

Differential effects of mate competition and mate choice on eastern tiger salamanders

R. D. HOWARD*, R. S. MOORMAN* & H. H. WHITEMAN†

*Department of Biological Sciences, Purdue University

†Department of Biological Sciences, Murray State University

(Received 17 June 1996; initial acceptance 19 August 1996;

final acceptance 20 September 1996; MS. number: A7630)

Abstract. Male tiger salamanders, *Ambystoma tigrinum tigrinum*, are slightly larger in body size and have considerably higher and longer tails than females. To determine how these dimorphic traits affected reproductive performance and success, we conducted breeding trials using 12 males and six females per trial and monitored male–female and male–male interactions. Larger males had an advantage in most aspects of mate competition investigated. Males with higher tails had no advantage in either mate competition or mate choice. Males with longer tails also had no advantage in mate competition but were preferred as mates by females. Larger males interrupted courting males more often than smaller males did. The form of male–male interference was conditional on body size and not on either tail dimension. If the intruder was larger than the courting male, it would shove the female away from the courting male and initiate courtship; if the intruder was smaller, it adopted a female mimicry tactic in which it positioned itself between the courting male and female and performed female behaviours to the courting male while simultaneously courting the female. Our trials indicated that the two components of sexual selection may influence the evolution of different male morphological traits in tiger salamanders. Mate competition may favour increased male body length; mate choice may select for greater male tail length.

© 1997 The Association for the Study of Animal Behaviour

Sexual selection has produced dramatic patterns of sexual dimorphism in morphology, behaviour and life history (e.g. Andersson 1994). Such selection consists of two components: interactions between members of the same sex for mating opportunities (mate competition) and proclivities to mate with individuals of the opposite sex that have particular characteristics (mate choice). These two selection components often interact in complex ways (e.g. Bradbury & Davies 1987) that can therefore complicate interpretation. For example, after reviewing 232 studies on 186 animal species, Andersson (1994) noted that determining the relative importance of mate competition and mate choice on the evolution of secondary sexual characters is hindered by problems such as disproportionate attention given

to mate choice by researchers, direct and indirect selection on correlated characters and lack of experimental data to separate the effects of each component. Some traits, such as body size, appear to be affected primarily by mate competition in some species, but by both sexual selection components in others. Other traits, such as male visual ornaments or displays, appear to be favoured mainly by mate choice in some species, but by mate competition in others. More rarely, the two sexual selection components may favour different traits in the same species (e.g. Evans & Hatchwell 1992a, b). Here we document the degree of sexual dimorphism in morphology for a population of eastern tiger salamanders, *Ambystoma tigrinum tigrinum*, and present results of breeding trials that reveal that mate competition and mate choice favour different male attributes in this species.

Two prerequisites appear to be particularly important in the evolution of sexually selected traits in urodeles (Verrell 1989a). In many species, operational sex ratios are male-biased because overall sex ratios of breeders are male-biased

Correspondence: R. D. Howard, Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907, U.S.A. (email: rhoward@bilbo.bio.purdue.edu). H. H. Whiteman is at Department of Biological Sciences, Murray State University, P.O. Box 9, Murray, KY 42071-0009, U.S.A.

(Halliday & Verrell 1984) and because the sexes differ in potential reproductive rates (Clutton-Brock & Parker 1992). In addition, about 90% of extant salamander species use an indirect method of sperm transfer in which courting males deposit spermatophores on the substrate that are then picked up by females for internal fertilization (Halliday 1975a; Arnold 1976, 1977). This courtship mode has produced two distinct forms of mate competition, sexual defence and sexual interference (Arnold 1976), and facilitates mate choice because females can easily reject both males and any deposited spermatophores. Multiple mating by females also results in a third form of mate competition, sperm competition, which has received relatively little attention (Halliday & Verrell 1984; Verrell 1989a; but see Houck et al. 1985a).

Many urodele species have sexually dimorphic characters, including body size, coloration, tail characteristics, and cloacal and skin glands (reviewed by Verrell 1989a). Although detailed data on the effect of male trait variation on mating success are lacking for most species (Verrell 1989a; Halliday 1990), some studies have revealed intense mate competition (Arnold 1976; Verrell 1984; Houck 1988; Janzen & Brodie 1989; Raxworthy 1989) as well as evidence for mate choice by males (Verrell 1989b) and females (Houck et al. 1985b). Reproductive benefits obtained by discriminating males are often straightforward: males may prefer larger females because they produce larger clutches. Benefits that discriminating females obtain by mating with particular types of males are uncertain, however, because in most urodele species males only provide sperm (Verrell 1989a). Nutrient transfer from spermatophores is unknown, and paternal care is limited to a few species in which fertilization is external and courtship sites are also used for oviposition (Nussbaum 1985).

In the present study, we concentrated on three morphological characteristics: body length, tail height and tail length. Body length and tail height are influenced by sexual selection in several urodele species, and both tail dimensions are sexually dimorphic in *A. tigrinum* (Arnold 1976). In some salamander species, larger-bodied males have a mating advantage due to apparent success in mate competition (e.g. Houck 1988; Janzen & Brodie 1989); in other species, males with greater tail heights have increased mating success due to

either mate competition (Janzen & Brodie 1989) or mate choice (Malacarne & Cortassa 1983; Green 1992). In great crested newts, *Triturus cristatus*, tail height correlates with body condition and could influence female mating decisions by indicating the resource acquisition ability of potential mates (Baker 1992).

