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Reproductive Ecology of a Population of the California Tiger Salamander

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We studied breeding migrations and variation in reproductive traits of the California tiger salamander, *Ambystoma californiense*, in Contra Costa County, California over two winter breeding seasons and three summer metamorphosis seasons (1992–1994). Initiation of adult breeding migrations followed major storm systems; in both 1993 and 1994, males arrived at the breeding pond first and stayed longer than females. Breeding population sizes of males and females varied annually and appeared to be determined by different mechanisms. Within a season, variation in weekly numbers of migrating adults was attributable only to rainfall; variation in numbers of emigrating juveniles could not be attributed to any measured environmental parameters. Sexual dimorphism in adults is expressed through longer tails in males. Annual numbers of juveniles produced varied substantially, ranging from over 1000 metamorphs in 1992 to only three in 1994. Timing and mean size at metamorphosis showed substantial annual variation.

SPECIES dependent on ephemeral breeding sites, such as many salamanders in the family Ambystomatidae, commonly exhibit high variability in life-history traits (Wilbur and Collins, 1973; Scott, 1994). Ambystomatids often have a "boom and bust" type of population dynamics in which recruitment is highly variable among years (Shoop, 1974; Semlitsch, 1983; Stenhouse, 1987). Breeding population structure also varies, potentially affecting sexual selection (Trivers, 1972; Douglas, 1979), genetic drift (Wright, 1940), and demographic traits (Cole, 1954). Variation in juvenile traits such as size at metamorphosis and timing of metamorphosis can have significant consequences for individual fitness (Berven and Gill, 1983; Smith, 1987; Semlitsch et al., 1988). Quantification of variability in life-history traits, as well as information on the factors influencing this variability, can help identify the factors regulating populations (Semlitsch, 1983). Migration patterns of several salamander species, for example, are influenced by environmental conditions such as rainfall and temperature (Semlitsch, 1985; Beneski et al., 1986; Sexton et al., 1990). Intrapopulation studies conducted over several years, as an alternative to comparisons between populations, are useful in the study of life-history variation because they reduce the number of ecological variables potentially responsible for this variation (Collins, 1979).

Insight into natural variation of life-history traits is especially important for rare or endangered species. The California tiger salamander, *Ambystoma californiense*, is endemic to California and is believed to have undergone substantial population declines in recent years. It is thus listed as a "species of special concern" by the state of California and as a Category I species on the federal Endangered Species List (Sorensen, 1994). Habitat loss and fragmentation, especially from urban development and conversion of natural habitat to agriculture, are considered the most significant threats to this species (Sorensen, 1994). Amphibian populations throughout many parts of the world have shown dramatic declines or extinctions, further emphasizing the need for knowledge of natural fluctuations in population parameters (Barinaga, 1990; Blaustein and Wake 1990; Pechmann et al., 1991). Though ambystomatid salamanders in general have been well studied, little is known about life-history variability of the California tiger salamander.

Ambystoma californiense is found in the Central Valley and adjacent foothills and coastal grasslands, an area with a Mediterranean climate of cool, wet winters and hot, dry summers (Storer, 1925; California Department of Fish and Game, unpubl., 1984). California tiger salamanders typically breed in ephemeral ponds that fill during winter and dry by summer. Breeding migrations are nocturnal and begin with the onset of the rainy season, usually in Nov. or Dec. (Storer, 1925; Barry and Shaffer, 1994). Metamorphosis of larvae begins in late spring or early summer and is followed by the departure of juveniles from their natal ponds into terrestrial habitat (Storer, 1925; Holland et al., 1990). Age at sexual maturity of *A. californiense* is unknown but is at least two years in *A. tigrinum*, its closest relative (Semlitsch, 1983).

TABLE 1. BREEDING POPULATION SIZES, SEX RATIOS, AND JUVENILE PRODUCTION OF *Ambystoma californiense* AND ASSOCIATED POND DRYING TIMES AT A BREEDING POND IN CONTRA COSTA COUNTY, CALIFORNIA.

