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TALL TAILS AND SEXY MALES: SEXUAL BEHAVIOR OF ROUGH-SKINNED NEWTS (*TARICHA GRANULOSA*) IN A NATURAL BREEDING POND.—Although courtship and other mating behaviors of many urodele amphibians in the laboratory have been described in great detail (Arnold, 1977; Halliday and Verrell, 1986; Verrell, 1989), little is known about such behavior in natural populations (MacMahon, 1964; Lynch and Wallace, 1987). Furthermore, although large-male sexual dimorphism for many traits has been reported in these animals (Shine, 1979), empirical information on the importance of such dimorphism to salamanders in the field is lacking. For example, male-male competition, a potential force in the evolution of sexually dimorphic traits, only recently has been observed in natural settings (Zuiderwijk and Sparreboom, 1986; Massey, 1988; Verrell and McCabe, 1988).

Observing reproductive behavior in salamanders presents tremendous methodological problems (Verrell, 1989), owing to the cryptic or nocturnal behavior of most salamanders. Still, researchers working on anurans have described sexual behavior in the field and also have documented both large-male mating advantage and positive assortative pairing by size in natural populations (Olson et al., 1986). These patterns

TABLE 1. RELATIONSHIPS BETWEEN BODY SIZE AND PAIRING STATUS IN MALE ROUGH-SKINNED NEWTS, *Taricha granulosa*. The mean \pm SD of four measures of male body size for four categories of pairing status are given. Also, the probability of significant differences between the means from a one-way ANOVA and results of tests of the least significant differences (LSD) between the means are presented. Three males were excluded from the analysis because their tails were missing a section.

Measure of body size	I Nonpairing n = 44	II Single-pair n = 15	III Intruding in ball n = 21	IV Amplexant in ball n = 8	P (df = 3,81)	LSD
Mass (g)	17.6 \pm 3.85	18.8 \pm 3.74	19.9 \pm 3.02	19.2 \pm 2.96	0.0371	III > I
SVL (mm)	73.9 \pm 4.34	76.1 \pm 4.36	77.5 \pm 3.93	78.3 \pm 4.74	0.0035	II, III, IV > I
TL (mm)	92.7 \pm 8.80	94.6 \pm 5.26	98.9 \pm 7.08	100.6 \pm 8.94	0.0082	III, IV > I
TLHT (mm)	14.8 \pm 2.20	16.5 \pm 2.23	17.5 \pm 1.73	16.1 \pm 1.87	0.0001	II, III > I

of mating behavior have been attributed to intrasexual competition and intersexual selection (Arak, 1983; Howard and Kluge, 1985; Sullivan, 1985; Woodward, 1982).

To further our understanding of sexual behavior of salamanders in natural populations, we studied a day in the life of a breeding aggregation of rough-skinned newts (*Taricha granulosa*). Herein we describe qualitative aspects of courtship behavior in the field and compare our findings to laboratory observations of courtship behavior (Arnold, 1972). We also present information on the quantitative size relationships among rough-skinned newts of both sexes and of various pairing situations.

Materials and methods.—We observed newts at a small natural pond near Tenmile Creek, Lane Co., Oregon on 22 March 1988. During this study there was intermittent drizzle, ambient temperature was 10.6 C, and water temperature was 12.0 C. We collected a representative sample of animals (88 males and 23 females; we observed many females on land, but excluded them from this study) from all regions of the pond. Our presence did not disrupt ongoing courtship behavior.

We captured animals with a dipnet, separated them with respect to pairing status, and placed them individually in bags. We define general categories for pairing status as follows: 1) nonpairing—any animal not engaged in discernible sexual activity, such as amplexus or attempting to gain amplexus; 2) single-pair pairing—a male and female in amplexus who are not disturbed by intruding males; 3) intruding—a male who attempts to displace another male from amplexus, thereby forming a mating ball (many males attempting to court a single female); and 4) amplexant in mating ball—a male and fe-

male in amplexus who are disturbed by at least one intruding male. For each animal, we recorded sex, pairing status, and the following measurements (in mm): SVL, tail length (TL), and tail height (TLHT) at mid-tail (from the top of the crest to the bottom of the tail). Also, we measured the mass (in mg) of each tow-dried newt with a Quantum portable electronic balance. We released all animals at the edge of the pond after completion of the study. Shapiro-Wilk tests of all variables indicated normal distributions. We used version 6 of Statistical Analysis System (SAS) for personal computers to analyze the untransformed data.

Results.—Nonpairing animals, single-pair pairings, and mating balls occurred throughout the pond. However, we found many more females than males on land and the overall adult sex ratio in the pond was skewed towards an excess of males (3.8:1), indicating that the operational sex ratio (Emlen and Oring, 1977) also may be skewed (given that all males and females observed were attempting to pair).