To determine the role of sexual selection on male morphological characters, we first considered whether allometric relationships differ between the sexes. Allometric patterns may provide insight into trade-offs that have been favoured by an evolutionary history of differential selection pressures acting on the sexes. Inferring adaptation from allometric patterns remains controversial (e.g. Harvey & Pagel 1991), however, particularly in intraspecific analyses such as ours. Factors such as age, environmental and genetic differences between individuals can influence the relative growth rates of both body size and morphological characters. Information concerning the specific costs and benefits of trait development in the sexes, as well as the form of selection operating (e.g. mate competition or mate choice on males), must come from additional sources (e.g. Green 1992; Petrie 1992) that reconcile trait expression with current performance. To accomplish this, we conducted breeding trials to assess the relationship between male morphology and several reproductive behaviours. We hypothesized that some male behaviour patterns are influenced more by mate competition than by mate choice (e.g. female encounter rates, spermatophore deposition rates and interference rates). Other behaviour patterns, such as a male's rate of sperm transfer, could be influenced by one or both sexual selection components: more by mate competition if a male's sperm transfer rate is solely a reflection of his overall rate of spermatophore deposition; more by mate choice if a male's sperm transfer rate is related more to some aspect of his phenotype than to his overall spermatophore deposition rate. Other behaviour patterns are assumed to indicate mate choice more than mate competition; for example, if females abandon courting males (possible mate rejection) or attempt to pick up their sperm masses (possible mate choice). We examined the overall effect of male trait variation on the two forms of sexual interference observed (displacement and female mimicry) as well as whether an intruder's interference tactic depends on his size relative to that of the courting male. In

these interactions, displacement occurred when the intruder shoved the female away from the courting male; female mimicry occurred when the intruding male performed female behaviours to the courting male while simultaneously courting the female (Arnold 1976).

Our breeding trials provide a novel way to assess mate choice. Males in the trials spanned the range of body sizes observed in our study pond, and each female had free access to 12 males, with multiple encounters possible with each male. We monitored all male–female encounters; as a result, we could specify the distribution of trait values of males encountered for each mating female and determine whether the ‘chosen’ male differed from this average trait value. Such a protocol provides a sensitive way to detect non-random mating due to mate choice, in the absence of pair-wise mate choice trials.

MATERIALS AND METHODS

Study Organism

Tiger salamanders are distributed throughout most of the central two-thirds of the United States and parts of southern Canada, and consist of several subspecies (Conant & Collins 1991). Breeding occurs in early spring in ephemeral habitats and in permanent ponds that lack fish (Minton 1972; Conant & Collins 1991). The breeding season is short, typically lasting about 1 week in our study population, and the overall sex ratio of breeders is highly male-biased with about five males to every female. Our population contained a minimum of 100–200 individuals during each year of the study.

Study Site

Our study site was a 1.5-ha temporary pond in an approximately 3.5-ha second-growth woodlot 5 km west of West Lafayette, Indiana, U.S.A. Woods bordered three sides of the pond and an agricultural field bordered the fourth. During the study, the pond reached its maximum depth (0.5 m) in mid-February to mid-March as a result of snow melt and spring rains. The pond was located in the floodplain of the Wabash River, and heavy spring rains flooded the entire area between the pond and river in some years.

The pond usually dried completely by late June. Several anuran species and one another salamander species, *A. texanum*, also bred in the study pond.

Collection Techniques

We collected individuals in mid-February to mid-March (1991–1993), either on land as they migrated to the pond from terrestrial overwintering sites or in the pond. All individuals used in breeding trials were collected using an aluminium-flashing drift fence with pit-fall traps that we installed in the wooded area about 15 m from the pond edge. This capture method ensured that females would not be inseminated prior to use in trials. Some individuals also were collected in the pond using minnow traps, dip nets or by hand to obtain additional morphological data. Males and females used in trials were housed separately in 40-litre aquaria containing moistened leaf litter in a refrigerator at 5°C. All salamanders were released within 72 h of the conclusion of trials.

We measured body length (distance between the snout and posterior end of the vent), tail height and total length (all to within 1 mm), and weighed all individuals (to within 0.1 g). Both body length and total length were measured with a standard metric ruler; we measured tail length by subtracting body length from total length. Tail height was measured using dial or digital calipers just distal to the cloaca where tail height was maximal. Sample sizes reported below vary slightly because we neglected to measure tail height for two males. Data on body mass were obtained using Mettler PL-3000 and Ohaus GA 110 balances. All individuals were permanently marked with unique toe clips prior to release.

Experimental Design

We conducted three replicate breeding trials during 1993 using 2-m diameter polyethylene cattle-watering tanks as breeding arenas. The tanks were filled with well water to 15 cm. All trials were performed outdoors at Purdue University’s Ross Biological Reserve to maintain natural temperatures and photoperiods. Because we could discern no effects of light on mating activity, we ran trials both at night and during the day. For night trials, incandescent light was used

to observe animals. Water temperature varied from 7 to 10°C in the trials, similar to the temperature range measured in our study pond.

Each trial involved 6 females and 12 males. The females were of various sizes. We selected three males from each of four body length categories (<98 mm, 98–102 mm, 103–107 mm and >107 mm). These categories represent the quartiles of the 1991 and 1992 male size distribution. Each individual was only used in one trial. To identify individuals during the trials, we placed a rubber band with a numbered tag on each animal just anterior to the hind limbs. Bands had no apparent effect on behaviour. Trials ended when all breeding activity had ceased (approximately 4 h).

We continuously recorded all behaviours on cassette tape and later transcribed tapes for analysis. We report data on six of the eight behavioural categories described by Arnold (1976): (1) female encounter (male touching a female with its head), (2) shoving (male pushing a female by butting the female with his snout and swimming vigorously; the distance that a female is shoved can vary from a few centimetres to more than a metre), (3) tail-tapping (male repeatedly raising and lowering his tail while stationary and in front of the female; usually the ventral surface of the male's tail contacts the female's head and dorsum), (4) spermatophore deposition (depositing a spermatophore on the substrate, usually performed when the female is immediately behind the male's cloaca), (5) sperm transfer to a female (female walks over the deposited spermatophore and picks up the sperm mass with her cloaca) and (6) courtship interruption. Two types of courtship interruptions were noted: when an intruding male shoved the female away from the courting male and when the intruding male adopted female mimicry behaviour (Arnold 1976). In the latter case, the intruder positioned itself between the courting pair, then responded as a female would to the courting male (female follow nudge behaviour; Arnold 1976) while simultaneously courting (tail-tapping) the female.