Year	Breeding adults		Sex ratio	Metamorphosing juveniles		Pond drying date
	Males	Females	(M: F)	Juveniles	Juveniles per female	
1991–1992	—	—	—	1248	—	1–2 Aug.
1992–1993	65	81	0.8:1	481	5.94	never dried
1993–1994	121	15	8.1:1	3	0.2	21–24 July

We studied a population of *A. californiense* for three years. Our objectives were to document variation in reproductive traits and to identify environmental factors that may cause this variation.

MATERIALS AND METHODS

The study site was located at Concord Naval Weapons Station, Contra Costa County, California. The pond was approximately 12 m in diameter when full and held water year-round in years of normal rainfall but dried out by late summer in drought years (Table 1). Western toads, *Bufo boreas*, and Pacific tree frogs, *Hyla regilla*, also breed in the pond; and red-legged frogs, *Rana aurora*, were occasionally found in the immediate vicinity. Surrounding habitat is typical of the Central Valley of California and consists of open, rolling grassland hills with scattered oaks, *Quercus* spp. Several other small ephemeral ponds are in the area, and California tiger salamanders breed in at least four (unpubl. data). We monitored the pond continually for three summer seasons (May through July 1992, May through Aug. 1993, and May through July 1994) when juvenile salamanders metamorphosed and left the pond and for two winter seasons (Dec. 1992 through March 1993 and Nov. 1993 through April 1994; hereafter referred to as winter 1993 and winter 1994) when breeding adults migrated to and from the pond. Salamanders were studied under California Fish and Game Scientific Collector's Permits numbers 6121, 6633, and 7109.

We used a drift fence and pitfall traps (Gibbons and Bennett, 1974) to capture adult and newly metamorphosed salamanders as they left the pond. The pond was completely encircled by a drift fence constructed of 50-cm high aluminum flashing, with the lower edge buried 10–15 cm into the ground. Pairs of pitfall traps were buried flush with the ground every 5–10 m, one trap on either side of the fence. We checked traps every night in the summer and every rainy night or at least every other night during the winter. Each adult salamander was marked individually by clipping toes. Juvenile salamanders were individually marked in 1992 and cohort-marked as year classes in subsequent years. Sex of adults was recorded, and all individuals were measured for total length (TL) and snout–vent length (SVL) to the nearest millimeter. Salamanders were then immediately released on the opposite side of the fence.

Length of stay at the breeding pond for each adult was the time elapsed from the first date of entrance until the last date of exit from the pond as determined by capture in pitfall traps. Time of metamorphosis of juveniles was considered to be the date that each individual was first captured emigrating from the pond.

We recorded four environmental variables (precipitation, temperature, cloud cover, and moon phase) that might influence salamander migration patterns. We measured precipitation in a rain gauge and temperature with a minimum-maximum thermometer at a location 1.25 km from the pond; these measurements were recorded at the start of each visit to the pond. Thus they represent conditions one to two days immediately preceding the night's migration. We visually estimated percent of cloud cover upon arrival to the pond (approximately 2100 h). Moon phase was recorded as nightly fractional illumination values from an astronomical almanac.

We analyzed the influence of environmental factors on migrations of *A. californiense* by performing stepwise multiple regressions using the number of individuals caught as the dependent variable and several environmental conditions as independent variables (Semlitsch, 1985). Nightly numbers of adults caught were summed over one-week periods and regressed using weekly cumulative rainfall and weekly means of maximum temperature, minimum temperature, percent of cloud cover, and lunar illumination for each of the 1993 and 1994 seasons. Nightly numbers of juveniles caught were regressed with percent of cloud cover, minimum temperature, maximum temperature, and lunar illumination for each of the 1992 and 1993 seasons; rainfall was excluded because rain fell on only 1–3 days each summer. All stepwise regressions were run with an F-to-enter and F-to-remove = 4.0.

Means were compared using *t*-tests; *t*-tests assuming unequal variances were used when an *F*-test for the assumption of equality of variances warranted ($P < 0.05$). Prior to statistical analysis, values of length of stay at the breeding pond were uniformly reduced by a constant of 0.5 and log-transformed to minimize deviations from normality.

