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COURTSHIP BEHAVIOR OF THE SMALL-MOUTHED SALAMANDER (AMBYSTOMA TEXANUM): THE EFFECTS OF CONSPECIFIC MALES ON MALE MATING TACTICS

by

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(With 2 Figures)

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Summary

1. The courtship behavior of *A. texanum* consisted of a rapid nudging period followed by males producing many spermatophores, some of which were picked up by the female. Neither amplexus or leading by the male were integral components of courtship. Consequently, proposed geographic variation in *A. texanum* courtship remains unsubstantiated.
2. Courtship behavior of *A. texanum* and *A. barbouri* (formerly pond and stream form *A. texanum*, respectively) is very similar; only the location of courtship and perhaps the frequency of sexual interference tactics are different for these two sibling species.
3. *A. texanum* courtship is rapid, males produce large numbers of spermatophores per courtship and invest little courtship time per spermatophore, and intermale competition is extreme.
4. Male *A. texanum* promote their sexual success using sexual interference behavior (*e.g.* covering other spermatophores with their own) and to a lesser degree sexual defense behavior (*e.g.* forcefully nudging rival males).
5. Male sexual success is primarily enhanced directly — *A. texanum* males increase the number of spermatophores produced when at least two other males are courting the same female. The temporal allocation of these additional spermatophores is adaptive only if males are maximizing the number of ejaculates per female or breeding typically occurs in polygamous aggregations.

Introduction

Intrasexual selection results when individuals of the same sex can increase their fitness by competing for more or better mates (DARWIN, 1871).

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Because it is the relative fitness of an individual which is important in natural and sexual selection, increases in individual fitness can occur when the absolute reproductive success of an individual is increased or when a competitor's success is decreased. Males can promote their reproductive success by interfering with rival males (ARNOLD, 1972; VERRELL, 1989), defending receptive females (ARNOLD, 1972; VERRELL, 1989), or by adopting alternative strategies of sexual resource allocation (PARTRIDGE & HALLIDAY, 1984).

Quantification of sexual resources and their allocation in ambystomatid salamanders is simplified compared to many other vertebrates because males and females provide no parental care, typically leaving breeding ponds soon after mating and egg laying (DUELLMAN & TRUEB, 1986). In addition, all *Ambystoma* have internal fertilization but transfer sperm indirectly via spermatophores. Consequently, allocation of the majority of a male's sexual resources is readily quantifiable by counting the number of spermatophores and recording when they are deposited.

The primary objective of this study was to experimentally investigate how numbers of rival males affect sexual resource allocation strategies of the small-mouthed salamander (*Ambystoma texanum*). Salamander sexual interference tactics include placing their own spermatophores on top of rival males producing "multiple spermatophores" and mimicking female behavior so that rival males deposit their spermatophores in locations where females have little chance of locating them (ARNOLD, 1976; HALLIDAY, 1990). Salamander sexual defense tactics include actively defending females by biting and chasing rival males or isolating a female by moving her away from rival males. The sexual resources of male salamanders are limited within a breeding season (ADAMS, 1940; ARNOLD, 1976; HALLIDAY, 1976). Thus, the distribution of male sexual resources during a breeding season is an important determinant of male reproductive success.

The second objective of this study involved resolving a controversy concerning the type of courtship behavior characteristics of *A. texanum*. *A. texanum* reportedly exhibits intraspecific variation in courtship behavior (ARNOLD, 1977) and also alternative mating and life history strategies between different ecological morphs with similar courtship behavior (PETRANKA, 1982a, 1984). Five descriptions of *A. texanum* courtship have been published. WYMAN (1971), studying populations from north-central Illinois, found males performed amplexus and leading behavior and extensively nudged females during courtship. In contrast, GARTON (1972), and LABANICK & DAVIS (1978), studying populations from southern Illinois, found no amplexus or leading. Instead, pairs performed prolonged bouts of mutual nudging during courtship. ARNOLD (1972) and PETRANKA (1982a), studying populations from southern Michigan and cental Kentucky, respectively, observed courtship behavior similar to that observed by GARTON (1972).

Two hypotheses have been proposed concerning why WYMAN (1971) may have seen different courtship behavior: 1) introgression of *A. texanum* and *A. laterale* is known to occur (DOWNS, 1978; BOGART *et al.*, 1987) and the individuals WYMAN (1971) observed courting may have been hybrids of these two species (GARTON, 1972; ARNOLD, 1977; PETRANKA, 1982a); 2) intraspecific geographic variation in breeding habits may occur in *A. texanum* (ARNOLD, 1977).

In this paper I report quantitative descriptions of *A. texanum* courtship using animals collected from southern Iowa, the northwestern limit of *A. texanum's* geographic range (CONANT, 1975). If large scale geographic variation in courtship behavior occurs, *A. texanum* from this part of the range should have amplexus courtship behavior like that observed by WYMAN (1971).