Statistical Analyses

All statistical analyses were performed using the SYSTAT statistical package (Wilkinson 1990). Parametric tests (e.g. regression, analysis of covariance) were used provided assumptions were

not violated; if assumptions could not be met despite transformations, we used an appropriate non-parametric test and report median and range values rather than means and standard deviations.

To examine sex differences in morphological characters, we pooled data from all 3 years because between-year differences were minimal ($P > 0.05$). We did not analyse data from recaptured individuals to avoid pseudoreplication, but we did use these data to examine yearly growth patterns in morphological traits. To evaluate relationships between tail characteristics and body mass, we used reduced major axis regression (e.g. Harvey & Pagel 1991). We log-transformed all variables and tested for allometry by determining whether the 95% confidence interval of regression coefficients excluded 1.0. We tested for sex differences in slope and intercept in these relationships using procedures outlined in Steel & Torrie (1960).

To obtain a mass-based measure of body condition for each male, we obtained residuals after regressing the cube root of mass against body length, and expressed these residuals relative to body length to obtain a 'condition index' (Baker 1992). Because tail length and tail height were both significantly correlated with body length ($R^2 = 0.43$, $P < 0.001$, $N = 273$; $R^2 = 0.50$, $P < 0.001$, $N = 275$, respectively), we removed the effects of body length on each tail measure by obtaining residual values for each male by regressing each variable against body length.

The six behaviour patterns described above and the percentage of interruptions involving female mimicry were regressed against each of the four male morphological traits (body length, condition index, residual tail height and residual tail length). In these analyses, we sought to determine whether individual differences in behaviour patterns depend on morphology. Thus, we considered a single male as a sampling unit and trials as blocks. We expressed behavioural data for each male as a rate (i.e. number of times observed per hour for each individual). We tested whether the 36 males from all three trials could be pooled in analyses (i.e. whether there was no block effect) by comparing the separate regression lines for the three trials following the procedure outlined in Zar (1984, page 293) with an analysis of covariance. This procedure first tested for differences in slopes between trials, then for differences in intercepts. We executed 28 ANCOVAs, one for

each combination of behaviour pattern and morphological trait. In all analyses, the interaction between male morphological trait and trial was non-significant (all $F_s < 2.14$; all $P_s > 0.14$), indicating that use of a common regression slope for the three trials was justified. We found significant differences in intercept between trials in about half of the analyses (13 of the 28), indicating that overall rates of some behaviour patterns differed between trials. To simplify presentation of results, we report the partial R^2 between behaviour and male trait for all analyses, thereby adjusting for the effect of trials regardless of whether intercepts differed between trials. To adjust for multiple testing in these regressions, we used the sequential Bonferroni test, using 0.05 as our 'overall' significance level for each trait (Rice 1989). We report P -values and relevant alpha values for comparison.

We used a paired t -test to examine morphological differences between courting and interrupting males. Separate analyses were performed for interruptions involving female shoving and female mimicry, and for each analysis we included only pairs involving the same males once in the dataset.

We tested for female mate choice by determining whether male morphology influenced either female rejection of males (females leaving during some stage of courtship) or female selection of males (courtships in which females picked up or attempted to pick up a deposited sperm mass). In the latter analysis, we used a sign test to determine whether selected males exceeded expected values for each of three morphological traits (body length, tail height and tail length). We obtained expected values for each female by calculating the average male trait value using data from all of her male encounters. A female commonly encountered the same male multiple times during a trial; as a result, we based the expected value of each male trait on all male encounters involving the female rather than on just the males that were encountered at least once. Although this criterion involves pseudoreplication of the males involved, it also provides a more conservative test of mate choice. Females are encountered by larger males more often than smaller males; hence, the expected male trait value based on all encounters is always higher if based on encounters rather than just on males. In addition, we defined a tie as any selected male that was within 2 mm of the

expected value of encountered males. We included in these analyses all interactions in which sperm transfer was attempted because female mating preferences were clearly evident in these situations.

RESULTS

Morphological Trends

Males had slightly longer bodies than females (mean \pm SD = 103.32 \pm 7.24 mm, $N=275$; 100.98 \pm 7.72 mm, $N=79$, respectively; $t=2.50$, $P=0.013$). Similarly, relative to females, males had higher tails (median for males = 17.24 mm, range = 10.92–24.29 mm, $N=273$; median for females = 14.62 mm, range = 11.03–19.22 mm, $N=79$; Mann-Whitney U -test: $U=18031$, $P<0.001$), and longer tails (males = 104.40 \pm 13.94 mm, $N=275$; females = 85.28 \pm 11.77 mm, $N=79$; $t_{352}=11.01$, $P<0.001$). Both tail measures showed significant allometry in males and females. A reduced major axis (RMA) regression analysis of tail height estimated the male slope to be 1.85 (95% CI = 1.66–2.03) and the female slope to be 1.55 (95% CI = 1.26–1.85; Fig. 1a); for tail length, the male slope was 2.50 (95% CI = 2.21–2.78) and the female slope was 1.83 (95% CI = 1.61–2.05; Fig. 1b). The slopes for both the tail height and tail length allometries were similar between the sexes ($t_{348}=0.68$, $P=0.32$; $t_{350}=1.24$, $P=0.19$, respectively), but the intercepts differed for each relationship ($t_{349}=2.23$, $P<0.03$; $t_{349}=3.46$, $P<0.001$, respectively). Body mass was isometric for both males and gravid females (male slope based on RMA of log cube root of body mass versus log body length: 1.04 (95% CI = 0.98–1.09); for females, the slope was 1.09 (95% CI = 0.95–1.24).