RESULTS

Breeding migrations and population dynamics.—Males were the first to arrive at the pond in both the 1993 and 1994 winter breeding seasons, on 8 Dec. and 29 Nov., respectively. Initiation of migration followed pond filling and was preceded by several rainstorms. In both years, the rainy season began in Oct. (> 15 mm monthly totals), followed by sparse rainfall (< 1 mm per week) until major storm systems in Dec. 1992 and Nov. 1993 deposited at least 28 mm of rain within 6–7 days. In both years, salamander migration began on the last day of these storm systems. Total numbers of adult males and females varied between years (Table 1). At least 45 of the 121 males and two of the 15 females captured as adults in 1994 were marked as juveniles in summer 1992. Other adults may have been from the 1992 juvenile cohort as well, but there was some regrowth of clipped toes so identities were uncertain. Age at sexual maturity is unknown but appears to be at least two years because no one-year-old males or females were identified during either breeding season. Sex ratios did not differ significantly from 1:1 in winter 1993 ($\chi^2 = 0.88$; df = 1; $P > 0.3$) but did in winter 1994 ($\chi^2 = 48.71$; df = 1; $P < 0.0005$). Numbers of metamorphosing juveniles varied considerably and declined in each successive year (Table 1).

Males stayed at the pond longer than females in both years. In winter 1993, males stayed an average of 54.2 days (SD = 20.4, range = 1–94, n = 53), and females 13.6 days (SD = 13.3, range = 1–62, n = 74). In winter 1994 both males ($\bar{x} = 20.0$ days, SD = 28.1, range = 1–111, n = 74) and females ($\bar{x} = 6.4$ days, SD = 4.0, range = 2–12, n = 5) stayed for shorter periods. Variation in length of stay at the breeding pond was attributable to both year (F = 20.25, $P < 0.001$) and sex (F = 22.04, $P < 0.001$), with a significant interaction term (F = 7.49, $P < 0.01$).

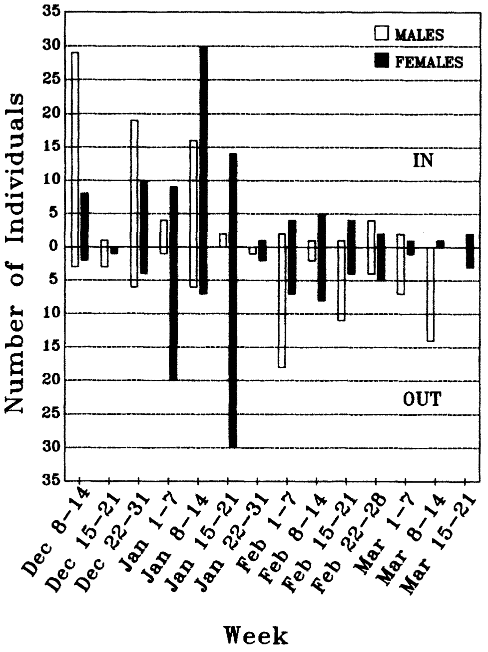

Fig. 1. Weekly number of adult *Ambystoma californiense* migrating into and out of a breeding pond during winter 1993, Contra Costa County, California. Numbers of individuals include original captures and recaptures.

Within a season, there was considerable weekly variation in the number of adults captured (Figs. 1–2). In the regression models to explain this variation, only total weekly rainfall entered

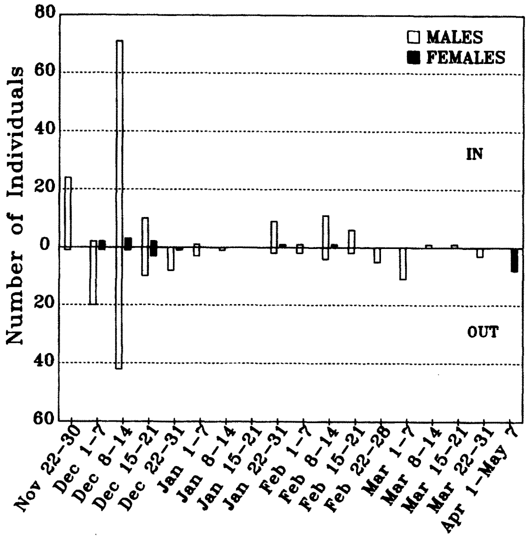

Fig. 2. Weekly number of adult *Ambystoma californiense* migrating into and out of a breeding pond during winter 1994, Contra Costa County, California. Numbers of individuals include original captures and recaptures.