The quantitative descriptions reported here will also enable comparisons of courtship behavior between two ecological morphs of *A. texanum* which differ in morphology, life history, and reproductive biology (PETRANKA, 1982a, 1984; KRAUS & PETRANKA, 1989). PETRANKA (1982b) categorized the population variation into two ecological forms — a stream form and a pond form. More recently, KRAUS & PETRANKA (1989) have argued that these population differences warrant sibling species status for the stream form and named this form *A. barbouri*. The salamanders used in this study are from a pond form (*A. texanum*) population.

Interspecific differences in duration of breeding season have often been invoked as primary selective forces shaping amphibian mating behavior (ARNOLD, 1976; WELLS, 1977; ARAK, 1983; VERRELL, 1989). *A. texanum* is an explosive breeder (BURGER, 1950), with immigration to breeding ponds, courtship and egg laying, and emigration occurring over a relatively short period of time (MCWILLIAMS & BACHMANN, 1988). *A. barbouri* is a nonexplosive breeder (PETRANKA, 1984) and lays larger but fewer eggs than pond form breeders (PETRANKA, 1982b). Because these two species are so recently diverged (KRAUS & PETRANKA, 1989), a comparison of these two sibling species' courtship behavior may offer insights into the rates at which different components of courtship evolve.

Methods

Salamander capture.

All 45 salamanders used in this experiment were captured on 3 or 4 February 1985 while migrating to breeding ponds at Flaming Prairie Preserve, Louisa Co., Iowa. The dates of capture, adult sex ratio, and estimated size of the entire breeding population using these flooded woodland ponds have been published elsewhere (McWilliams & Bachmann, 1988). Briefly, *Ambystoma texanum* is a synchronous migrator with males generally migrating earlier than females. The sex differences in migration make it likely that variable numbers of males and females encounter each other during courtship.

Salamanders were captured using drift fences. Only *A. texanum* salamanders were captured. Since only one other *Ambystoma* species (*A. tigrinum*) occurs in southern Iowa (Christiansen, 1981; Camper, 1988), and since sympatric populations of *A. tigrinum* and *A. texanum* do not occur at my study area, I assume the study animals are not hybrids. When a salamander was captured, its sex and weight were recorded. Then each animal was placed in its own one gallon plastic container lined with moist sand and leaf litter. On 4 February 1985, all animals were placed in an environmental chamber with a 12:12 L:D cycle and a 15°C constant temperature. All trials were completed under these conditions within 20 days after capture. The 45 salamanders used in this study and the resulting 15 clutches of eggs were returned to Flaming Prairie Preserve upon completion of the experiment.

Experimental design.

Individual females were placed in a tank with either one, two, or three males. Treatment (*i.e.*, number of males) order and subjects for each treatment were randomly selected. The resulting completely randomized design included five replicates of each treatment totalling 15 trials. Each animal was used only once so that 30 males and 15 females were used in this experiment.

Two 10 gallon aquaria with gravel substrate and 10-12 cm of dechlorinated water were used for all 15 trials. Gravel was thoroughly scrubbed and rinsed between each trial. Fresh dechlorinated water was used for each trial.

The appropriate number of males and females were then randomly selected and each salamander was weighed. When two or three males were used the tail fin of one or two males, respectively, was clipped so individuals could be identified. A red light source placed 5 m from the aquaria was the only illumination used during a trial. Red light conditions are thought to simulate night-time conditions since salamanders apparently have low sensitivity to red light (Grusser-Cornehls & Himstedt, 1976). Earlier trials revealed that no courtship occurred when fluorescent lights were used.

Males were placed in the aquaria and allowed a 30 minute acclimation period. The female was then introduced and behavior recording initiated. Using a Datamyte 1000 recorder (DataMyte Corp., Minnetonka, Minnesota) specific courtship events and the corresponding time were recorded. Four events were recorded: 1) when the female was added to the aquarium, 2) first contact between a male and the female, 3) first and subsequent spermatophores deposited and picked up by each male and the female, and 4) intermale displacements and chases. Since the Datamyte recorded the time at which each event occurred, courtship behavior could then be quantified using the phase distinctions of Salthe (1967) and Garton (1972) (Fig. 1). In addition, the number of spermatophores observed deposited on top of other spermatophores was recorded. Behavior recording ended when the last spermatophore was deposited. Observations ended 30 minutes after sexual activity had stopped.

Statistical analysis.