The condition index was positively correlated with both residual tail height ($r=0.43$, $N=273$, $P<0.001$) and residual tail length ($r=0.40$, $N=275$, $P<0.001$). The similarity of these relationships is influenced by the strong correlation between tail height and tail length ($r=0.64$, $N=272$, $P<0.001$) that persisted even after examining residuals (with respect to body length) of the two variables ($r=0.28$, $N=272$, $P<0.001$). Tail heights of 25 recaptured males were only weakly correlated between years ($R^2=0.16$, $P=0.05$), and condition index values were uncorrelated ($R^2=0.13$, $P=0.08$); however, tail lengths were

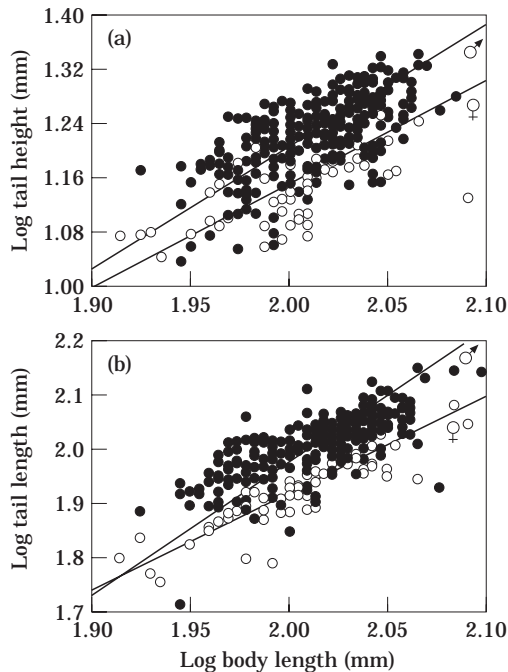


Figure 1. Reduced major axis regression analyses testing for allometry within and between the sexes in (a) tail height and (b) tail length. ●, Males; ○, females.

strongly correlated between years ($R^2=0.61$, $P<0.001$).

Behavioural Observations

We observed 1825 encounters between males and females in the three trials (Fig. 2). Most encounters (1147/1825 or 63%) ended during some courtship phase because males either lost contact with females or stopped courting; the remaining interactions either ended because of interruptions by rival males or rejection by females; only 1% of the encounters resulted in sperm transfer (Fig. 2). We never observed males depositing spermatophores on top of previously deposited spermatophores, as reported by Arnold (1976).

Overall, spermatophore deposition was relatively rare, occurring in only 4.5% of observed encounters. In these 83 encounters, typically one spermatophore was deposited (74 of 83 encounters or 89%); in six encounters, two spermatophores were deposited; in three cases, more than two spermatophores (three, four and five, respectively) were deposited. In some cases,

spermatophore deposition did not occur during courtship because courting males lost contact with their females or abandoned them, rather than being rejected by females or disrupted by interfering males.

Sperm transfer occurred (or was attempted) for 28 of the 98 deposited spermatophores (29%), and involved 15 of the 18 females. Ten of these females (67%) were involved in only one sperm transfer; two females were involved in two sperm transfers; and three were involved in more than two (three, four and seven, respectively).

Male-Male Competition

Males with longer bodies had higher rates of female encounters; male residual tail height (log transformed), residual tail length and condition index were not correlated with encounter rate (Table I). Shoving rate and rate of spermatophore deposition also increased with male body length, but were unrelated to both residual tail measures and to the condition index (Table I). Rate of tail-tapping was not related to body length or to the other three male characters (Table I).

Males with longer bodies interrupted courting pairs more frequently; however, interruption rates were unrelated to the other three male morphological traits (Table I). The percentage of interruptions involving female mimicking behaviour declined linearly with the body length of the intruding male, and was unrelated to the other three male characters (Table I). When an interruption involved female shoving behaviour by the intruding male, the intruder had a longer body length than the courting male (paired $t_{151}=3.08$, $P<0.002$); when female mimicking occurred, the intruder was smaller than the courting male (paired $t_{38}=2.63$, $P=0.012$). No differences between courting and intruding males existed for the other three male characters (all $P>0.70$).

Males varied considerably in the number of successful or attempted sperm transfers. Thirty of the 36 males deposited at least one spermatophore. For the 30 males, their rate of spermatophore transfer was positively related to their spermatophore deposition rate ($R^2=0.20$, $P=0.014$), but unrelated to their body length, residual tail length or condition index (all $R^2<0.09$, $P<0.10$). Similarly, the ratio of sperm transfer events to spermatophores deposited was

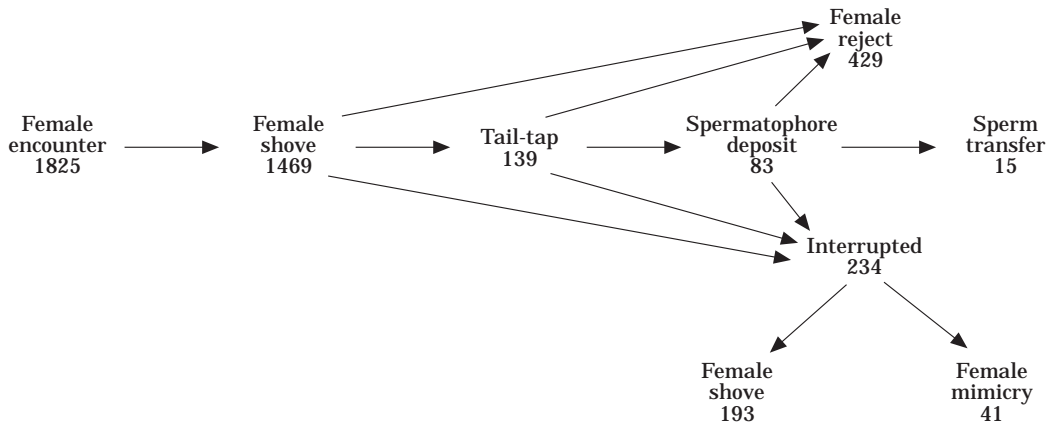


Figure 2. Summary of observations of reproductive behaviours observed during breeding trials. Numbers below each activity indicate the number of encounters in which at least one of the behaviours was performed. Data were pooled from all three breeding trials.

not related to any male trait measured (all $R^2 < 0.10$, $P > 0.08$).

