

differences in response are significant and repeatable. The common albumins of *P. kentucki* from Big Black Mt. and High Knob have been found to have a different electrophoretic mobility than the albumin alleles seen in the other 6 *P. kentucki* populations (Highton and MacGregor, 1983). Thus, albumin variation within the species *P. kentucki* is detectable both by gel electrophoresis and micro-complement fixation.

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### Critical Thermal Maxima in Populations of *Ambystoma macrodactylum* from Different Elevations

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Although Miller and Packard (1974) have indicated that "the CTM [critical thermal maxima] of ectothermic vertebrates provided a convenient index of adaptations to the thermal environment . . .", intraspecific variation in CTM among populations from different altitudes has been examined in only a few anurans (Heatwole et al., 1965; Brattstrom, 1968, 1970; Miller and Packard, 1974, 1977; Hoppe, 1978). Even fewer altitudinal studies have been conducted on salamanders (Cupp and Brodie, 1972; Delson and Whitford, 1973).

Significant differences in CTMs of coastal and piedmont *Eurycea quadridigitata* were reported by Cupp and Brodie (1972) and intra- and inter-specific altitudinal differences in CTM were discovered in frogs of the genus *Eleutherodactylus* (Heatwole et al., 1965). Strong differences in CTMs were found between desert and montane populations of *A. tigrinum*, but only in neotenic animals (Delson and Whitford, 1973). An altitudinal cline of CTM in adult chorus frogs (*Pseudacris triseriata*) was reported by Miller and Packard (1977).

*Ambystoma macrodactylum*, the long-toed salamander, is widely distributed in the Pacific northwest and exists in a variety of habitats (Knudsen, 1960; Ferguson, 1961; Anderson, 1967) ranging from coastal rainforests to desert pools and alpine lakes. The objective of this study was to investigate CTMs for evidence of local adaptations to different thermal environments in three populations of *A. macrodactylum* from different altitudes.

Adult salamanders were collected from three sites in northeastern Oregon and western Idaho (Table 1). Site 1 is a shallow permanent pond (420

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TABLE 1. Mean critical thermal maxima for the three collection sites.

| Site no. | CTM<br>Acclimation temperature |             | Elevation (m) | Approximate size (ha) | Approximate maximum depth (m) | Range of H <sub>2</sub> O temperatures |                          |
|----------|--------------------------------|-------------|---------------|-----------------------|-------------------------------|--|--------------------------|
|          | 8°C 95% CI                     | 20°C 95% CI |               |                       |                               | (°C)                                   | (n)                      |
| 1        | 33.4 ± 0.59                    | 34.9 ± 0.63 | 420           | 0.03                  | 1                             | 1.18–21.0                              | 19<br>February–September |
| 2        | 34.3 ± 0.63                    | 35.0 ± 0.80 | 1140          | 3.00                  | 4                             | 5.0–25.0                               | 13<br>March–September    |
| 3        | 33.2 ± 1.20                    | 34.4 ± 0.71 | 2470          | 2.00                  | 6+                            | 7.4–18.4                               | 12<br>June–September     |

m in elevation) 5 km E of Lewiston, Nez Perce County, Idaho, and is fed by a small stream. Site 2 is a frequently temporary, irrigation pond at 1140 m, 5 km N of Halfway, Baker County, Oregon, filled by run-off from melting snow. The high elevation pond (Site 3) is located in a small cirque basin about 31 km NE of Site 2 in Wallowa County, Oregon. It is a permanent lake (elevation 2470 m) fed by several small streams.

Water temperatures were taken at a depth of 20 cm at each site once or twice a month in 1977 and 1978 during the main period of salamander activity (egg deposition to larval metamorphosis). A depth of 20 cm was chosen to represent a region of high diurnal activity of larval salamanders.

All animals were collected from these sites during the breeding season and were held at room temperature for a minimum of two months prior to final acclimation. They were exposed to natural daylength during this period and fed earthworms. After this period, 15 animals from each population were acclimated for two weeks without food or light in an environmental chamber at 8°C and approximately 100% relative humidity. A duplicate set of animals (15 from each population) was held in another environmental chamber at 20°C under the same conditions.

