survival value. Rapid growth is advantageous in both the larval stage (numerous experimental studies, e.g. Wilbur, 1977; Wilbur and Collins, 1973) and in attaining early maturity, a selective advantage.

In most anurans (e.g. Clarke, 1974; Collins, 1975), but not in our sample of *B. quercicus*, fecundity increases with body size. *Bufo quercicus* may also follow this pattern but our sample contained females of a narrow range of body size making a correlation difficult to detect. Given the increase in fecundity with female body size, a female should choose a mate that will confer a large body size on her sons (mating advantage) and her daughters (larger clutches and perhaps larger eggs).

Both Licht's and our field observations demonstrate that females will move past calling males to initiate amplexus with a

male of their choosing. Numerous behavioral and neurophysiological studies demonstrate that females could be capable of aurally discriminating among males of different sizes. Martof and Thompson (1958), Blair (1955), Gerhardt (1974) and others have demonstrated that females can receive sufficient information to initiate courtship from males' calls alone.

Several aspects of anuran calls are related to male body size. Zweifel (1968) has shown in *Bufo fowleri* that larger males call at lower frequencies than smaller males. Sounds with lower frequencies in general attenuate less rapidly with distance because there is less reflection and scattering than sounds with higher frequencies (Morton, 1975; Lyon, 1973). Larger males have a larger lung volume and produce more powerful calls than small males. The combined effect of more power and lower frequencies is that calls of large males travel farther before attenuation reduces the sound pressure level below the auditory threshold of a female. This alone would confer a mating advantage on larger males.

A female's perception of male calls of different signal intensities may be ambiguous. Differences in distance between two males and a female may confound the acoustic distinctions between males of different body sizes. Most *Bufo*s emit mating calls which contain several frequencies of high intensity. Because sounds of higher frequencies attenuate more rapidly over distance than sounds of lower frequencies, a female could determine the distance to a calling male by comparing the relative intensities of the peak frequencies of the call. Differences in intensities of the high and low frequency components within a call increase with distance.

The size of a calling male could be similarly determined relative to that of another calling male, regardless of the distance of either to the female. If both males are equidistant or if the larger male is closer than the smaller male to the female, all peak frequencies of the larger male's call

will be perceived as louder by the female than the frequencies of the smaller male. If the closer male is smaller, the low frequency component of the calls of both males will be of similar intensity, but the high frequency part of the large male's call will be less intense than that of the small male's call.

Anuran mating calls are usually discussed as interspecific isolating mechanisms. Because auditory thresholds of female anurans are narrowly tuned to the frequencies produced by conspecific males (Capranica et al., 1973; Lombard and Straughan, 1974; Narins and Capranica, 1976), females do not appear to be very sensitive to calls of males of other species and can use a conspecific male's call to evaluate his suitability as a mate.

These physical and neurophysiological considerations support the assumption that females are able to choose a male on the basis of his body size without being confounded by spatial relationships among males in the chorus. This is not to say that the spatial relationships and temporal interactions among males of the same species are not important.

One would expect the following results from Licht's hypothesis: (1) There should be significant sexual dimorphism with the male smaller than the females in species with axillary amplexus. (2) There should be a positive correlation between the sizes of males and females in amplexus. Larger females should choose males slightly smaller than themselves and smaller females should choose even smaller males to optimize the difference in body sizes of the pair. (3) Successful males should not necessarily be larger than unsuccessful males although this prediction depends on the size distribution of females and the optimal size differences between members of an amplexing pair.

All *Bufo* have axillary amplexus, but sexual dimorphism is not strongly developed in *B. quercicus*. Efficiency of amplexus need not be the primary reason for sexual dimorphism. Delayed reproduction

to increase fecundity of females may be more important.

Licht's hypothesis of assortative mating would result in a correlation of sizes within pairs. Our hypothesis would result in a correlation between male success and his body size. However, the two hypotheses differ only with respect to the mates of smaller females. Licht predicts they will choose mates smaller than themselves by an optimal amount. Our hypothesis predicts they should choose the largest available males.

Licht's data support his hypothesis; mating is assortative ($r = 0.783$, 82 d.f., $P < 0.01$; Licht, pers. comm., 11 Feb 1977) and there is no significant mean difference in body size between successful and unsuccessful males ($t = 1.23$, 132 d.f., $P > 0.20$; Licht, pers. comm., 11 Feb 1977). Our data do not confirm his hypothesis; there was no assortative mating in any of the populations. The data for *B. quercicus* fit our hypothesis of a mating advantage for large males. Our data for the *Bufo americanus* complex did not show a mating advantage for large males. The small samples make it difficult to evaluate assortative mating.

Thus it appears that among *Bufo* species there are at least two different criteria used by females to discriminate among males. In spite of the sexual selective advantages to large male body size only *Bufo quercicus* females choose the largest males as mates. Efficiency of amplexus, which necessitates an optimal male-female size differential, appears to influence the size of mates chosen by females of the *Bufo americanus* complex.

We have demonstrated for *Bufo quercicus* that female behavior acts on the male's phenotype but it has not been demonstrated that this differential reproductive success affects gene frequencies. We know of no direct test of heritability of body size in anurans. If body size is heritable, then our results predict directional selection for increased male body size. The adult niche (Nevo, 1973) and the balance between the

sexual selective advantage of large body size and the disadvantage of delayed reproduction (Wilbur et al., 1974) may both act to stabilize male body size. Therefore demographic and ecological considerations as well as efficiency of amplexus may be involved in the optimization of male body size.

SUMMARY

Sexual selection can act either by interactions among individuals of one sex in which successful contestants have increased access to the opposite sex (e.g. male territoriality or dominance relationships) or by members of one sex choosing among alternative mates. Both modes may operate in anuran breeding systems. Behavioral and neurophysiological observations indicate that female anurans ought to be able to choose mates by call characteristics that are correlated with body size.

Licht (1976) has suggested that the selective basis of body size is related to the optimal size difference between a male and a female that permits efficient amplexus and fertilization. This hypothesis predicts that positive assortative mating should occur. We present data from six mating aggregations of *Bufo quercicus*, *B. americanus*, *B. terrestris* and *B. americanus* × *terrestris* intergrades in which mating is not assortative. Large male *B. quercicus* have a clear advantage in attracting females compared to smaller males in the chorus.

As an alternative we present a hypothesis that females chose the largest males available. Large males in a chorus are either older or have grown faster than small males. Older males have demonstrated their survival value by their age. Efficient feeding and rapid growth is advantageous in the highly competitive larval stage and in attaining early maturity, a demographic advantage. Careful observation of the breeding behavior of toads will be necessary before it is possible to understand why different species exhibit different criteria for female choice.

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