Female Mate Choice

Female rejection of courting males occurred at all stages of male courtship in the 1825 encounters. Females left or showed no response during 317 of the 2164 times that they were shoved by males (14.6%), 9 of the 146 times that males performed the tail-tapping display (6.2%) and 16 of the 98 times that males deposited a spermatophore (16.3%). The percentage all male–female encounters that ended with female rejection was unrelated to all the male morphological characters examined (Table I).

Female rejection of courting males after spermatophore deposition was random with respect to male morphology. Rejected males did not differ, on average, from other males in the same trial in any of the four morphological traits measured (t -tests; all $t_{49} < 1.61$, $P > 0.11$). Thirteen females were involved in at least one sperm transfer event and had multiple male encounters (210.08 ± 153.43 ; range = 110–677). Tail length was the only male trait that distinguished males with successful or attempted sperm transfers from the average male encountered (sign test; $P = 0.02$; Fig. 3a). Chosen males did not differ from average encountered males in either body length (sign test; $P = 0.08$; Fig. 3b), tail height (sign test; $P = 0.83$; Fig. 3c), or number of spermatophores deposited (sign test; $P = 0.41$).

DISCUSSION

The influence of mate competition and mate choice differed for the three sexually dimorphic traits we considered in *A. tigrinum*. Longer body length in males provided advantages in many aspects of mate competition, but was not influenced by mate choice. In contrast, longer tail length in males was influenced by mate choice, but provided no advantages in mate competition. Higher tails in males was unrelated to both mate competition and mate choice.

The processes of mate choice and mate competition may commonly interact to influence the evolutionary maintenance of secondary sexual traits in organisms, and such interactions may occur at both the ultimate (evolutionary) or proximate (mechanistic) levels. The complexity of such interactions may impede assessment of the relative contribution of each sexual selection component to trait evolution. Mate choice and mate competition often, but not always, favour the same male trait expression (see Table 6.A in Andersson 1994), an understandable outcome at the ultimate level of analysis. When males contribute directly or indirectly to female reproductive success (Kirkpatrick & Ryan 1991), females should be favoured to base their mating decisions on male phenotypic characteristics that determine superiority in mate competition. In contrast, if females base mate choice on ‘arbitrary’ male traits (Heisler 1985), preferred male traits need not also influence success in mate competition. By definition,

Table I. Relationships between male morphological characters and rates of mate competition behaviours

	Partial R^2	P	α^*
Body length and rate of:			
Female encounter	0.23	0.001	0.010
Shoving	0.29	0.001	0.008
Tail-tapping	0.10	0.047	0.025
Spermatophore deposition	0.12	0.016	0.017
Interruption	0.31	<0.001	0.007
% Female mimicry	0.20	0.008	0.013
% Rejection	0.01	0.682	0.050
Residual tail height and rate of:			
Female encounter	0.07	0.090	0.008
Shoving	0.06	0.163	0.010
Tail-tapping	0.00	0.935	0.050
Spermatophore deposition	0.06	0.117	0.013
Interruption	0.02	0.346	0.025
% Female mimicry	0.04	0.284	0.017
% Rejection	0.07	0.071	0.007
Residual tail length and rate of:			
Female encounter	0.01	0.582	0.013
Shoving	0.01	0.672	0.025
Tail-tapping	0.01	0.635	0.017
Spermatophore deposition	0.01	0.517	0.010
Interruption	0.00	0.904	0.050
% Female mimicry	0.04	0.234	0.008
% Rejection	0.06	0.087	0.007
Body condition and rate of:			
Female encounter	0.01	0.485	0.010
Shoving	0.01	0.632	0.025
Tail-tapping	0.01	0.504	0.013
Spermatophore deposition	0.01	0.420	0.008
Interruption	0.00	0.851	0.050
% Female mimicry	0.02	0.385	0.007
% Rejection	0.01	0.529	0.017

* α based on sequential Bonferroni test.

preferred male traits are random with respect to female fitness (Lande 1981).

At the proximate level, complications exist because mate competition may pre-empt mate choice if one or a few males dominate access to mating females and thus prevent females from assessing or choosing mates. For females in nature, male interference may limit mate choice to situations in which the intensity of mate competition is low (e.g. Borgia 1981). If mate competition and mate choice favour different male traits, then selection for mate discrimination in females as well as for the male traits they prefer may be weak.

In addition, mate choice always involves some form of assessment; mate competition need not. As a result, the types of male traits included in

mate choice may be a consequence of how well females can discriminate between males that differ in trait expression. For example, analyses of female preference for male vocal attributes in anurans indicate that females can resolve only gross differences in the spectral features of male calls (Gerhardt 1994) despite considerable variation between males. In contrast, other call properties that may be resolved more easily, such as call rate and call duration, are often used in mate choice (Gerhardt 1994). Whether the latter cues are better indicators of male genetic or competitive quality or just more distinguishable characteristics is unclear.