Because a single aquarium represented the experimental unit, data taken on individual males within the same aquaria represented repeated measures taken on the same experi-

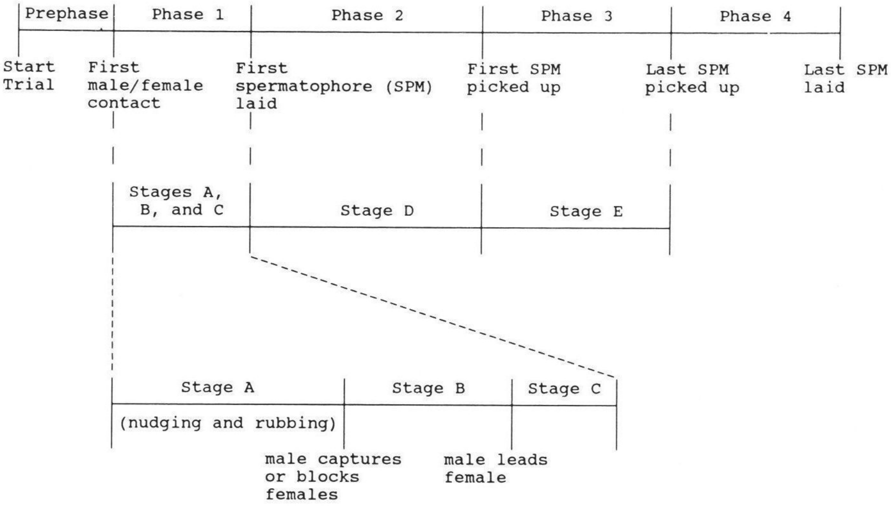

Fig. 1. Salamander courtship and its partitioning into distinct Phases or Stages of courtship. Phases and Stages are as defined by Garton (1972) and Salthe (1967), respectively. Stages D and E are not exactly comparable to Phases 2 and 3 when many spermatophores are laid and picked up during a single courtship.

mental unit. Consequently, a completely randomized design, split-plot analysis of variance (ANOVA) with conservative degrees of freedom (Snedecor & Cochran, 1980) was used to analyze these aspects of the experiment. Otherwise, a standard ANOVA model for a completely randomized design was used (Snedecor & Cochran, 1980). All values used in the ANOVA were tested for normality and homogeneity of variance and found to conform to the assumptions of ANOVA. The Waller & Duncan (1969) test was used for multiple means comparisons when significant main effects were found. Pearson product-moment correlations were used for all tests of association (SAS Institute Inc., 1985).

Results

Three trials were excluded from the analysis because at least one individual exhibited no sexual activity. Additionally, one trial was excluded because sexual activity began after the initial observation period, making counts of spermatophores deposited and picked up incomplete. Consequently, only four replicates for the one and two male treatments, and three replicates for the three male treatment were used in the statistical analysis.

A. texanum courtship behavior.

Since courtship behavior in my study was similar to that described by Arnold (1972), Garton (1972) and Petranka (1982a), no specific descriptions of courtship behavior are provided here. Generally, *A. texanum* courtship proceeded as follows: males never deposited spermatophores or exhibited any other sexual activity prior to female introduction. Initially, inter- and intrasexual contacts were nudges primarily directed towards the cloacal and head regions. After initial contact with a female, male(s) began moving quickly around the aquarium, resulting in more contact and nudges with conspecifics. Interactions between males and females often included intertwining and mutual nudging. Males often used a stiff-legged, waddling motion (called vent-shuffling by ARNOLD, 1972) just before and during spermatophore deposition. Amplexus using the forelimbs was never observed. Males led females and oriented them to specific spermatophores twice out of 1550 spermatophores observed deposited.

Males assumed a characteristic posture while depositing spermatophores (described by ARNOLD, 1972, p. 180) and laterally fanned their tail slowly as a spermatophore was deposited. During spermatophore deposition, males grasped their cloaca with both hindlegs (as observed by GARTON (1972) and LABANICK & DAVIS (1978)), but also regularly grasped a piece of gravel on the substrate while depositing a spermatophore (as observed by UZZELL (1969)). Individual males deposited at least five spermatophores before the female began picking up spermatophores (Phase 2, Fig. 2). When picking up spermatophores, females assumed a posture like that of males depositing spermatophores. The number of spermatophores picked up by females varied among individuals (Table 1).

Once females stopped picking up spermatophores they became rigid and unresponsive to male nudging. Females often would gulp air and then remain at the water's surface. Males always continued to deposit spermatophores and nudge conspecifics after the female had stopped picking up spermatophores (Phase 4, Fig. 2).

A few unusual observations of *A. texanum* courtship require further comment. Three males performed "amplexus" using their hind feet to grasp the female. The amplexus posture was similar to that used by males when they grabbed gravel on the substrate and deposited a spermatophore. All three males subsequently deposited spermatophores on the back and head of the female. In each case the female seemed disturbed by the spermatophores and performed somersaults and rolls on the gravel substrate (apparently trying to dislodge the spermatophores).

