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LATE SUMMER MOVEMENT AND MASS MORTALITY IN THE CALIFORNIA TIGER SALAMANDER (*AMBYSTOMA CALIFORNIENSE*)

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Overland movements to and from breeding sites by adults are a well-documented aspect of the life history of many ambystomatid salamanders (Douglas and Monroe, 1981; Semlitsch, 1983a; Stenhouse, 1985; Beneski et al., 1986). By comparison, movements of juveniles are poorly understood, although some data imply that juveniles are vulnerable to dehydration or heat stress during overland movement (Webb and Rouche, 1971; Shoop, 1974; Semlitsch, 1981). That limited understanding leads us to report the circumstances associated with a unique, unseasonal overland movement by juvenile California tiger salamanders (*Ambystoma californiense*) and their subsequent mass mortality. These data are also significant because this poorly known California endemic has been listed as being of special concern

(Jennings, 1983); large temporary pools, its major breeding habitat (Feaver, 1971), are rapidly disappearing (Jain, 1976; Zedler, 1987).

Observations were made during August through October 1983 at Grant's Lake, a large (20 ha), shallow (<1.5 m) sag pond on the San Andreas fault in the inner Coast Ranges of central California. Although this lake often dries by June, it held water throughout 1983. Based on rainfall, this region approaches a desert (Major, 1977). Mean annual precipitation is 268 mm (records from 1936 to 1984 for a station 5 km north of Grant's Lake), although 1983 had the second highest annual rainfall (508 mm) on record. An annual grassland (Heady, 1977) with scattered woody shoreline vegetation surrounds the lake. Surface cover (e.g., cottonwood (*Populus fre-*

montii) logs, planks, trampled shrubs) was abundant on the east shore but scarce or absent elsewhere.

On 21 and 22 August, J. Grant (pers. comm.), a local, 50-year resident, noted extensive surface activity of *A. californiense*. Movements were observed at night between 1900 and 2200 h and before 0800 h. Grant noted that all salamanders were moving towards the north shore of the lake, that little variation was apparent in body size among individuals, and that individuals observed were much smaller than those observed during late winter-early spring breeding migrations. Grant also found hundreds of salamander trackways, each with a similar north-south or northeast-southwest orientation, in the fine-textured soil 120 m from the north shore; trackways were still visible on 15 September. Salamander activity was preceded by an unseasonal storm that deposited 12 mm of rain on 19 August and an additional 3 mm on the following day. Prior to 19 August, it had not rained since 2 April (2 mm) and, after 20 August, it did not rain again until 21 October (21.5 mm).

On 15 September, over 100 post-metamorphic *A. californiense* were found under surface cover along the north shore of Grant's Lake during a 1-h search. Twenty-three were aggregated under a large barrel approximately 30 m from the waterline. Four others were found wedged in a crack in the soil under a dried algal mat. Salamanders were found only in areas near the lake shore. All individuals were alive, showed no obvious signs of stress and appeared similar in size; 21 collected had a mean snout-vent length (SVL) of 62.4 mm (range of 56.0 to 69.0 mm, UCSB 15457-15477, recorded to the nearest 0.5 mm after preservation).

On 24 September, the east shore was surveyed at 1900 to 1930 h. Three dead larvae of *A. californiense* (SVL = 59, 67 and 70 mm, UCSB 19500-19502) found in shallow (60 cm) water of 24.0°C showed no signs of decomposition. No salamanders were found on the surface or under cover along the east shore. On 2 October, the north, east, and south shores were surveyed at 1400 to 1730 h. One hundred sixty-seven metamorphosed *A. californiense* were found along the north shore; 165 of these were dead. The two live individuals died within 2 h despite efforts to rehydrate them. Over 70% of the salamanders were found in cattle hoofprints, and most of the pieces of surface cover had at least one salamander un-

derneath. Twenty-nine individuals were tightly packed into a ball in a nest of a cricetid mouse under a plank. A 20-min search of the east shore revealed 15 additional carcasses on exposed ground or in hoof prints. Carcasses were not found under the abundant surface cover less than 10 m away. No carcasses were found along the south shore, but two living individuals were found under a cottonwood log. These salamanders died within 48 h despite efforts to rehydrate them. All salamanders observed on 2 October appeared similar in size, but most were desiccated to the point of mummification. Twenty-eight individuals (\bar{X} SVL = 63.9 mm, range of 59.0 to 69.0 mm, UCSB 19504-19531) were flexible enough to be measured, and this sample did not differ significantly in size from those collected on 15 September (Mann-Whitney *U*, $P = 0.075$). Extensive seining produced two dead larvae along the east shore and a single live larva (SVL = 66.0 mm, UCSB 19503) from the water of 24.5°C along the south shore. This animal swam erratically, could not right itself, and died within 24 h.

