

# CRITICAL THERMAL MAXIMA IN SEVERAL LIFE HISTORY STAGES IN DESERT AND MONTANE POPULATIONS OF *AMBYSTOMA TIGRINUM*

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**ABSTRACT:** Montane neotenic *Ambystoma tigrinum* had lower critical thermal maxima (CTM) than desert neotenic *A. tigrinum*. In all other life history stages studied there were no differences in CTM between montane and desert populations. Comparison of life history stages in a desert population showed that larvae and neotenic adults had higher CTM than transformed animals or animals in the process of transforming. The CTM differences in life history stages reflects the potential thermal stresses to which these stages may be subject.

In New Mexico, the tiger salamander, *Ambystoma tigrinum*, ranges from desert scrub habitats at elevations of 900–1500 m to spruce-fir forests at 2500–3000 m. In the desert habitats, water temperatures may reach 30–35 C for brief periods and when desert ponds dry, migrating *A. tigrinum* could be subjected to temperatures above 30 C. In montane areas water temperatures rarely exceed 20 C and migrating salamanders would unlikely be exposed to air temperatures above 25 C. Apparent contrast in thermal environments of desert and montane populations of *A. tigrinum* provided an opportunity to examine possible evolutionary shifts in physiological tolerances within these populations.

Brattstrom (1970) demonstrated that there were significant differences in the critical thermal maxima (CTM) of anurans of the same species from different elevations. However, the patterns of the differences were not constant and in some species, animals from low elevation populations had lower CTM's than higher altitude populations of the same species. Similar inconsistencies were noted in metabolic response of anuran populations of the same species from different elevations (Packard and Bahr, 1969; Jameson et al., 1970).

Hutchison (1961) showed that the CTM in transforming larvae of *Diemictylus v. viridescens* was lower than that of the eft and newt stages and suggested that determination of CTM in different developmental stages would be useful in describing the changes in thermal tolerance that occur

with development. Since populations of *A. tigrinum* may include larvae, transformed adults and neotenic adults within a single mountain or desert pond, we decided to examine both the influence of elevation on the CTM and the relationship between thermal tolerance and life history stage of *A. tigrinum*.

## METHODS

*Ambystoma tigrinum* used in this study were collected in May and June of 1970 from three localities in southern New Mexico. One of the sites, an ephemeral desert pond 1036 m elevation, was located 48 km NW of Las Cruces, Dona Ana County. The other sites, one permanent and one ephemeral, were located at approximately 2500 m elevation in the Sacramento Mountains near Mayhill and Sunspot, Otero County, New Mexico. All tiger salamanders were acclimated in the laboratory at 10 or 20 C and 12-hour photoperiod for at least one week prior to use in the experiments.

Salamanders brought to the laboratory were placed in aquaria filled with aged tap water. None of the animals were fed prior to the experiments. The salamanders from the montane ponds included larvae (22–38 mm snout-vent length) from an ephemeral pond and neotenes (30–134 mm SVL) from a permanent pond. These animals did not metamorphose in the laboratory. Salamanders from the desert ponds exhibited a variety of responses. Some rapidly metamorphosed into air breathing adults (desert