Generally, males did not deposit spermatophores until after making direct contact with the female. However, in two of the three-male trials, a male which had not yet deposited spermatophores, and which had not yet

TABLE 1. Effects of conspecific males on success rates of spermatophores (SPM)

No. of males	Repl.	No. SPM deposited	No. SPM picked up	Spermatophore success rates (%) Overall[1]	Corrected[2]	Corrected max.[3]
1	1	49	24	41	71	71
	2	48	25	52	56	56
	3	44	17	39	59	59
	4	91	41	45	48	48
2	1	51, 59	16	15	18	40, 33
	2	102, 65	18	11	17	41, 29
	3	56, 52	17	16	20	40, 40
	4	23, 32	20	36	36	87, 63
3	1	106, 94, 73	19	7	16	48, 44, 58
	2	118, 127, 128	23	6	11	33, 39, 30
	3	104, 52, 76	67	29	35	78, 100, 100
ANOVA (testing for number of male effects):						
	$F_{2,8}$ = 4.39			9.45	16.46	0.46
	P value = 0.05			0.008	0.002	0.65

[1] (no. SPM picked up/total no. SPM deposited) × 100.

[2] (no. SPM picked up/total no. SPM deposited during Phases 2 and 3) × 100.

[3] (no. SPM picked up/no. SPM deposited per male during Phases 2 and 3) × 100.

TABLE 2. Effects of varying numbers of conspecific males on courtship duration

No. of males	Pre-phase	Duration (sec) of courtship periods (mean+SD) Phase 1	Phase 2	Phase 3	Phase 4	Total length of courtship
1	315±30	165±72	425±293	1695±1056	1306±815	4000±1084
2	216±246	1073±1191	841±806	1393±1012	2503±2165	5087±1242
3	51±47	943±839	1039±871	2196±1267	2123±957	6321±1663

Phases are defined in Fig. 1.

encountered the female, began depositing spermatophores after encountering a male depositing a spermatophore. Thus, direct contact with a female was not a necessary stimulus for the initiation of male spermatophore deposition.

Effects of conspecific males on the duration of courtship phases. About 70% of the courtship period involved females picking up spermatophores (Phase 3) and males depositing spermatophores after the female had stopped picking up spermatophores (Phase 4, Table 2). Males began depositing spermatophores soon after contact with the female

TABLE 3. Effects of conspecific males on spermatophore investment (total courtship time/no. of spermatophores)

No. of males	Repl.	Overall courtship time per SPM[1]	Individual male courtship time per SPM[2]
1	1	63	63
	2	79	79
	3	61	61
	4	46	46
2	1	43	92, 80
	2	25	65, 42
	3	45	87, 94
	4	79	189, 136
3	1	14	45, 42, 42
	2	36	79, 159, 108
	3	20	51, 58, 74
ANOVA (testing for number of male effects):			
	$F_{2,8}$ = 4.48		1.10
	P value = 0.05		0.38

[1] Courtship duration (sec)/total no. spermatophores (SPM) deposited.
[2] Courtship duration (sec)/no. SPM deposited by individual males.

(Table 2, $\bar{x} = 734$ s, SD = 909). Females began picking up spermatophores on average 752 s after the males began depositing spermatophores (Table 2). Increasing numbers of males did not cause a consistent change in the duration of courtship phases ($F_{2,9}=0.35$, $p>0.05$, original df = 8,36).

Courtship time and spermatophore deposition.

The total duration of courtship (Table 2) increased significantly as more conspecific males were present ($F_{2,8} = 7.35$, $p = 0.01$). More conspecific males also resulted in more spermatophores being deposited per male (Table 1). Consequently, spermatophore investment (Table 3) did not change significantly in response to different numbers of males. Males depositing more spermatophores simply spent more time courting. From a female's perspective, however, more males resulted in a significantly faster rate of spermatophore production (Table 3, overall courtship time per SPM). A new spermatophore was deposited on average every 23.3 s when three males were present as opposed to every 62.3 s with only one male present (Table 3).

Temporal aspects of spermatophore deposition.