The movement of salamanders on 21 and 22 August appeared to be an en masse immigration of juvenile *A. californiense* toward Grant's Lake. Observation of movement only towards the lake makes unlikely the alternative of an emigratory event by recent metamorphs; timing and size and reproductive condition of immigrants eliminate the possibility of a breeding migration. In this area, breeding migrations of *A. californiense* have been observed only from January to March (pers. obser.); elsewhere in California, this species migrates from November through April, when breeding pools fill (Storer, 1925; Twitty, 1941; Anderson, 1968; Feaver, 1971; J. Medeiros and S. Sweet, pers. comm.). Dissection of all Grant's Lake specimens indicated little gonadal differentiation, and body sizes were smaller than the smallest reproductive *A. californiense* we could find in an examination of 96 post-metamorphic specimens surveyed from museum collections (adult males, 80 to 108 mm SVL, $n = 26$; adult females, 79 to 119 mm SVL, $n = 37$). Moreover, the relative uniformity in body size among individuals found on 15 September and 2 October and Grant's parallel observation for 21 and 22 August suggests that salamanders belonged to a single cohort. Twitty (1941) observed two juveniles moving with adults during a breeding migration, but observations parallel to ours have not been reported for any ambystomatid salamander.

Three plausible, non-exclusive explanations exist for why juvenile *A. californiense* migrate to water. First, response to environmental cues that initiate movement may differ in adults and juveniles. Semlitsch (1983a) observed that despite rain, adult salamanders would not migrate if seasonal trends in air temperature were unsuitable. The lack of adults being observed on 21 and 22 August and among the 190 individuals subsequently found appears to support this hypothesis. Second, return to water may be important to the growth of metamorphosed *A. californiense*. Temporary pools frequently support large numbers of prey organisms (Anderson, 1968; Jain, 1976; Zedler, 1987), so they may consistently have more food than terrestrial habitats used by salamanders. Webb and Rouche (1971) concluded that juvenile *Ambystoma tigrinum mavortium* return to water based on finding spadefoot (*Scaphiopus multiplicatus*) tadpoles the most frequent prey item in stomachs of members of that age group. An examination of the stomachs of 12 (57%) and 17 (60%) of the *A. californiense* with stomach contents collected on 15 September and 2 October, respectively, failed to reveal the obligately aquatic prey that would provide convincing support for this hypothesis. Still, lack of such evidence should not be construed as excluding this hypothesis since conditions in Grant's Lake may have been unfavorable to salamanders remaining there. Third, California's Mediterranean climate is believed to have become established through the gradual diminution of summer rains (Axelrod, 1973), so the observed movement may simply reflect the historical repertoire of *A. californiense*. This reason alone cannot explain why only juveniles moved without invoking an explanation of why adults did not move (e.g., see first hypothesis).

Microsites and the aggregates in which dead and disoriented salamanders were found suggest that they experienced dehydrative conditions (Alvarado, 1967), which are known to decrease heat tolerance (Claussen, 1977). We suspect that a combination of the lack of surface moisture and high surface temperatures (air temperatures averaged 28°C, high of 38°C) fatally stressed salamanders that immigrated to the lake on 21 and 22 August. Shoop (1974) and Semlitsch (1981) suggested that desiccation was the cause of mortality for over half the juvenile ambystomatids they followed, but in neither case was mortality preceded by the circumstances we report. The presence of dead and disoriented larvae in the

lake suggests that conditions there may have precluded the use of this potential refugium by immigrants. What these conditions may have been is unclear, but larvae were presumably not temperature stressed because water temperatures observed on 24 September and 2 October were at least 5°C below those recorded at pools where healthy larvae have been observed (Anderson, 1968; R. Hansen, pers. comm.; pers. obser.). Burrowing (see Semlitsch, 1983b) or taking refuge in rodent burrows (Storer, 1925; J. Medeiros, pers. comm.) was not an option for most individuals because the clay hardpan around the lake precluded burrowing and rodent burrows were scarce within 40 m of the east shore and 60 m of the north shore. Previous observations of overland movement have always somehow been coupled with rain (Storer, 1925; Twitty, 1941; J. Grant, pers. comm.; pers. obser.). Without rain to allow retreat to burrow refugia, we believe juvenile *A. californiense* were forced to move to the most accessible, moist microenvironments available (i.e., surface debris or cattle footprints along the lake shore). There, salamanders were trapped by drying conditions that resulted in their eventual mass mortality.

In conclusion, juvenile *A. californiense* can engage in unseasonal overland movement. Other salamanders may engage in similar behavior (R. Semlitsch, pers. comm.), but the biological significance of this phenomenon is unclear. In *A. californiense*, some types of habitat loss and modification are already likely to result in consistently high mortality for juveniles, particularly if their movements are stereotyped (see Douglas and Monroe, 1981; Stenhouse, 1985; Phillips and Sexton, 1989). Unseasonal movements may exacerbate this problem, and long-term data are needed to establish the frequency of such events and their effect on population dynamics. Adults may continue to migrate successfully and reproduce for many years, but those populations risk extirpation if increased recruitment failures induced by such events go unrecognized.

We thank J. Grant for detailing his observations and providing weather data for Grant's Lake. Long-term precipitation records were obtained from H. Twisselman. We thank J. Vindum (California Academy of Sciences) and S. Sweet (University of California at Santa Barbara) for the loan of comparative material. J. C. Medeiros provided insight with his comments on the behavior of California tiger salamanders at the Hickman

vernal pools. Specimens are deposited at the University of California at Santa Barbara (UCSB). R. W. Hansen, J. F. Jackson, R. G. Jaeger, M. R. Jennings, C. M. Nelson, R. D. Semlitsch, S. S. Sweet, S. C. Walls and three anonymous referees reviewed this manuscript.

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