Data on the Life History of Ambystoma tigrinum californiense Gray

By Victor C. Twitty

SINCE relatively little information is available concerning the *Ambystoma* of California, it seems desirable to record certain data accumulated during the past few years, mostly incidental to the collection of embryos and adults for experimental purposes.

The first observations on the spawning migration of A. tigrinum californiense were made recently by Professor W. H. Rich. During the first heavy rain of the season, on January 1, 1940, he collected approximately 45 adults between 10 and 11 p.m. on the highway bordering Lake Lagunita near the Stanford golf course. Twenty-eight of these had been killed by passing cars. The living specimens were migrating in the direction of the lake-bed, although the latter had not yet begun to fill with the winter rains. Of the dead specimens, dissection revealed that 18 were males and 4 females, with the remaining 6 too mangled for identification of their sex. The living specimens included 7 males, 8 females, and 2 immature specimens. The males were readily distinguishable without recourse to dissection by their heavily swollen cloacae and more prominently developed tail fins, Three of the larger males measured 21, 22, and 23 cm., as compared with 17, 18, and 19 cm. for the same number of females.

The following evening, which was cool and clear, the writer visited the same half-mile stretch of road and found no animals. It was raining heavily again the next evening, January 3, however, and three excursions between 7:30 and 10 p.m. netted 15 females and 8 males. In addition, 5 or 6 injured or killed animals were observed. Two nights later Mr. L. E. DeLanney, also during a heavy rain, collected 4 females and one male in one trip along the same portion of road. The declining percentage of males in the three successive collections may or may not be indicative of a differential in onset of migration between the two sexes, which appears to be so marked for A. maculatum of the eastern United States (Moment, 1938).

A striking behavior was exhibited by the animals shortly after they were placed in a large tank of water on return to the laboratory. In several instances the male was observed to pursue the female actively around the aquarium, his head beneath her tail and appearing to nose her cloacal region. On the following morning a number of spermatophores were found attached to the floor of the aquarium. Although spawning of the females did not ensue, this is possibly attributable to the crowded and unnatural conditions afforded by the aquarium.

DATA ON SPAWNING

Most of our data on spawning have been collected from a temporary rain pool, roughly an acre in extent and scarcely more than a foot in depth, which forms each year during the winter rains in an open field on the Alpine Road

¹Ten of these specimens were preserved for the collections of the Stanford Natural History Museum, Nos. A4784-4793.

about 5 miles from Stanford University. Eggs are often laid in great abundance in this pool, attached to the stems of grass and other plants. As reported by Storer (1925: 65), they are generally deposited singly, although groups of 2 to 4 are not uncommon. In one unusual case about 15 were found attached to a plant stem in an elongated cluster suggestive of that typical for A. tigrinum of the eastern states. Following is a summary of our records from this pool. Unless otherwise specified, the visits were made during the daylight hours.

On January 13, 1936, several eggs in young cleavage stages were collected; they were probably deposited the previous evening. The pool was visited again about 10 P.M. on January 14, during a warm rain, and 9 females were found in the act of spawning. The females were observed to grasp the plant stems with their hind legs while the eggs were being deposited. Three days later, January 17, many eggs ranging in development from morulae to advanced neural plate stages were collected or observed.

The following year, 1937, many eggs ranging from 2-cell to gastrula stages were collected on January 12. About two weeks later, January 25, another collection yielded embryos varying in development from gastrula to "tail-bud" stages. Their development had presumably been retarded by the cold weather intervening since the date of last collection. Two weeks later, February 8, with the exception of a few young neurulae, the product of a more recent spawning, all the embryos observed were in the motile stage of development which precedes hatching. These presumably belonged to the group first observed on January 12.

The following winter the pond was first visited on December 13, 1937. Only a few eggs were found, in blastula and gastrula stages. They had probably been deposited during the last rain two or three nights previously. All embryos collected on the next trip eleven days later, December 24, were in tail-bud stages of development, and probably belonged to the same group noted on the preceding visit. There was in fact apparently no resumption of spawning until considerably later in the season. After two fruitless trips in January, a few blastulae were found on February 6, 1938.

On January 2, 1940, the day following Prof. Rich's observations on the migration of adult *Ambystoma*, the pond on Alpine Road had not yet begun to fill with water. At the next visit on January 13, however, it was well filled, and many embryos were taken. The great majority of these were in tail-bud stages, although several neurulae and a few gastrulae were found. The evidence thus indicates that heavy spawning occurred only a few days after the first onset of migration as recorded above, and almost immediately upon accumulation of water in the pool.