In general, males deposited significantly more spermatophores ($\bar{x} = 33.5$, SD = 8.8) while the female was picking up spermatophores compared to

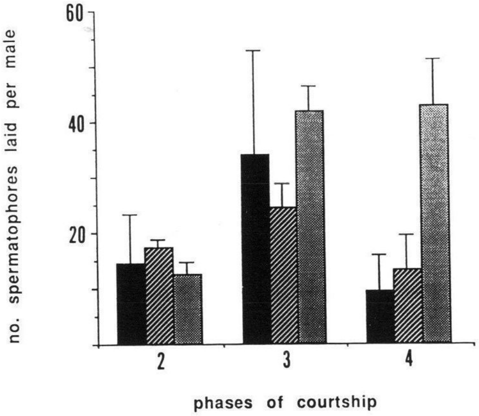

Fig. 2. Effects of conspecific males on temporal patterns of spermatophore laying (mean ± SE). Phases are defined in Fig. 1. black: one male; hatched: two males; spotted: three males.

other times during courtship (Fig. 2, $F_{1,23} = 12.4$, $p < 0.005$, original df = 2,46). Significantly fewer spermatophores were deposited during Phase 2 ($\bar{x} = 14.8$, SD = 2.3) compared to Phase 4 ($\bar{x} = 21.9$, SD = 18.3). The change in numbers of spermatophores deposited by males during Phase 2, 3, and 4 was not the same across treatments (Fig. 2, $F_{2,23} = 5.46$, $p = 0.01$). Males with two conspecific males continued to deposit large numbers of spermatophores after the female had stopped picking up spermatophores (Fig. 2, Phase 4). Numbers of spermatophores deposited by males alone ($\bar{x} = 58$, SD = 22.1), and with one other male ($\bar{x} = 55$, SD = 23.6) were significantly less than the number of spermatophores deposited by males with two other males present ($\bar{x} = 97.6$, SD = 26.2) (Table 1).

Males deposited spermatophores at similar overall rates regardless of the number of conspecifics present (Table 4, $F_{2,8} = 0.06$, $p>0.8$). Spermatophore deposition rates were highest before the female started picking up spermatophores, declined slightly while she picked up spermatophores, and then declined significantly once the female stopped picking up spermatophores (Table 4, $F_{1,8} = 16.6$, $p >0.005$, original df = 2,16). As more males courted the female, the degree of decline in deposition rate was less (though not significantly so: $F_{2,8} = 1.95$, $p = 0.2$, original df = 4,16).

Male weight ($\bar{x} = 9.7$ g, SD = 2.2) was not significantly correlated with the total number of spermatophores produced during courtship ($r = 0.02$, $p = 0.92$) or with spermatophore deposition rate during the interval when

TABLE 4. Conspecific male effects on spermatophore deposition rates1) during certain intervals of courtship

No. of males	Repl.	Courtship interval2) Before	 During	 After
1	1	2.5	1.6	0.1
	2	1.6	1.1	0.3
	3	2.3	1.1	1.3
	4	2.3	2.0	0.5
	mean±SD=	2.2±0.4	1.5±0.4	0.5±0.5
2	1	2.4±.08	1.9±.09	1.1±.09
	2	2.3±.41	2.1±.25	0.7±.04
	3	1.3±.19	1.2±.11	1.0±.00
	4	0.9±.21	0.4±.13	0.4±.21
	mean±SD3)=	1.7±0.71	1.4±0.76	0.8±.33
3	1	1.8±.03	2.3±.33	1.0±.25
	2	2.3±.30	1.7±.15	1.3±.23
	3	0.3±.43	1.3±.42	0.8±.19
	mean±SD3)=	1.5±1.07	1.8±0.50	1.0±.23
	Overall mean±SD+	1.8±0.72	1.5±0.56	0.8±.41

1) Pots of cumulative no. of spermatophores deposited by individual males over time were used in calculating slope values.

2) Defined as before, during, or after the female picks up spermatophores.

3) Means±SD for two and three male trials are based on values in the table, not individual male slope values.

females picked up spermatophores ($r = 0.25$, $N = 21$, $p>0.05$). Spermatophore deposition rate prior to females picking up spermatophores was not significantly correlated with the total number of spermatophores deposited by a given male ($r = 0.4$, $N = 19$, $p >0.05$), but was significantly correlated with male body weight ($r = -0.51$, $N = 19$, $p < 0.05$). In addition, spermatophore deposition rate during the interval when females picked up spermatophores was significantly correlated with total number of spermatophores deposited by a male ($r = 0.53$, $N = 21$, $p < 0.05$).

Spermatophore success.

Because I could not visually keep track of an individual male's spermatophores, only the number of spermatophores picked up by the female and not the paternity of the spermatophores was recorded. Females picked up an average of 26 spermatophores/courtship (SD = 14.6, Table 1). The number of males courting did not significantly affect the number of spermatophores picked up by the female ($F_{2,8} = 1,37$, $p = 0.31$). Female weight was not significantly correlated with the number of spermatophores picked up ($r = 0.02$, $p>0.8$).

Since most spermatophores are deposited during Phases 2 and 3 (Fig. 2), the success rate of spermatophores generally improves when spermatophores deposited during Phase 4 are excluded from the calculation (Table 1, corrected success rate). Solitary males had significantly higher overall and corrected spermatophore success rates (Table 1) compared with males in the presence of one or two other males.