CTM determinations were made during the summer at the end of this two week period. Each animal was placed in a 250 cm<sup>3</sup> flask containing 20 cm<sup>3</sup> of water. Flasks were submerged to the neck in a refrigerated 60.5 l bath. Water temperature at the initiation of each test was set at the acclimation temperature. The rate of temperature change was 0.5°C/min which was slow enough to allow the body temperature to change at the same rate as the water in the chamber. During trial runs, a thermocouple was placed 1–2 cm into the cloaca of experimental salamanders and in no case did the body temperature differ more than 0.1°C from the water bath. Heat rigor and failure to respond to stimuli were the most consistent and reliable indicators of CTM. Similar indicators were used in studies of *A. tigrinum* and *A. jeffersonianum* (Claussen 1977). The animals were prodded with a sharp probe when heat rigor was observed to determine if they would respond to intense stim-

ulation. In no case did any animal respond after heat rigor was observed. All tests were conducted between 1800 and 2400 hrs to minimize possible effects of circadian rhythm.

A stepwise multiple regression was used to determine the effect of acclimation temperature, highest recorded site water temperature, and altitude on observed CTMs. This procedure permitted us to evaluate which independent variables most influenced the dependent variable (CTM). It should be noted that since altitude and temperature (both independent variables) were not perfectly correlated it was possible to determine which of these most influenced the data.

The mean CTMs for the three populations acclimated at 8°C ranged from 33.2°C to 34.3°C and those acclimated at 20°C ranged from 34.4°C to 35.0°C (Fig. 1).

The stepwise regression procedure yielded the following model:  $C = .09(A) + .134(S) + 29.9$  ( $R^2 = .73$ ), where C = critical thermal maximum, A = the acclimation temperature, and S = the highest water temperature recorded at the site; thus the model explained 73% of the variability of the data. The stepwise procedure indicated that entering altitude into the model did not significantly increase the  $R^2$  term. Acclimation temperature explained 52.2% of the data and the highest recorded water temperature explained 20.8%.

The increase in CTM as a result of the higher acclimation temperature is an expected and widely documented phenomenon (Hutchinson, 1961; Brattstrom, 1968; Snyder and Weathers, 1975; Claussen, 1977). This response to higher acclimation temperatures is well known in amphibians as well as other vertebrates and specifically has been investigated in ambystomatid salamanders by Claussen (1977) and Delson and Whitford (1973), among others.

The maximum water temperatures measured at each site explained a significant part of the variation. Other studies (Heatwole et al., 1965; Delson and Whitford, 1973; Miller and Packard, 1974, 1977; and Hoppe, 1978) have shown a strong correlation between CTMs and altitude. As shown in Table 1, maximum water temperature does not consistently decrease with increasing altitude.

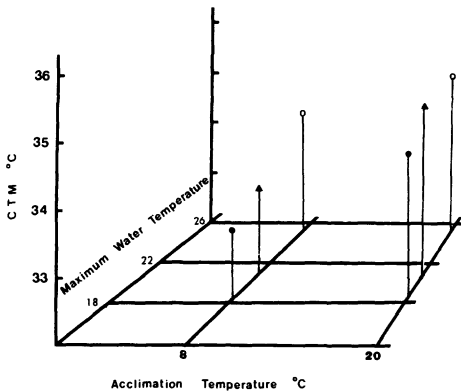


FIG. 1. The relationship between CTM and acclimation temperature and maximum water temperature for *Ambystoma macrodactylum*. Bar end points represent mean CTMs for respective acclimation temperatures and populations where ▲ = site number 1, ○ = site number 2 and ● = site number 3 (see Table 1).

Based on our analysis, the thermal history of the site (as indicated by maximum water temperature) is more important than altitude per se. Thermal history is a proximate factor which influences thermal tolerance; whereas altitude is an ultimate factor acting indirectly on thermal tolerance through its effect on the thermal history of the site.

Adult *A. macrodactylum* are rarely active above ground and usually then only when it is cool and moist. As a result they are unlikely to be subjected to the same thermal stresses as are the larvae (at least those larvae in shallow ponds). More of a variation in adult CTMs was explained by maximum water temperature than by altitude. For these reasons, we suggest that CTMs observed in adult long-toed salamanders represent a holdover of thermal adaptation in the larval stage and echo adaptations to aquatic thermal histories.

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## Behavioral Response of the American Alligator to Freezing Weather

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Little is known of winter behavior of alligators (*Alligator mississippiensis*) except that they seem to remain in their dens, surfacing only to breathe, or to bask if the day is warm (Chabreck, 1966; Kellogg, 1929; McIlhenny, 1935). Ice formation can limit an alligator's access to air, and deaths in