Urodeles such as tiger salamanders provide opportunities to minimize some potential complications involved in evaluating the relative effects

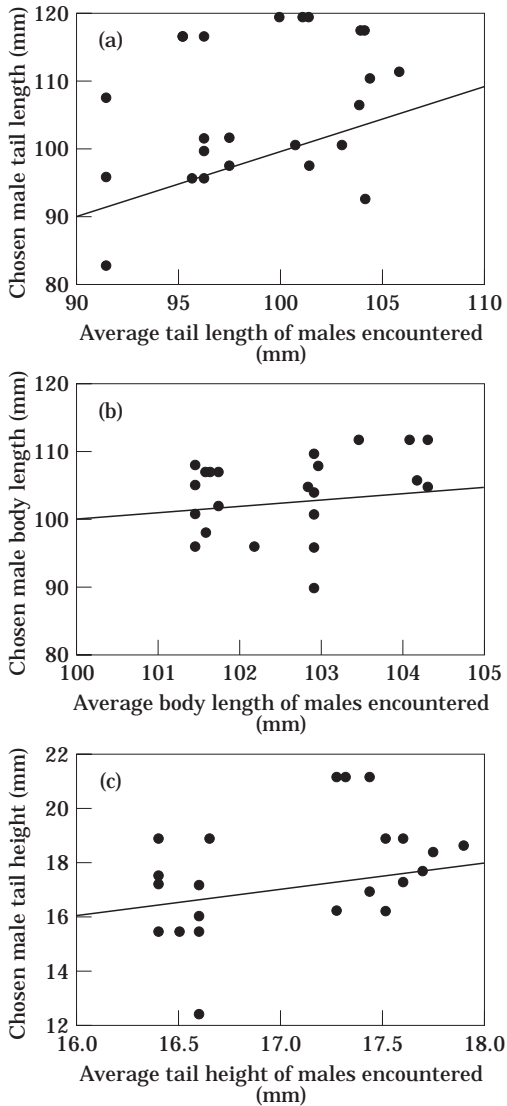


Figure 3. Morphological characteristics of 'chosen' males relative to the average trait expression of all males encountered by each female for (a) tail length, (b) body length and (c) tail height. Each point represents an interaction between a male and female in which a sperm transfer occurred or was attempted. The line refers to equality in 'chosen' male and average trait expression of encountered males. Symbols above line represent 'chosen' males that exceed average trait values, those below the line are the reverse.

of mate competition and mate choice on male trait evolution. Male traits affected by mate choice are likely to be either 'indicator traits' of male genetic

quality (Borgia 1985; Andersson 1994) or arbitrary traits because males do not control resources that affect female reproductive success. As a result, male traits that determine success in mate competition may differ from those influenced by mate choice. Although mate competition could impede choice at a proximate level, the indirect form of sperm transfer in urodeles increases the opportunity for mate choice even with intense mate competition because females cannot be forced to pick up spermatophores. In addition, the types of mate competition that occur in tiger salamanders, sexual defence (shoving females away from potential competitors) and sexual interference (depositing spermatophores on top of those laid by competitors) need not involve males assessing other males because combat is never involved. In contrast, mate choice by females must involve assessment. As a result, limitations of trait assessment mechanisms could also result in traits favoured by mate choice to differ from those selected by mate competition. To evaluate the effect of each component of sexual selection on male tiger salamanders, we first consider patterns of morphological differences between the sexes and then the processes that could have produced these patterns.

Morphological Trends

Urodele amphibians are sexually dimorphic in several traits; however, the role of mate competition and mate choice in the elaboration of these traits in males remains to be determined for almost all species (Verrell 1989a). Male and female *A. tigrinum* differed, on average, in all three morphological characters that we measured. Males had slightly longer bodies, greater tail heights and longer tails than females. All three traits were positively correlated with each other, and each could be positively related to reproductive success in both sexes.

We could not evaluate how current selection intensities on the three morphological characters differed between males and females, because data were lacking on how each trait was related to reproductive success (i.e. selection gradients; Arnold & Wade 1984; Arak 1988; Howard 1988) for either one or both sexes. Thus, we used allometric analyses to infer how past selection influenced tail characteristics in the sexes and breeding trials to evaluate how male body length

and residual tail dimensions influenced current success in mate competition and mate choice.

In a review of amphibian body size dimorphism, Shine (1979) reported that females are larger than males in 61% of the urodele species investigated, and suggested that species characterized by male combat are typically the exceptions to the general pattern of 'reverse' dimorphism (but see Halliday & Verrell 1986). We never observed male combat in *A. tigrinum* (see also Arnold 1976); thus, this form of mate competition did not explain the slight body size dimorphism that we observed. Male size did influence success in other forms of male-male interference behaviour. The degree to which such success translates into reproductive success was not evident in our breeding trials, however (see below), and merits further investigation. In contrast, large body size conferred an observable reproductive advantage for females in our population. As in many urodele species (e.g. Kaplan & Salthe 1979), larger females produced larger clutches ($R^2=0.60$, $P=0.007$, $N=12$ females; both variables log-transformed).

Arnold (1976, page 264) initially reported that male *A. tigrinum* have higher and longer tails than females and noted that these structural modifications of the male's tail in *A. tigrinum* are undoubtedly related to its use in the tail-nudging walk and in shoving the female. The degree of sexual dimorphism in tail length in our populations was much greater than that in body size or tail height. Tail dimensions are also sexually dimorphic in other salamander species, particularly in newts (e.g. Halliday 1975b; Raxworthy 1989) where they serve to enhance both visual and olfactory aspects of male courtship displays (Halliday 1990).