If females have preferences for a specific male's spermatophores, then spermatophore success rates can improve greatly (Table 1, corrected maximum success rate). The number of conspecific males had no significant affect on the corrected maximum spermatophore success rate (Table 1).

Interactions between conspecific males.

No sexual defense of females was ever observed. Males nudged each other forcefully at times, but these nudges did not appear to be associated with keeping other males away from the female.

Males did participate in sexual interference behavior. Disruptions of males while they were depositing spermatophores were infrequent ($\bar{x}$ = 2.8, SD = 1.4 interferences per male per courtship across all treatment groups). The primary sexual interference tactic involved males depositing their spermatophores on top of other spermatophores, thus creating multiple spermatophores of which the one on top has the best chance of being picked up by the female. Males placed their spermatophores on top of other spermatophores on average 7.2% of the time (range = 2-13%). Even males alone produced multiple spermatophores at approximately this same frequency. Unfortunately, the multiple spermatophore deposition rate is based on data from only seven males (two pairs of courting males, and three solitary males) because it often was impossible to keep track of where a male's spermatophore was being deposited when more than one male was present. Consequently, I was able to record only the least frequent occurrences of multiple spermatophores.

Discussion

Courtship behavior of pond form *A. texanum.*

Courtship behavior of *A. texanum* in this study conformed to that described by ARNOLD (1972) and GARTON (1972). The amplexus/leading type of courtship observed by WYMAN (1971) was not observed. Thus, large scale geographic variation in *A. texanum* courtship behavior seems unlikely.

Several aspects of WYMAN's (1971) study suggest he was observing hybrid individuals (most likely *A. texanum/A. laterale*). WYMAN (1971) observed courtship involving amplexus and leading (behavior characteristic of *A. macrodactylum* (ANDERSON, 1961), *A. jeffersonianum* (UZZELL, 1969), and *A. laterale* (STOREZ, 1969)) and also much rubbing and probing during a lengthly Phase 1 (behavior characteristic of *A. texanum* (GARTON, 1972; this study), *A. maculatum* (SALTHE, 1967; ARNOLD, 1976), *A. tigrinum* (ARNOLD, 1976), and *A. annulatum* (SPOTILA & BEUMER, 1970)). If WYMAN (1971) unknowingly used hybrid *A. texanum/A. laterale*, then he observed individuals with combined components from each species' courtship behavior.

Comparison with stream form *A. barbouri*.

Courtship behavior of *A. barbouri* and *A. texanum* is generally quite similar (ARNOLD, 1972; GARTON, 1972; PETRANKA, 1982a; this study). PETRANKA (1982a, 1984) and KRAUS & PETRANKA (1989) suggested *A. barbouri* courtship is different in that: 1) courtship and spermatophore deposition takes place beneath rocks in streams; 2) Phase 1 is abbreviated; 3) females nudge males less throughout courtship; and 4) intermale interference during spermatophore deposition tends to be more common.

No observations of *A. texanum* courtship behavior in the field have been published. GARTON (1972) and PETRANKA (1982a) found *A. texanum* spermatophores on top of leaf mats and twigs in lentic habitats. PETRANKA (1982a) observed spermatophores of *A. barbouri* only under flat rocks in lotic habitats. Consequently, spermatophore deposition sites and probably courtship sites are different for *A. texanum* and *A. barbouri.*

The duration of Phase 1 in this study was quite variable (28—2625 s), especially when single male treatments are compared with two and three male treatments (Table 2). PETRANKA (1982a) and GARTON (1972) found Phase 1 durations of 35-1080 s and 300-900 s, respectively. Phase 1 lasted less than 1 min in three of PETRANKA's (1982a) courtship trials and in three of the trials in this study (two with two males, one with three males). Thus, Phase 1 durations do not seem unequivocally shorter for *A. barbouri.*

I did not count nudges between males and females nor have any data on frequency of nudges been published elsewhere. Males and females in this study participated regularly in reciprocal nudging bouts. Whether the frequency of participation is less than observed in *A. barbouri* is unknown.

PETRANKA (1982a) reported six males violently nudging other males while they deposited spermatophores. Two of these intermale contacts resulted in successful interruption of spermatophore deposition. I observed males disrupting spermatophore deposition on average 2.8 (SD

= 1.4) times per courtship (though the success of these disruptions was not recorded). A total of 52 intermale interference attempts were observed during 11 successful courtships. Based on my observations and those of PETRANKA (1982a), it appears that *A. texanum* not *A. barbouri* participates in more intermale interferences.

Thus, the difference in duration of breeding season between the nonexplosive breeding *A. barbouri* (PETRANKA, 1984) and the explosive breeding *A. texanum* (PETRANKA, 1982b; MCWILLIAMS & BACHMANN, 1988) has not produced changes in courtship behavior (as observed in the laboratory), other than perhaps in the degree of sexual interference.

