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Author(s): Casey S. Berkhouse and Joe N. Fries

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ber of potential pollinators because many of the small bees present on the southwestern Edwards Plateau do not become active until later in the spring. Honey bees were one of the most frequent visitors to *A. tobuschii* during this study.

The initial survey was conducted with the help of David K. Stuart. The halictid bees were identified by George Eickwort, Evan Sugden, and J. L. Neff. David H. Riskind and Ray Emmett made suggestions on earlier drafts.

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CRITICAL THERMAL MAXIMA OF JUVENILE AND ADULT SAN MARCOS SALAMANDERS (*EURYCEA NANA*)

CASEY S. BERKHOUSE AND JOE N. FRIES

National Biological Service, San Marcos National Fish Hatchery and Technology Center,
500 East McCarty Lane, San Marcos, TX 78666

The San Marcos salamander (*Eurycea nana*) is endemic to the upper reaches of the San Marcos River, Hays County, Texas. The salamander occurs only in Spring Lake (the headwaters of the San Marcos River) and the portion of the river to a point 150 m below the Spring Lake dam (Nelson, 1993). Spring Lake receives its water from numerous springs emerging from the Edwards Aquifer. The water near the springs is thermally constant (21 to 22°C) and has a pH from 7.1 to 7.6, dissolved oxygen of about 4 mg O₂/L, and a moderate alkalinity (about 275 mg CaCO₃/L) (Ogden et al., 1985). Population estimates for the salamander range from approximately 21,000 (Tupa and Davis, 1976) to 54,000 (Nelson, 1993). Due to its limited distribution and dependence on spring flow, the San Marcos salamander has been listed as a threatened species (United States Department of the Interior, 1980).

Substantial reduction or complete cessation of spring flow would allow water temperature in the habitat of the San Marcos salamander to fluctuate daily and seasonally, which could adversely affect individual salamanders and population viability. However, the temperature tolerances of this species are unknown. The upper limit of temperature tolerance for the salamander, at a given acclimation temperature, can be determined

by calculating its critical thermal maximum (CTM) (Fry, 1967). Hutchison (1961) defined CTM as "the arithmetic mean of the collective thermal points at which locomotor activity becomes disorganized and the animals lose their ability to escape from conditions that will promptly lead to their death." The purpose of our study was to determine the CTM for juvenile and adult San Marcos salamanders acclimated to the temperature of their stenothermal environment.

Tests were done at the San Marcos National Fish Hatchery and Technology Center (SM-NFHTC), San Marcos, Texas, using a water bath that raised the temperature of 9.7 L of water about 1°C/minute, the same rate used by Hutchison (1961). A clear, perforated PVC test cell for holding the salamanders during CTM determinations was placed inside the water bath. An aquarium power head provided flow through the test cell and mixing within the water bath. A pH/mV/°C microprocessor and probe were used for all pH and temperature measurements. The probe was calibrated using commercial pH standards and a certified (National Institute of Standards and Testing) mercury thermometer. Preliminary tests were run on eight San Marcos salamanders that had been maintained at the SMNFHTC for 1–2 years. Results of these tests

indicated that the loss of righting response (LRR) or the onset of spasms (OS) (Claussen, 1977) should be objective endpoints for the CTM tests for this species, and supported the use of 160 mg/L of tricaine methanesulfonate (MS-222) as an anesthetic for the salamanders during weight and length measurements. Heat rigor followed OS but was not well defined.

Tupa and Davis (1976) reported that wild male San Marcos salamanders reached sexual maturity (based on testicular development) at a snout-vent length (SVL) of 19 mm and that wild females were sexually mature (based on egg maturation) at a SVL of about 21 mm. Based on these data, we assumed that salamanders with a SVL <19 mm were juveniles and a SVL >21 mm were adults (i.e., were sexually mature).

Salamanders were collected on 15 July 1994 (adults) and 1 September 1994 (juveniles) from the northern end of Spring Lake (Texas Parks and Wildlife Department scientific collection permit number SPR-0390-045). Water temperature and pH at the site during the first collection were 21.7°C and 7.64, and during the second collection were 21.9°C and 7.18, respectively. Dipnets were used to retrieve mats of vegetation (mainly *Amblystegium riparium*) from which we removed salamanders. Salamanders were transported to the laboratory and held in an ice chest containing water from the collection site. The water temperature in the ice chest was maintained (using ice in plastic bags) within $\pm 0.3^\circ\text{C}$ of the water temperature at the collection site.