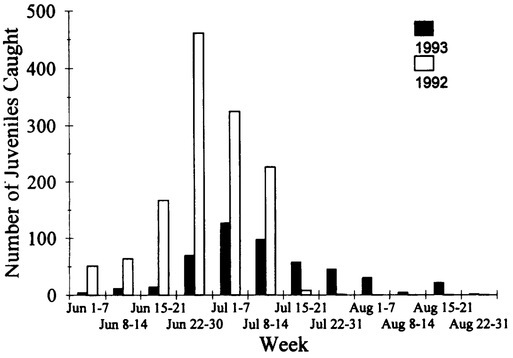

Fig. 3. Number of juvenile *Ambystoma californiense* caught by week in summer 1992 and summer 1993, Contra Costa County, California. Numbers of individuals include original captures and recaptures.

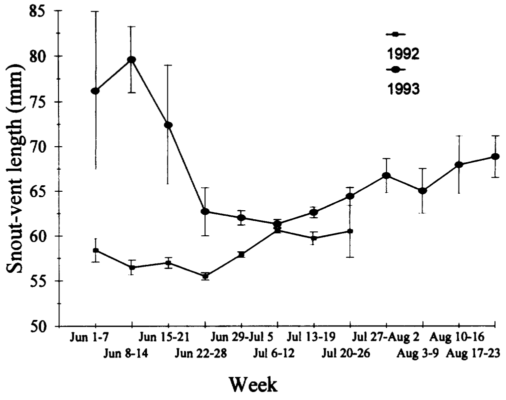

Fig. 4. Mean *Ambystoma californiense* snout–vent length at metamorphosis over time in 1992 and 1993, Contra Costa County, California. Vertical lines denote 95% confidence intervals.

in either 1993 ($r^2 = 0.72$; F = 31.38; df = 1,12; $P < 0.001$) or 1994 ($r^2 = 0.22$; F = 5.67; df = 1,20; $P < 0.03$). The proportion of variation explained by rainfall was lower during 1994, a year of low rainfall. Most adults (90% in 1993 and 81% in 1994) were captured on days in which rain fell.

Metamorphosis and emigration of juveniles occurred from 3 June through 27 July in 1992 and 1 June through 22 Aug. in 1993. Median emigration dates were on 29 June 1992 and 9 July 1993. Salamander reproduction evidently failed in 1994; only three metamorphs were caught, between 19 June and 3 July. Juvenile movement out of the pond each week appeared normally distributed (Fig. 3) in contrast to adults. None of the environmental variables accounted for a significant portion of the variation in juvenile emigration in either 1992 or 1993 ($P > 0.05$). Although summer rain is rare in California's Central Valley, one major storm did occur each year. In 1992, a storm deposited 4 mm of rain in the middle of the metamorphosis period; on that day 15.5% of all juveniles emigrated. In 1993, a storm deposited 9 mm of rain, but it occurred during the first three days of metamorphosis; only 0.6% of salamanders emigrated then.

Body size variation.—Adult size (SVL) did not differ between years (two-way ANOVA, F = 3.41, $P = 0.07$) or sexes (F = 1.48, $P = 0.24$) ($\bar{x} = 90.5$ mm, SD = 5.9). Total length also did not differ between years (F = 0.10, $P = 0.75$) but did differ between sexes (F = 167.36, $P < 0.001$). Males averaged 200.3 mm TL (SD = 15.6) and females 168.1 mm (SD = 13.6); sexual dimorphism in this species thereby is expressed through longer tails in males. Mean SVL of emigrating juveniles differed between years (58.0 mm in 1992, SD = 3.4, range = 46.0–80.0; 63.8 in 1993, SD = 6.2, range = 55.0–114.0; $t = 19.20$, $P < 0.001$; t-test assuming unequal variances). Mean SVL of juveniles in 1994 was 78.0 mm (SD = 2.6; range = 75.0–80.0) but was not included in the analysis because of the small sample size (n = 3).