Effects of multiple conspecific males on courtship behavior.

Other salamander studies which varied the number of males present during courtship generally found rival males inhibited or had no effect on each other. For example, UZZELL (1969) found that *A. laterale* males with rivals produced fewer spermatophores on average than solitary males. *Notophthalmus viridescens* responded to more than two rival males by adopting the amplexus mode of courtship more often than when solitary (VERRELL, 1983, 1985). Males directly interfered with other males while they clasped a female and induced him to deposit spermatophores by nudging his cloaca (VERRELL, 1983; MASSEY, 1988). Thus, both *A. laterale* and *N. viridescens* usually court females using amplexus and their response to rival males often involves strategies of sexual defense.

Studies of salamanders which do not clasp and defend females generally found rival males had no effect or had a stimulatory effect on each other. PETRANKA (1982a) observed no differences in courtship behavior in trials with one or two *A. barbouri* females and 2, 4, or 5 males. ARNOLD (1976) found that *A. maculatum* males deposited similar numbers of spermatophores when alone with a female compared to when one rival male was present. With a rival present, males did increase the rate at which they deposited spermatophores. GARTON (1972) observed one courtship between three *A. texanum* males and a single female. He observed extensive intermale nudging and an increase (relative to single male/female parings) in total spermatophore production.

I found general courtship behavior, the duration of specific phases, and the number of spermatophores picked up by females were not affected by the number of conspecific males. In addition, sexual interference and sexual defense behavior did not change when more competing males were present. Males with two other males and a female did significantly increase their spermatophore production, but not the average deposition rate (Table 4). Interestingly, the additional spermatophores were primarily deposited after the female had stopped picking up spermatophores.

Comparison with *A. maculatum*.

A. texanum courtship behavior is very similar to that observed in *A. maculatum* (ARNOLD, 1976). Both species emphasize courtship speed, deposit many spermatophores, and have relatively low spermatophore success rates (ARNOLD, 1976; this study). Both species also have similar life histories (ARNOLD, 1976; MCWILLIAMS & BACHMANN, 1988).

Both *A. texanum* and *A. maculatum* have been described as breeding in a polyandrous frenzy (GARTON, 1972; ARNOLD, 1976). In the field, *A. maculatum* breeds in congresses of 10-50 males with one or a few females (ARNOLD, 1976). No field observations of *A. texanum* courtship have been published. Previously, concentrations of 70-100 spermatophores have been interpreted as evidence that *A. texanum* breeds in congresses of at least two or three males (GARTON, 1972; ARNOLD, 1972). However, individual males in my study commonly deposited as many as 100 spermatophores. Thus, no published observations of *A. texanum* courtship under natural conditions confirm breeding in groups.

The most significant difference between *A. texanum* and *A. maculatum* courtship apparently involves the sexual resources of the male and their temporal allocation. ARNOLD (1976) concluded that the total sexual resources of *A. maculatum* males was less than 100 spermatophores, with males depositing ca. 50% of this total supply during their first courtship. The total spermatophore capacity of *A. texanum* males is unknown, but males deposited up to 128 spermatophores during their first courtship. Since it is unlikely, but not yet empirically demonstrated, that a male's total capacity approaches 200 spermatophores, *A. texanum* males are probably depositing a greater proportion of their total capacity per courtship.

What determines the number of spermatophores deposited by a given male in a courtship? I found males increased their spermatophore production in the presence of conspecific males. Thus, intermale competition is one important determinant. If females pick up spermatophores regardless of paternity, male success is reduced to a numbers game — always deposit more spermatophores relative to the number deposited by conspecific males. The "numbers game" male strategy requires that more spermatophores picked up by the female results in more patrimonial contribution for a given male. In fact, no "last in" or "first in" spermatophore dominance like that seen in some insects seems to occur in salamanders (HOUCK *et al.*, 1985; VERRELL, 1989), although the potential for sperm competition exists (TILLEY & HAUSMAN, 1976; HALLIDAY & VERRELL, 1984). If females exercise selection while picking up spermatophores it would directly alter male courtship strategy. Studies are needed which record which male's spermatophores are picked up, the order in which they are picked up, and the paternity of offspring.

Constraints on allocation of male sexual resources.

A spermatophore was produced by a male every 1.06 min when alone, every 0.84 min when one other male was present, and every 1.04 min when two conspecific males were present ($F_{2,8}$ = 0.04, p = 0.96). The constancy of spermatophore deposition rate across treatments (also see Table 4) suggests a physiological limit on deposition rate. Males do deposit successive spermatophores faster than every minute (it only takes approx. 10-20 s for a male to deposit a single spermatophore (GARTON, 1972; LABANICK & DAVIS, 1978; pers. obs.)), this limit refers to an average for a given courtship. If *A. texanum* males are constrained by deposition rate and adopt a strategy whereby they produce more spermatophores per courtship, then males can do so only by increasing the time they spend depositing spermatophores.