The CTM tests were run on individual salamanders ($N = 10$ for both juveniles and adults) on the day of collection. For each test, the water bath was filled with chilled (19°C) Edwards Aquifer water (pH = 7.67 for tests with adults and pH = 7.37 for tests with juveniles). After raising the water temperature to that of the collection site, a single salamander was placed into the test cell. Salamander behavior, water temperature, and time were monitored during the tests; temperatures at LRR and at OS also were recorded. The salamanders then were quickly removed from the test cell, placed inside numbered recovery chambers (one salamander per container), and returned to the ice chest. After all CTM tests were completed, salamanders were anesthetized and SVL was measured for each. Weight (WT) also was measured for the adults (we were unable to accurately measure WT for the juveniles). Salamanders were returned to their re-

covery chambers and held in aquaria at approximately 21°C. After three days, the salamanders were removed from their recovery chambers, mortality was recorded, and the survivors were released into the aquaria. Statistical analyses followed the methods of Zar (1984) and significance was set at $P \leq 0.05$.

Salamander behavior was fairly consistent during the tests. Typically, the salamanders showed little activity until the water temperature reached 29–30°C. As the temperature increased beyond that, the salamanders became more active and occasionally would break the surface of the water along the side of the test cell. Often there were episodes of “false LRR” where the animals would lie on their backs or sides and, after being gently probed with a blunt instrument, would right themselves and continue swimming. These episodes were followed by true LRR. After LRR, the salamanders became still and often, while lying on their backs or sides, assumed a “C-shape” from which they would slowly straighten. It was during this time that OS usually occurred. The intensity of spasms was variable and ranged from total body convulsions to spasms of only the head and upper body. The spasms generally were more pronounced for the juveniles.

For the adults, the mean temperature at LRR was 35.8°C and was significantly lower (paired t -test: $t = 6.56$, $P < 0.001$) than the temperature at OS (37.2°C) (Table 1). For the juveniles, the mean temperatures at LRR and OS were 34.3°C and 35.8°C, respectively. These means also were significantly different (paired t -test: $t = 7.99$, $P < 0.001$). The mean difference between OS and LRR temperatures for the adults was 1.3°C and for the juveniles was 1.5°C. These means were not significantly different (unpaired t -test: $t = -0.48$, $P > 0.05$). Claussen (1977) reported that LRR temperatures averaged 0.8°C below OS for the salamanders *Ambystoma jeffersonianum* and *A. tigrinum* (presumably pooled for both species) and Hutchison and Rowland (1975) reported that the temperature at LRR for *Necturus maculosus* was highly variable and ranged from 1.0 to 4.4°C below OS.

Hutchison (1961) listed several responses of salamanders to heating (LRR, OS, increased mucous secretions, and heat rigor) and found that OS usually was the least variable for 26 species tested. We found OS to be less variable (coefficient of variation (CV) = 1.8%) than LRR (CV = 2.4%) for juvenile San Marcos salamanders and

TABLE 1.—Mean snout-vent length (SVL, mm), mean weight (WT, g), and mean temperatures (°C) at loss of righting response (LRR) and onset of spasms (OS) for San Marcos salamanders (*Eurycea nana*) used in critical thermal maxima tests ($n = 10$ for both juveniles and adults). Means in a column followed by different letters are significantly different ($P < 0.05$).

	SVL			WT			LRR			OS		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Juveniles	10.7a	0.58	8-14	—	—	—	34.3a	0.26	33.1-35.5	35.8a	0.21	34.8-36.9
Adults	25.8b	1.04	22-30	0.240	0.013	0.18-0.32	35.8b	0.10	35.3-36.2	37.2b	0.20	36.3-38.1

more variable (CV = 1.7%) than LRR (CV = 0.9%) for adults.

The mean temperature at LRR for adults was significantly greater than that for juveniles (unpaired t -test: $t = 5.55$, $P < 0.001$) (Table 1). This was true also for the mean temperature at OS (unpaired t -test: $t = 4.82$, $P < 0.001$). Hutchison (1961) found that the mean CTM (using OS as the endpoint) for adult *Diemictylus* (= *Notophthalmus*) *viridescens viridescens* was significantly greater than that for larvae. On the other hand, Delson and Whitford (1973) found that larval and neotenic *A. tigrinum* from an ephemeral desert pond had a higher CTM (using the completion of spasms as the endpoint) than did transforming or completely transformed adults from the same habitat. They speculated that this was an adaptation to life in this habitat; transformed adults can move from drying ponds at night and thus avoid severe thermal conditions (up to 30°C) in the ponds during the day while larvae and neotenes may be trapped in those ponds.