Hyla regilla also spawns abundantly in the pool on Alpine Road, the onset of breeding seeming to coincide closely with that of A. t. californiense. Triturus torosus has never been observed to inhabit the pool, although it spawns regularly in a permanent pond only a few hundred yards distant. Conversely, A. t. californiense has not been known to spawn in the latter pool. In fact, as indicated by Storer (1925), this species appears to prefer the shallow waters of temporary bodies of water for its breeding activities. The two other loca-

tions where eggs of A. t. californiense have been taken by us, namely the margins of Lagunita as this lake fills during early winter, and a small pond on the Portola Road about 2 miles distant from the one on Alpine Road, both conform to this description.

Storer (1925: 65) records finding A. t. californiense embryos in advanced stages of development on February 15, 1924, in eastern San Joaquin County, and gives additional data concerning larval stages collected from pools in that region. On May 12, 1937, a Stanford student presented the writer with several larvae measuring approximately 80 to 90 mm., taken that day from Lagunita. Although the gills were still unreduced, these specimens were probably approaching metamorphosis, judging from the size at which transformation may occur in larvae reared in the laboratory.

DEVELOPMENT

It is of interest to compare the developmental stages of this species with those of A. tigrinum tigrinum, since such a comparison serves to establish well marked differences as well as the fundamental affinities between the two forms. The eggs and embryos are very similar in size, both measuring about 2.0 mm. in diameter in the gastrula stage. The embryonic and larval stages also conform closely to the same morphological type, including general proportions of the body and such special features as absence of the 'balancer.' The eggs and embryos of A. t. californiense are less heavily pigmented than those of A. t. tigrinum, a distinction which also applies to the larval stages, although the general pattern of chromatophore arrangement is similar in both.

At least two features have been observed, however, which sharply differentiate the larvae of t. californiense and t. tigrinum. One of these is the rate of growth. Although we shall not attempt to present absolute data on this point, repeated experience has shown that under identical laboratory conditions the rate of larval growth is much higher in t. tigrinum. This difference has, of course, no utility as a taxonomic criterion, but it nevertheless serves to substantiate the genetic distinction between these two forms. The second feature concerns the relative size of the larval eye, which is markedly greater in t. tigrinum than in t. californiense. Incidentally, the size of the eye in t. californiense is almost identical with that of Siredon mexicanum, for larvae of any given length. Attention was called in an earlier paper to the smaller eye-size in mexicanum as compared with t. tigrinum (Twitty and Elliott, 1934: fig. 21).

It may be recorded here that the writer has artificially hybridized A. t. californiense with S. mexicanum. Highly viable offspring, all of which metamorphosed, were obtained and reared to maturity. An equally viable backcross resulted when eggs of S. mexicanum were fertilized with sperm from one of the hybrid males.

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Evidence of Venom in Hypsiglena ochrorhynchus

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S PECIMENS of Hypsiglena ochrorhynchus, the spotted night-snake, have been found to feed freely on Xantusia vigilis, the yucca night-lizard. Where this lizard is not available it may be presumed that Hypsiglena may also feed on other small scaled lizards such as Uta stansburiana, U. graciosa and Coleonyx variegatus, as well as the very small young of other species. The availability of a food supply for juvenile individuals of Hypsiglena presents a different problem, for the young of this species are so small that in areas where Xantusia are not present the juveniles must perforce subsist on invertebrates as the adult Sonora occipitalis are known to do.¹ It is probable that those occurring in the habitat of the yucca night-lizard may augment this arthropod diet by feeding on the minute newly born young of these lizards, which appear in large numbers during late August, September, and well into November. Most of our juvenile Hypsiglena have been captured during this period and the chronological juxtaposition of juveniles of these species would appear to be an advantage to the snakes.

Repeated feeding episodes have suggested that the quiescence of captured lizards has been due to something more than the normal habitual docility of lizards once they have been overpowered by a snake, namely the presence of a functional venom. On several occasions lizards which have been captured and held by only one limb or the tail have been liberated and kept under observation with a view to determining whether or not visible evidence of toxemia might appear. In many there was no apparent evidence of toxemia, but in a number of instances death took place within a very few minutes after being bitten. Such deaths were attributed to possible mechanical injury resulting from deep punctures caused by the enlarged posterior maxillary teeth.

The enlarged posterior maxillary teeth have no more than a slight sug-

¹ Scorpions have been found in several freshly collected individuals of this species and have been fed to them in captivity. Under the latter condition they have also captured and consumed relatively large centipedes. Other arthropods presumably supply the small snakes with most of their food, especially the wingless burrowing cockroach, which is so abundant in the sandy areas inhabited by this species.