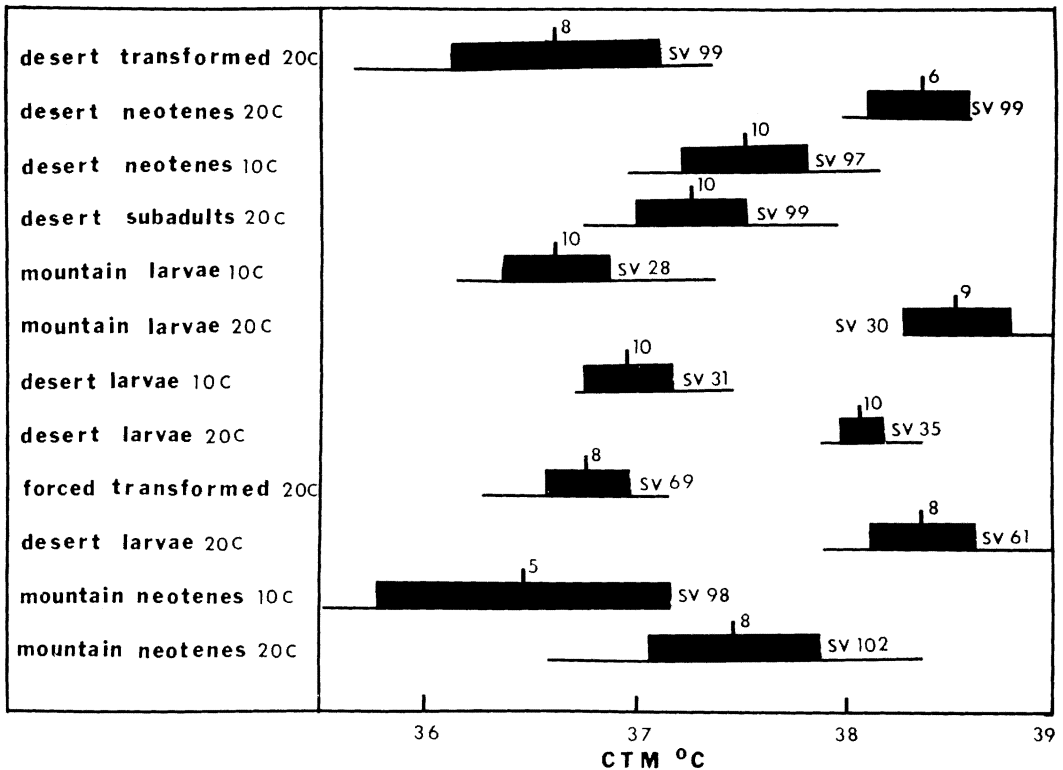


FIG. 1.—Critical thermal maxima in different life history stages of montane and desert *Ambystoma tigrinum*. The horizontal line is the range; the vertical line the mean. Solid bars on each side of mean are 95% confidence intervals. SVL indicates snout-vent lengths in millimeters. Numbers adjacent to mean give sample size.

transformed 91–113 mm SVL or forced transformed 59–76 mm SVL), some exhibited a much slower rate of metamorphosis (subadults) and others (neotenes) (90–105 mm SVL) and larvae (28–90 mm SVL) failed to transform. These groups were treated separately in the CTM measurements.

CTM were determined by the methods of Hutchison (1961). Deep body temperatures were monitored by Yellow Springs Instrument thermistors inserted deep into the gut via the cloaca. Salamanders were placed in flasks containing 100 ml of constantly aerated water at their acclimation temperature. The flasks were heated in heating mantles connected to a variable transformer adjusted to provide a heating rate of approximately 0.5 C/min. All CTM

measurements were made between 0900 and 1700 h MST. The CTM was the temperature of the salamander at which body spasms ceased and an open mouth gape was apparent. Each salamander was used in only one CTM determination. Each sample consisted of CTM obtained over this time span and therefore includes any variance attributable to circadian shifts in CTM.

Montane larvae ( $\bar{x}$  SVL = 30 mm) from the ephemeral pond acclimated at 20 C had significantly higher CTM ( $t = 3.4, P < .01$ ) than small desert larvae ( $\bar{x}$  SVL = 35 mm) acclimated at 20 C. However, there was no significant difference in CTM results, between montane larvae and larger desert larvae (from a later collection) acclimated at 20 C. In comparisons of neotenes acclimated at 10 C and 20 C, salamanders from

the desert population had significantly higher CTM than the montane population ( $t = 3.7$  and  $3.4$  respectively,  $P < .01$ ). There was no significant difference in CTM in montane and desert larvae acclimated at 10 C (Fig. 1).

Desert neotenes acclimated at 20 C had significantly higher CTM than subadults, transformed, and forced transformed desert salamanders acclimated at 20 C (Fig. 1). There was no significant difference in CTM of desert neotenes and large ( $\bar{x}$  SVL = 61 mm) or small ( $\bar{x}$  SVL = 35 mm) larvae acclimated at 20 C. In all comparisons larval animals had higher CTM than the transformed animals acclimated at the same temperature. Transformed *A. tigrinum* acclimated at 20 C had CTM similar to montane and desert larvae acclimated at 10 C.