Tail length and tail height were allometric traits in both male and female *A. tigrinum*, as was also true in *T. vulgaris* (Green 1992). For each trait in *A. tigrinum*, the slopes for males and females were similar when regressed against body length; however, the intercepts of both regression relationships were significantly higher in males than in females. Such differences in intercept might result from an early ontogenetic divergence between the sexes in the onset of growth in each tail dimension as a result of a sex-specific difference in some trade-off (e.g. differential energy allocation to gamete production or gonadal structures in the sexes) prior to sexual maturation or a differential selection pressure on the sexes (e.g. intense sexual

selection to increase male trait expression) at or after sexual maturation. Distinguishing between these alternatives requires data on the growth trajectories of each sex during ontogeny and is currently under investigation.

Mate Competition

The low overall rate of spermatophore deposition in our study (only 98 spermatophores deposited by 30 of the 36 males during 4 h observation periods) was similar to that observed by Arnold (1976) under conditions of high mate competition and was almost certainly affected by our use of enclosures in the breeding trials.

Larger male body size provided advantages in almost every aspect of mate competition. Larger males had more encounters with females, shoved females more often to initiate courtship, deposited spermatophores more often and interrupted other courting males more often. Similar size-related advantages in mate competition have been suggested to occur in the newt *Taricha granulosa* (Janzen & Brodie 1989). In *A. tigrinum*, the tactic used by an interrupting male was conditional on the interrupter's size relative to the courting male: if the interrupter was larger, he usually shoved the female away to gain sole access to her; if the interrupter was smaller, he used female mimicry to deceive the courting male. Female mimicry was initially described in *A. tigrinum* (Arnold 1976), and appears to be a fairly common alternative mating tactic in urodeles (Verrell 1989a). The tactic is conditional in some species, however (e.g. *T. granulosa*; Janzen & Brodie 1989), but not in others (e.g. *Notophthalmus viridescens*; Massey 1988). In sum, most of the advantages of larger body size in *A. tigrinum* occurred because of greater performance levels; body size assessment by competing males was evident only in affecting the tactic used by interrupting males to gain access to courted females.

Residual tail heights did not influence any aspect of mate competition in male tiger salamanders. Support for an effect of tail height on pairing success (or mating success) in other urodeles is mixed and limited. For example, males with higher residual tail heights had greater pairing success in *T. granulosa* because of advantages in mate competition (Janzen & Brodie 1989), and greater mating success because of one or

both sexual components in *Triturus cristatus* (Malacarne & Cortassa 1983); however, paired and intruding males did not differ in tail height in *N. viridescens* (Massey 1988).

Residual tail length was also not related to any aspect of mate competition that we measured. Thus, we obtained no support for Arnold's (1976) prediction of an effect of tail length variation in female shoving or other aspects of courtship. We measured only rates of behaviour patterns, however, not performance levels (e.g. distances that females were shoved). Thus, residual tail length still could have some role in mate competition in addition to its influence on mate choice as discussed below.

Mate Choice

In our breeding trials, mate choice was determined by how male traits influence patterns of mate rejection and sperm transfer to females. Mate choice also could have been ascertained by the degree to which each female distinguished mating males from all encountered males. Unfortunately, mate rejection rates did not provide a sensitive method to detect mate choice with our protocol. Most females encountered each male multiple times; as a result, even mating males were often rejected. Thus, lack of sperm transfer during a courtship might have resulted more because females were still sampling for potential mates than rejecting them. Differences between males in the sperm transfer rates may also provide little insight into mate choice because they may be a function of spermatophore deposition rates by males as well as mate choice by females. That is, some males might have had higher sperm transfer rates than others only because their spermatophore deposition rates were higher. This was true for our study; the only correlate of sperm transfer rate that we detected was spermatophore deposition rate. When the mating decisions of individual females were considered in the context of the distribution of encountered males, however, females selected mates with longer than average tail lengths, even though these males did not deposit more spermatophores than other encountered males did, on average. These results support the prediction by Arnold (1976) that male tail length is a sexually selected character. Whether male tail length is an indicator trait or an arbitrary trait is unknown. Both residual tail length and

residual tail height were correlated with the condition index, but the degree to which either tail measure or the condition index was related to male genetic quality remains to be determined. At the proximate level, females may be able to assess male tail length better than male tail height or body length because males stroke females with their entire tail during the tail-tapping phase of courtship. Given the typically low visibility in natural breeding habitats, tactile and pheromonal cues may be used more than visual ones.

ACKNOWLEDGMENTS

We are indebted to G. Borgia, M. Brown, J. Lucas, S. Howard, P. Verrell and P. Waser for their comments and help on earlier versions of this manuscript. We thank two anonymous referees and P. L. Schwagmeyer for their diligence and thoughtful comments. We thank N. Hilliard, John Gutrich, J. Hale, T. May, R. Pingel and K. Whitten for field assistance. We also thank Dr J. Barany for generously allowing us to use his pond as our study site. This research was supported by grants from the Indiana Academy of Science, Animal Behavior Society, Purdue University Research Foundation and National Science Foundation grants BSR-89-58253 and IBN-93-18099. Manuscript preparation was supported in part by contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

REFERENCES

- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arak, A. 1988. Sexual dimorphism in body size: a model and a test. *Evolution*, **42**, 820-825.
- Arnold, S. J. 1976. Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. *Z. Tierpsychol.*, **42**, 247-300.
- Arnold, S. J. 1977. The evolution of courtship behavior in New World salamanders with some comments on Old World salamandrids. In: *The Reproductive Biology of Amphibians* (Ed. by D. H. Taylor & S. I. Guttman), pp. 141-183, New York: Plenum Press.
- Arnold, S. J. & Wade, M. J. 1984. On the measurement of natural and sexual selection: theory. *Evolution*, **38**, 709-719.