Male rough-skinned newts remained stationary in the pond until a female, either unpaired or in amplexus, approached. If the female was alone, the male pursued and usually captured her by dorsally clasping her pectoral region with his forelimbs. During amplexus the male rubbed his chin several times from side-to-side on the dorsum of the female's head. If an amplexant pair encountered a single male, the unpaired male occasionally pursued the pair. The amplexant male vigorously transported the female away with powerful strokes of his tail, either to escape the intruder or simply to surface for air. If the amplexant pair did not escape the intruder, the latter usually tried to displace the amplexant male by nudging his head on the

TABLE 2. RELATIONSHIPS BETWEEN BODY SIZE AND PAIRING STATUS IN FEMALE ROUGH-SKINNED NEWTS, *Taricha granulosa*. The mean \pm SD of four measures of female body size for two categories of pairing status and the probability of significant differences between the means from a one-way ANOVA are given.

Measure of body size	Single-pair n = 15	Amplectant in ball n = 8	P (df = 3,19)
Mass (g)	10.9 \pm 1.33	11.8 \pm 2.88	0.2200
SVL (mm)	66.5 \pm 2.95	67.4 \pm 4.03	0.4529
TL (mm)	74.3 \pm 6.65	77.3 \pm 9.69	0.2035
TLHT (mm)	7.1 \pm 0.90	7.3 \pm 0.65	0.7918

side of the amplectant male's head. The intruding male sometimes tried to grasp the female laterally or ventrally, but more often clasped the amplectant male dorsally. We observed neither spermatophore deposition nor displacement of an amplectant male.

A one-way ANOVA revealed important differences in body size among males of different pairing statuses (Table 1). Generally, nonpairing males were smaller than pairing males of any pairing status. Males intruding in mating balls were significantly larger than nonpairing males for all morphometric variables. Single-pair males also were significantly larger than nonpairing males in SVL and TLHT; likewise, amplectant males in mating balls were significantly larger than nonpairing males in SVL and TL.

Because male rough-skinned newts have conspicuously tall tails compared to females and because such sexually dimorphic traits usually are attributed to sexual selection (Verrell, 1989), we examined the relationship between size-adjusted TLHT (i.e., the height of the tail holding SVL constant) and pairing status in males. An analysis of covariance, treating SVL as the covariate, showed that tails of intruding males were significantly higher than those of nonpairing males and those of amplectant males in mating balls ($F_{3,81} = 4.20$, $P = 0.0082$), independent of body size. ANOVA indicated no significant differences in any morphological measure between females amplectant in pairs or in mating balls (Table 2).

To determine if male and female rough-skinned newts pair according to size, data for four measures of body size for all amplectant pairs were submitted to Pearson product-moment correlation analysis. Males and females

did not exhibit positive assortative pairing with respect to any of the morphological measures (Mass: $r = -0.16$, $P = 0.45$, $n = 23$; SVL: $r = -0.06$, $P = 0.79$, $n = 23$; TL: $r = -0.45$, $P = 0.04$, $n = 22$; TLHT: $r = +0.003$, $P = 0.99$, $n = 22$).

Discussion.—Our observations of courtship behavior of rough-skinned newts in a natural breeding pond generally corroborate the laboratory findings of Arnold (1972). Males captured females with a dorsal clasp to the pectoral region, but we observed no preliminary snout nudging, hindlimb jerking, or hindlimb treading by the males. Although Arnold states that chin rubbing by the male occurs on the female's snout, we found that chin rubbing took place on the dorsum of the head. The discrepancies between our observations and Arnold's (1972) should be viewed as inconclusive, however, because of our inability to observe complete matings and because our observations were made on a single day.

Our finding that nonpairing male newts were significantly smaller than pairing and intruding males suggests that larger male *T. granulosa* have greater access to females than smaller males. However, unpaired males may have mated previously or may have mated later. Further, because reproductive success also may depend on insemination and sperm competition, our results only suggest that large-male advantage in access to female translates into reproductive success.

Intruding males have absolutely taller tails than nonpairing males and disproportionately taller tails than nonpairing males and amplectant males in mating balls in contrast to findings for *Notophthalmus viridescens* (Massey, 1988). The height of the tail may be very important to males in capture and retention of females. The tail may be valuable for sustaining sexual activity in newts, which often breed in anoxic ponds (Halliday, 1977, 1987). A larger (taller?) tail presumably is advantageous in both cases, improving swimming speed and increasing the surface area through which respiratory gases are exchanged (Feder and Burggren, 1985). Experimental analyses of the ecophysiological importance of tail size are needed to resolve this intriguing problem.

Positive assortative pairing by body size was not found, despite the occasional incidence of this phenomenon in anurans (Olson et al., 1986). However, Olson et al. (1986) also reported in-

traspecific and intrapopulation variation in mating patterns in anurans and suggested that this variation is a response to differences in environmental conditions and to demographic parameters. Similar sources of variation and the lack of observations from more than 1 d may explain the absence of positive assortative pairing by body size documented by this study. Our frequent observations of aggressive interactions among males, which occurred only when one of the males was paired to a female, suggest that the pairing patterns were due to intrasexual competition rather than to intersexual selection. Whether the same would hold true for mating patterns is unknown.

The results reported here represent the first observations of sexual behavior and pairing patterns of *T. granulosa* in the field. Additional studies are needed to determine whether sexually dimorphic characters, particularly TLHT, are important to mating success and if so how. Further, field studies which follow several populations through time would yield significant information on spatial and temporal variation in pairing patterns of rough-skinned newts.

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