There were no differences in CTM that could be attributed directly to size differences, i.e. there was no significant difference in CTM in the two groups of desert larvae. When the CTM of all desert larvae acclimated at 20 C were pooled, there was no significant difference in CTM between these larvae and montane larvae.

A difference of 10 C in acclimation temperature resulted in an increase in the CTM between 1 and 2 C. The groups most responsive to acclimation were the montane larvae which exhibited a 2 C shift in CTM. Other groups shifted the CTM approximately 1 C with the 10 C difference in acclimation.

#### DISCUSSION

The higher CTM in larval and neotenic *Ambystoma tigrinum* when compared to transforming or completely transformed adults is a surprising result on *a priori* grounds. We originally hypothesized that larval *A. tigrinum* would have lower CTM than adults based on the data of Hutchison (1961) for transforming newts. The interpretation of these results is simplified when the ecological relationships of desert populations of *A. tigrinum* are considered. Desert *A. tigrinum* of all life history stages remain

in ponds for as long as ponds hold water. Drying ponds in early summer may incur water temperatures as high as 30 C (Webb and Roueche, 1971; pers. observ.). We have observed that as a pond dries, the transformed salamanders emigrate at night and consequently avoid the high temperatures of the drying pond. Emigrating *A. tigrinum* apparently seek shelter in rodent burrows (Hamilton, 1946; pers. observ.). Consequently, emigrants can avoid temperatures as high as 30 C. That portion of the population which, because of apparent genetic differences, transforms slowly may be trapped in this severe thermal environment for several days (pers. observ.; Webb and Roueche, 1971). High CTM in larval and neotenic desert salamanders would be important in insuring the survival of a greater portion of the population which would help to insure retention of those genes which result in retardation of metamorphosis, an important adaptation in populations of desert salamanders (Delson and Whitford, unpubl. data).

If we consider the pooled data for untransformed *A. tigrinum* the only significant differences in CTM were between the desert and montane neotenes. In montane situations, neotenes are only found in permanent ponds which characterized by relatively low water temperatures. Neotenes in desert ponds may be subjected to high temperatures as discussed previously and are really facultative neotenes. The variation in CTM with elevation appears to reflect the manner in which selective pressures of a specific environment affects different stages in the life history of these animals rather than a generalized relationship with habitat.

Thus the lack of difference in CTM between montane and desert larvae may reflect the characteristics of the pond from which the larvae were obtained. Montane larvae were taken from a shallow ephemeral pond with a black silt bottom. During dry years in such a pond, larvae might be trapped in a shallow drying pond and subjected, due to the high isolation characteristics in these mountains, to thermal stress

similar to that experienced by desert populations.

Since we were unable to obtain larvae and neotenes from the same pond, we were unable to determine if larvae from a population with the genetic make-up of montane neotenes would have the same CTM as the montane larvae from a temporary pond.

The results of this study suggest that in *A. tigrinum* the CTM has been evolutionarily adjusted to protect the salamanders from the thermal stresses to which particular life history stages are subjected. We propose that the shifts in the CTM may reflect important adaptations in the life history stages of *A. tigrinum* and provide a tool for examining the complex genetic patterns in southwestern populations of this species.

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## A NEW SPECIES OF *BUNOPUS* (REPTILIA: GEKKONIDAE) FROM IRAN AND A KEY TO LIZARDS OF THE GENUS *BUNOPUS*

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**ABSTRACT:** *Bunopus aspratilis* is a new species of gekkonine lizard differing from other members of the genus in having all scales of body, tail, limbs, and head, with exception of labials, chin shields, and nasals, prominently keeled. A key to the five species of *Bunopus* recognized currently is provided.

RECENTLY, Tuck (1971a) reported on Iranian amphibians and reptiles in the United States National Museum, including material collected by himself and J. W. Neal, Jr. from 1963–1965. Subsequently, a few additional specimens resulting from that field work have come to light. Included are two specimens which I believe represent a hitherto undescribed species of gecko.

*Bunopus aspratilis* new species  
(Figs. 1, 2A-C)

*Holotype.*—United States National Museum 193961 ♀. 35 km E Gach Sārān (30° 20' N, 50° 48' E), Fārs Province (Ostan 8), Iran; collected 10 February 1964 by John William Neal, Jr.

*Paratype.*—USNM 193962 ♀. Same data as holotype.

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