Juvenile size at metamorphosis varied with time in a pattern that was similar in both 1992 and 1993 (Fig. 4). Early metamorphosing juveniles were relatively large, especially in 1993; mean SVL subsequently decreased, and later gradually increased.

DISCUSSION

Breeding migrations and population dynamics.—Breeding migrations of *A. californiense* began at the onset of the winter rainy season as the pond began to fill with water. Natural selection may delay amphibian breeding migrations until there is a high probability that the breeding pond is sufficiently full of water, thereby leading to an environmental influence on the timing of migrations (Semlitsch, 1983, 1985). Our data support this hypothesis; the onset of breeding migrations differed between years and in each year was preceded by the first major storms of the rainy season.

Males arrived first and stayed at the breeding site longer than did females, a pattern that has been demonstrated for other ambystomatid salamanders (Douglas, 1979; Semlitsch, 1983; Beneski et al., 1986). Douglas (1979) proposed that male salamanders are more sensitive than females to environmental cues initiating breeding migrations because males that arrive earlier and spend more time at the breeding site have opportunity to mate with a greater number of females. Conversely, females may maximize reproductive success by waiting for a prolonged period of favorable environmental conditions before migrating (Douglas, 1979). This delay probably minimizes the environmental dangers of terrestrial migration and may afford females a greater array of males to choose from (Douglas, 1979).

If environmental conditions are inadequate, some females may not migrate at all. Thus, yearly variation in number of breeding females may be a consequence of the differences in breeding season (15 Nov. to 31 March) precipitation totals. The 1993 season had above-average rainfall (37.7 cm) and followed a six-year drought, whereas the 1994 season had below-average rainfall (19.0 cm). Females invest more energy in offspring than do males and would consequently lose more if early pond drying prevented juvenile metamorphosis. Therefore, a greater proportion of males than females should participate in breeding migrations under poor conditions, as we documented in winter 1994. Yet despite low rainfall in 1994, almost twice as many males were caught compared with 1993. Recruitment from the large juvenile cohort of 1992 may have been responsible for this pattern. At least 37% of the 1994 males were marked as juveniles in 1992. This may represent the first substantial recruitment to the population since the drought began.

Variation in time spent at the breeding site may also be a response to environmental conditions (Semlitsch, 1983). Both sexes spent less time at the pond in winter 1994, during a drought when conditions were presumably not as favorable for breeding, than in winter 1993. The significant interaction term between sex and year suggests that the difference between sexes in length of stay is dependent on the year. During winter 1993, the difference between the sexes in length of stay was 40.6 days, whereas for winter 1994, it was 13.6 days. Many males in 1994 stayed at the pond for only one day, perhaps departing quickly upon discovering poor breeding conditions or few females, especially in proportion to the large number of males, which may represent increased competition for mates.

Weekly variation in numbers of adult salamanders was attributable only to total weekly rainfall. Salamanders typically enter ponds not en masse but in successive waves or pulses (Baldauf, 1952; Husting, 1965). In our study, waves in salamander movement corresponded to periods of rainfall; most adult movement was restricted to nights preceded or accompanied by rainfall. Variation in movement of juveniles could not be attributed to any of the environmental variables measured. However, when a storm did occur in the middle of the metamorphosis period, a disproportionate number of juveniles emigrated, suggesting that rainfall can have an influence.