The endpoint for CTM appears to be species-dependent and open to interpretation. Claussen (1977) chose heat rigor, which occurred after OS, as the endpoint for CTM tests with *A. jeffersonianum* and *A. tigrinum*. Hutchison and Rowlan (1975) chose OS for tests with *N. maculosus*, though the spasms were characterized only by "twitching of the limbs and trunk" and "tetany of the hyoid musculature." Hutchison (1961) preferred OS for 26 species of salamanders tested. We feel that at LRR the San Marcos salamanders conceivably could have escaped local high temperatures by random whole body movements. At OS, however, the salamanders effectively were immobile. Also, LRR was a more ambiguous endpoint than OS. We chose OS for the CTM endpoint for this species because it was less subjective than LRR and fits Hutchison's (1961) definition of CTM better than LRR. Claussen (1977) and Hutchison (1961) mentioned the copious secretion of mucus as a possible endpoint, but this was not observed in our tests.

Test animals typically survive CTM tests if they are removed from the test cell immediately after reaching OS and placed at a lower temperature (Hutchison, 1961). All of the San Marcos salamanders were alive after the completion of the last CTM test. One adult, however, was very inactive. This salamander had the highest CTM (38.1°C). Three days after testing, this salamander and two additional adult salamanders were

dead. The two additional salamanders had CTMs of 37.2°C and 37.6°C and were among the shortest adult salamanders tested (SVL, 22 mm and 23 mm). One of the juvenile salamanders was dead three days after testing. This salamander had the lowest CTM (34.8°C) and a SVL of 10 mm. Brattstrom (1968) and Miller and Packard (1977) did not consider data from frogs that did not recover immediately after CTM tests. Our salamanders, however, had the additional stress of exposure to MS-222 and handling for length and weight measurements. These stresses could have been at least a partial cause of the mortalities, so we used all the data in our analyses.

There was no significant correlation between CTM and WT for adult salamanders (Pearson's $r = 0.22$, $P = 0.54$). Hutchison (1961) likewise found no correlation between adult WT and CTM for 26 species of salamanders tested. We also found no significant correlation between CTM and SVL for either juveniles (Pearson's $r = 0.43$, $P = 0.22$) or adults (Pearson's $r = 0.23$, $P = 0.53$), but when the data were pooled there was a significant correlation between CTM and SVL (Pearson's $r = 0.77$, $P < 0.001$).

No previous CTM tests or temperature tolerance studies have been conducted on the San Marcos salamander. We found the CTM of this species to be higher than the CTM of two congeners and less than that of one congener that Hutchison (1961) acclimated at 20°C: *E. bislineata wilderae* (32.1°C, $N = 3$ "juveniles"), *E. lucifuga* (35.0°C, $N = 10$ "adults") and *E. longicauda guttolineata* (35.9°C, $N = 3$ "adults"). Tupa and Davis (1976) reported that when an aquarium holding San Marcos salamanders was inadvertently allowed to reach 30°C, the salamanders "went into convulsions and died." Norris et al. (1963) noted that San Marcos salamanders held at 30°C during oxygen consumption tests had higher mortality than those held at 25°C under the same conditions. They speculated that this species may be less tolerant of temperature change than the congeners also tested (*E. pterophila* and *E. neotenes*).

The San Marcos salamander shares its habitat with the endangered fountain darter (*Etheostoma fonticola*). Brandt et al. (1993) found the mean CTM of 18 fountain darters was 34.8°C. Because of differences in procedure, however, we cannot compare our results to theirs. Spring Lake is listed as critical habitat for both of these species (United States Department of the Interior, 1980),

and the use of one of these species as a temperature-sensitive indicator for this environment could be useful.

The results of this study should be considered only within the limited definition of CTM. Exposure to temperatures elevated above that of the spring environment, and below CTM, could have detrimental effects on this species. No studies have been done to assess exposure to elevated subcritical temperatures on aspects of this salamander's life history (e.g., fecundity, mating, feeding, larval development).

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