- Baker, J. M. R. 1992. Body condition and tail height in great crested newts, *Triturus cristatus*. *Anim. Behav.*, **43**, 157–159.
- Borgia, G. 1981. Mate selection in the fly *Scatophaga stercoraria*: female choice in a male-controlled system. *Anim. Behav.*, **29**, 71–80.
- Borgia, G. 1985. Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behav. Ecol. Sociobiol.*, **18**, 91–100.
- Bradbury, J. W. & Davies, N. B. 1987. Relative roles of intra- and intersexual selection. In: *Dahlem Workshop on Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 143–163. Chichester: John Wiley.
- Clutton-Brock, T. H. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.*, **67**, 437–456.
- Conant, R. & Collins, J. T. 1991. *A Field Guide to Reptiles and Amphibians of Eastern/Central North America*. 3rd edn. Boston: Houghton Mifflin.
- Evans, M. R. & Hatchwell, B. J. 1992a. An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. the role of pectoral tufts in territorial defence. *Behav. Ecol. Sociobiol.*, **29**, 413–419.
- Evans, M. R. & Hatchwell, B. J. 1992b. An experimental study of male adornment in the scarlet-tufted malachite sunbird: II. the role of the elongated tail in mate choice and experimental evidence for a handicap. *Behav. Ecol. Sociobiol.*, **29**, 421–427.
- Gerhardt, H. C. 1994. The evolution of vocalization in frogs and toads. *A. Rev. Ecol. Syst.*, **25**, 293–324.
- Green, A. J. 1992. Positive allometry is likely with mate choice, competitive display and other functions. *Anim. Behav.*, **43**, 170–172.
- Halliday, T. R. 1975a. An observational and experimental study of sexual behaviour in the smooth newt, *Triturus vulgaris* (Amphibia: Salamandridae). *Anim. Behav.*, **23**, 291–322.
- Halliday, T. R. 1975b. On the biological significance of certain morphological characteristics in males of the smooth newt *Triturus vulgaris* and of the palmate newt *Triturus helveticus* (Urodela: Salamandridae). *Zool. J. Linn. Soc.*, **56**, 291–300.
- Halliday, T. R. 1990. The evolution of courtship behavior in newts and salamanders. *Adv. Study Behav.*, **19**, 137–169.
- Halliday, T. R. & Verrell, P. A. 1984. Sperm competition in amphibians. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 487–508. New York: Academic Press.
- Halliday, T. R. & Verrell, P. A. 1986. Review: sexual selection and body size in amphibians. *Herpetol. J.*, **1**, 86–92.
- Heisler, I. L. 1985. Quantitative genetic models of female choice based on 'arbitrary' male characters. *Heredity*, **55**, 187–198.
- Harvey, P. H. & Pagel, M. D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Houck, L. D. 1988. The effect of body size on male courtship success in a plethodontid salamander. *Anim. Behav.*, **36**, 837–842.
- Houck, L. D., Tilley, S. G. & Arnold, S. J. 1985a. Sperm competition in a plethodontid salamander: preliminary results. *J. Herpetol.*, **19**, 420–423.
- Houck, L. D., Arnold, S. J. & Thisted, R. A. 1985b. A statistical study of mate choice: sexual selection in a plethodontid salamander (*Desmognathus ochrophaeus*). *Evolution*, **39**, 370–386.
- Howard, R. D. 1988. Reproductive success in two species of anurans. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed. by T. H. Clutton-Brock), pp. 99–113. Chicago: The University of Chicago Press.
- Kaplan, R. H. & Salthe, S. N. 1979. The allometry of reproduction: an empirical view in salamanders. *Am. Nat.*, **113**, 671–689.
- Kirkpatrick, M. & Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature, Lond.*, **350**, 33–38.
- Janzen, F. J. & Brodie, E. D. III 1989. Tall tails and sexy males: sexual behavior of rough-skinned newts (*Taricha granulosa*) in a natural breeding pond. *Copeia*, **1989**, 1068–1071.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. natn. Acad. Sci. U.S.A.*, **78**, 3721–3725.
- Malacarne, G. & Cortassa, R. 1983. Sexual selection in the crested newt. *Anim. Behav.*, **31**, 1256–1264.
- Massey, A. 1988. Sexual interactions in red-spotted newt populations. *Anim. Behav.*, **36**, 205–210.
- Minton, S. A. 1972. *Amphibians and Reptiles of Indiana*. Indiana Academy of Science Monograph No. 3. Indianapolis: Indiana Academy of Science.
- Nussbaum, R. A. 1985. The evolution of parental care in salamanders. *Misc. Publs Mus. Zool. Univ. Mich.*, **169**, 1–50.
- Petrie, M. 1992. Are all secondary sexual display structures positively allometric and, if so, why? *Anim. Behav.*, **43**, 173–175.
- Raxworthy, C. J. 1989. Courtship, fighting, and sexual dimorphism of the banded newt, *Triturus vittatus ophryticus*. *Ethology*, **81**, 148–170.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Shine, R. 1979. Sexual selection and sexual dimorphism in the amphibia. *Copeia*, **1979**, 297–306.
- Steel, R. G. D. & Torrie, J. H. 1960. *Principles and Procedures of Statistics*. New York: McGraw-Hill.
- Verrell, P. A. 1984. Sexual interference and sexual defense in the smooth newt, *Triturus vulgaris* (Amphibia: Urodela: Salamandridae). *Z. Tierpsychol.*, **66**, 242–254.
- Verrell, P. A. 1989a. The sexual strategies of natural populations of newts and salamanders. *Herpetology*, **45**, 265–281.
- Verrell, P. A. 1989b. Male mate choice for fecund females in a plethodontid salamander. *Anim. Behav.*, **38**, 1086–1088.
- Wilkinson, L. 1990. *SYSTAT: The System for Statistics*. Evanston, Illinois: SYSTAT.
- Zar, J. H. 1984. *Biostatistical Analysis*. 2nd edn. Englewood Cliffs, New Jersey: Prentice-Hall.