Several factors may influence production of juveniles among ambystomatid species, but none adequately explains variation in our study. Our results agree with others that have failed to show a consistent relationship between juvenile production and number of breeding females (Shoop, 1974; Semlitsch, 1987). Juvenile production has been positively correlated with pond duration in other studies (Shoop, 1974; Semlitsch, 1987; Scott, 1990) but not in ours; juvenile production was highest in 1992 though pond duration was longer in 1993. Other possible influences include floods and freezes (Anderson et al., 1971; Petranka and Sih, 1986), which did not occur in our study, and predation and intraspecific competition (Anderson et al., 1971; Semlitsch and Caldwell, 1982; Stenhouse, 1987), which were not measured. Determining patterns in juvenile production may likely require many years of data because of the high variability. Therefore, our data set may be too short to adequately discern correlations. The cause of reproductive failure in 1994 remains uncertain.

Body size variation.—Among adults, males had longer tails than did females. Arnold (1976) found proportionately longer tails in male *A. tigrinum*, the closest relative of *A. californiense*, and proposed that this difference arose as a result of the tail's importance in courtship during which males perform a tail-nudging walk to lead females to spermatophore deposition sites. Tail size may play a similar role in *A. californiense* courtship.

In both 1992 and 1993, large juveniles metamorphosed early; later developing juveniles gradually increased in size at metamorphosis as the season progressed. Both early timing of and large size at metamorphosis have been positively correlated with fitness traits including age at first reproduction, survival, and adult size (Smith, 1987; Semlitsch et al., 1988; Berven, 1990). Large larvae may thus be under selection to metamorphose early, whereas smaller larvae may benefit from increased growth before metamorphosis. The advantage accrued by delaying metamorphosis, however, may be outweighed if the pond dries before metamorphosis is complete. Thus, in addition to any body size cues, pond duration can influence timing of metamorphosis (Wilbur, 1980; Semlitsch and Wilbur, 1988; Semlitsch et al., 1988). In our study, the period of peak metamorphosis occurred later in a year when the pond did not dry (1993) than when it dried by midsummer (1992).

California tiger salamanders showed substantial variation in life-history traits among years. Environmental conditions, specifically breeding season rainfall and pond duration, are important influences on breeding population sizes and sex ratios, adult movement patterns, juvenile production, and timing and size at metamorphosis. High annual variation in reproductive traits may be a common feature among ambystomatids (Shoop 1974; Semlitsch 1983; Stenhouse 1987) and may represent selection for phenotypic plasticity as an adaptation to highly variable, transient environments (Wilbur and Collins, 1973; Caswell, 1983; Scott, 1994). The geographic region encompassing the range of the California tiger salamander commonly experiences periodic droughts lasting several years. Juvenile recruitment may be minimal during drought conditions, yet the species may be maintained by periodic "boom" years during which recruitment is very high.

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Perulibatrachus kilburni, a New Toadfish from East Africa (Teleostei: Batrachoididae)

DAVID W. GREENFIELD

A third species of *Perulibatrachus* is described from Natal, southeastern South Africa. The other two species in the genus, *P. elminensis* and *P. rossignoli*, are known only from the west coast of Africa. *Perulibatrachus kilburni* differs from both species in having 19 pectoral-fin rays (vs 23 or 26), bony interorbital width 49.1‰ SL (vs 108–116.3‰), eye 145.5‰ SL (vs 75.7–83.7‰), and distinctive color pattern, especially an intense-white bar between eyes and a similar white spot on upper body at center of second dorsal fin. It differs from each of the described species in a number of additional characters.

ROUX (1971) erected *Parabatrachus* for the toadfish *Batrachus elminensis* Bleeker (1863) and also included *Batrachus rossignoli* Roux (1957) in the genus. Roux and Whitley (1972) proposed *Perulibatrachus* as a substitute name for *Parabatrachus*, which was preoccupied. The title of their paper refers to Roux (1970), but the paper acutally was published in 1971. Both known species of *Perulibatrachus* occur only on the west coast of Africa: *P. elminensis*, from Ghana south to Walvis Bay, Namibia, and *P. rossignoli*, from Gabon south to Walvis Bay (Roux, 1981; Hutchins, 1986).

The most recent key to toadfish genera is that of Smith (1952). In that key, *Perulibatrachus* would fall in section B III, which includes *Chatrabus*, *Barchatus*, *Tharbacus*, *Batrachoides*, and *Halobatrachus*. Hutchins (1986) considers *Thar-*