

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 = 31	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-

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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 (Zuidervijk 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

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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 1.93	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	0.2085
TL:HT (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 TL:HT; 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 TL:HT (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

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 TL:HT, 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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