Sexual interference tactics.

The number of multiple spermatophores produced by males in this study was generally low (ca. 7%) and did not change in frequency when rival males were present. Similarly, *A. laterale* and *A. maculatum* males did not increase the number of multiple spermatophores produced when in the presence of rival males (UZZELL, 1969 and ARNOLD, 1976, respectively). However, the frequencies of multiple spermatophores I observed are much lower than the 45-64% frequency reported for *A. texanum* by LABANICK & DAVIS (1978). Other *Ambystoma* also produce high frequencies of multiple spermatophores (*e.g.* 57% for *A. maculatum* and 63% for *A. tigrinum* (ARNOLD, 1976)). These results are derived from laboratory experiments in which courting groups are confined, possibly increasing the frequency of multiple spermatophores. The low frequency of multiple spermatophores reported here may result from: 1) the use of gravel substrate which provided males with many alternative projected surfaces upon which to deposit spermatophores, and 2) the small and biased sample from which the frequencies are derived (see Results). It seems likely that multiple spermatophores represent the primary sexual interference tactic of male *A. texanum*.

Male choice and mating strategy of *A. texanum.*

Females picked up a relatively fixed number of spermatophores regardless of the number of conspecific males present or the number of spermatophores produced (Table 1). The infrequency of leading behavior, and the behavior of females, suggests females are picking up spermatophores as they encounter them, without any apparent selection.

If mate choice occurs in *A. texanum,* it is probably very subtle (*e.g.* HALLIDAY, 1983). Spermatophore deposition rate was significantly correlated with total spermatophore production during courtship only for the time interval when females were picking up spermatophores. HALLIDAY (1976) and HALLIDAY & HOUSTON (1978) found male newts (*Triturus vulgaris*) were "honest salesman" because the rate of display early in courtship was a good indicator of spermatophore production later in courtship. It remains to be demonstrated whether *A. texanum* females use spermatophore deposition rate or other potential indicators of male quality in a selective manner.

Because the life history strategy of *A. texanum* includes no parental care and a short breeding season, there is less *a priori* reason to suspect strong female choice (TRIVERS, 1972; VERRELL, 1989). A given female can only participate in courtship for certainly less than 48 hrs and probably less than 24 hrs (due to egg laying constraints), making her a very limiting resource (especially relative to males in a strongly male-biased breeding population). Because the male's strategy includes depositing increasing numbers of spermatophores per courtship when at least two males are present, it seems unlikely males are trying to maximize the number of females inseminated. Males more likely are trying to ensure that the number of "ejaculates" with a given female ensures effective paternity (DEWSBURY, 1982).

However, if females are attracted to breeding aggregations (but see VERRELL, 1984), then a male's ability to inseminate many females is directly related to the number of spermatophores he can produce per courtship. Under these circumstances, males can increase both the number of females inseminated and the number of ejaculates per female. Because the additional spermatophores deposited by males with two other males were primarily deposited after the females had stopped picking up spermatophores, polygynous aggregations would provide the ecological conditions making this strategy adaptive.

Evolution of *A. texanum* courtship tactics.

The temporal and spatial crowding of *A. texanum* breeders caused by synchronous migration to small woodland ponds, combined with the typically male-biased sex ratio, may have provided the conditions selecting for males producing large numbers of spermatophores per courtship, little courtship time investment per spermatophore, and extreme intermale competition.

Compared to other salamanders (ARNOLD, 1976), *A. texanum* courtship is rapid and involves males depositing unusually large numbers of spermatophores. This large capacity may result from extreme intermale competition or because males normally court many females over a short period of time (perhaps even simultaneously). LABANICK & DAVIS (1978) found *A. texanum* spermatophores were smaller than those of most other *Ambystoma* species (the only exceptions being *A. annulatum* and *A. laterale*). Consequently, species differences can be explained in part by simple spermatophore size/number redistribution strategies (SMITH & FRETWELL, 1974).

My results provide the first quantitative evidence that rival males of a species with rapid courtship are able to increase the number of spermatophores they produce per courtship in response to male competition. This modification in sexual resource allocation can effectively compensate for any reduced success caused by spermatophores deposited by rival males. When the "numbers game" strategy is combined with a sexual interference tactic like the use of multiple spermatophores, males can simultaneously reduce a rival male's probability of success and increase the number of his spermatophores available to the female. What remains to be demonstrated is whether these male tactics influence paternity directly and whether female choice plays any role in determining male reproductive success.

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