Physiological Responses to Temperature in the Horned Lizards, Phrynosoma cornutum and Phrynosoma douglassii

Author(s): Andrew A. Prieto, Jr. and Walter G. Whitford

REFERENCES
Linked references are available on JSTOR for this article:
https://www.jstor.org/stable/1442447?seq=1&cid=pdf-
reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

Physiological Responses to Temperature in the Horned Lizards, *Phrynosoma cornutum* and *Phrynosoma douglassii*

Andrew A. Prieto, Jr. and Walter G. Whitford

In the laboratory, *Phrynosoma cornutum* and *Phrynosoma douglassii* from central New Mexico had mean preferred body temperatures of 38.5° C and 35° C respectively. The mean critical thermal minimum established in the laboratory for *P. douglassii* was 2.75° C and 9.46° C in *P. cornutum*. The mean critical thermal maximum in *P. douglassii* was 43.5° C and 47.9° C in *P. cornutum*. The range of thermal tolerance in *P. douglassii* was 2.3° greater than that of *P. cornutum*.

Oxygen consumption and heart rate increased with temperature. There were no significant differences between the heart rates of *P. douglassii* and *P. cornutum* at various temperatures. Oxygen consumption in *P. douglassii* at 5° C and 15° C was almost double that in *P. cornutum* at those temperatures, but their rates of oxygen consumption were not significantly different at 25, 35, and 40° C.

Differences in the oxygen pulse values of these species at high and low temperature extremes indicate differences in the cardiac output and efficiency. It is suggested that *P. douglassii* may have a more efficient transport of oxygen by the respiratory pigments at low temperatures than *P. cornutum*.

INTRODUCTION

A number of investigators have studied physiological responses to temperature in lizards in an effort to determine the nature and possible physiological significance of thermal adjustments in reptiles. Most of these studies have dealt with species that inhabit hot, arid environments such as *Crotaphytus collaris* (Dawson and Templeton, 1963), *Amphibolurus barbatus* (Bartholomew and Tucker, 1963), *Sauromalus obesus* (Templeton, 1964) and others reviewed by Dawson (1967). Some studies have included data on the thermal tolerances of *Phrynosoma cornutum* (Ballinger and Schrank, 1970; Kour and Hutchison, 1970) and certain aspects of the behavioral responses to temperature in *P. cornutum* and *Phrynosoma douglassii* (Heath, 1965).

Less has been published concerning nonthermophilic lizards. Dawson and Templeton, (1966) found significant differences in thermal tolerance and the metabolism-temperature curve in the alligator lizard, *Gerrhonotus multicarinatus*, in comparison to thermophilic species. Hudson and Bertram (1966) found similar differences in the physiological responses to temperature in the skink, *Lygosoma laterale* in comparison to more thermophilic species.

P. cornutum, a thermophile, is essentially limited to open desert shrub habitats while *P. douglassii* is found in a variety of habitats ranging from open shrub-grassland communities to coniferous forests high in the mountains (Stebbins, 1966). We have collected *P. douglassii* from an elevation of 3494 m on Sierra Blanca peak in the Sacramento Mountains. In this part of southern New Mexico, *P. douglassii* is restricted to the coniferous forest. Comparative physiological studies of these forms could provide a basis for a better understanding of the ecology and distribution of these species of *Phrynosoma* and provide insights into the adaptations of reptiles capable of inhabiting high elevations.

METHODS AND MATERIALS

Lizards used in this study were collected during the spring and summer of 1966 and 1967. The *P. cornutum* were taken within a ten mile radius of University Park, Dona Ana Co., New Mexico. The *P. douglassii* were taken at Haynes Canyon, 2591 m, Lincoln National Forest, Otero Co., New Mexico and at the Dale Ressler Boy Scout Camp, 1.5 miles ESE, Cloudcroft, 2652 m, Otero Co., New Mexico.

As it is known that the thermal tolerance limits of poikilotherms respond to acclima-

498

tion (Lowe and Vance, 1955; Licht *et al.*, 1966), the lizards used in this study were kept in the laboratory under constant conditions for one month. Both species were maintained in separate terraria measuring $12'' \times 12'' \times 60''$ in which a temperature gradient of 24° C to more than 50° C was provided by incandescent lamps. The lizards were kept on a 14 hr light and 10 hr dark photoperiod centered at noon M. S. T. This provided acclimation at a preferred temperature diurnally with acclimation to ambient temperature (24° C) at night. Water was available at all times. All animals were fed ants and/or mealworms (*Tenebrio* larvae at least once a week).

Critical thermal minima and maxima.— The definition of critical thermal minimum (CTMin) in this study is the body temperature at which a lizard loses its ability to escape from conditions which, if continued, would result in its death (when organism is cooled at a relatively constant rate). The CTMin is thus an ecological lethal in the same sense as the critical thermal maximum (CTMax) of Lowe and Vance (1955). To determine CTMin's lizards were placed in a 1-gal jar which contained about two inches of sand on the bottom. The temperature of the jar was lowered at a known rate by cooling coils wrapped around it. A mixture of ethylene glycol and water precooled to below 0° C in a compressor cooled water bath was pumped through the cooling coils by a centrifugal pump. Body temperatures were measured by placing a thermistor deep into the gut via the cloaca. Substratum, air and deep body temperatures were recorded with Yellow Springs Instrument (YSI) thermistors and a YSI telethermometer. At the beginning of and at intervals during each test, temperatures of substrate, air, and lizard were recorded in order to determine the rate of cooling. The loss of muscular coordination and righting response was selected as the end point for CTMin.

The critical thermal maximum (CTMax) of ten individuals of each species was determined by placing a lizard in a 500 ml Erlenmeyer flask which was submerged in a water bath provided with heating coils. Body, air, and water temperatures were recorded as previously described for the CTMin. The temperature of the water bath was raised approximately 1°/min until the CTMax was reached. The loss of muscular coordination

and righting response was used as the end point.

Preferred temperature.—Body temperatures were measured by YSI small animal thermistor inserted deep into the cloaca. Temperatures were monitored by the YSI thermistor connected to a YSI telethermometer. The lizards were allowed free movement in the temperature-preference chamber while body temperatures were recorded. For several hours before any body temperatures were recorded, the lizards were placed in the gradient with the thermistors in place. A stop-watch was used to measure the length of time spent at any body temperature and the body temperature for each time interval was recorded. Each lizard was kept under close observation for at least one hour, but most were observed for longer periods.

Oxygen consumption and heart rate.—The apparatus used to measure oxygen consumption was a modification of that used by Whitford and Hutchison (1963). Two 500 ml Erlenmeyer flasks closed with rubber stoppers and connected by means of a tygon tubing-glass manometer were used as respirometers. One flask contained the lizard and the other served as a thermobarometer. The flask with the animal was provided with an attachment for the insertion of a syringe filled with oxygen. The thermobarometer was filled with sand or water equal to the volume of the lizard as determined by displacement. A vial containing 20% NaOH solution (carbon dioxide absorbent) and small strips of filter paper were placed in each flask. The respirometers were then placed in a temperature controlled bath at the desired temperature. Comparable sized animals of both species were selected to avoid size related differences in metabolism. Gas volumes were corrected to standard temperature and pressure.

Heart rate and oxygen consumption were recorded simultaneously. Small pins or fine insulated wire leads were attached to each experimental animal, one on the thorax over the heart, the other below the axilla. The leads, sealed into the stoppers on the respirometers, were connected to a high-gain preamplifier and the electrocardiograms recorded on an E and M Physiograph recorder.

RESULTS

Critical thermal minimum and maximum. —The mean CTMin of *P. douglassii* was
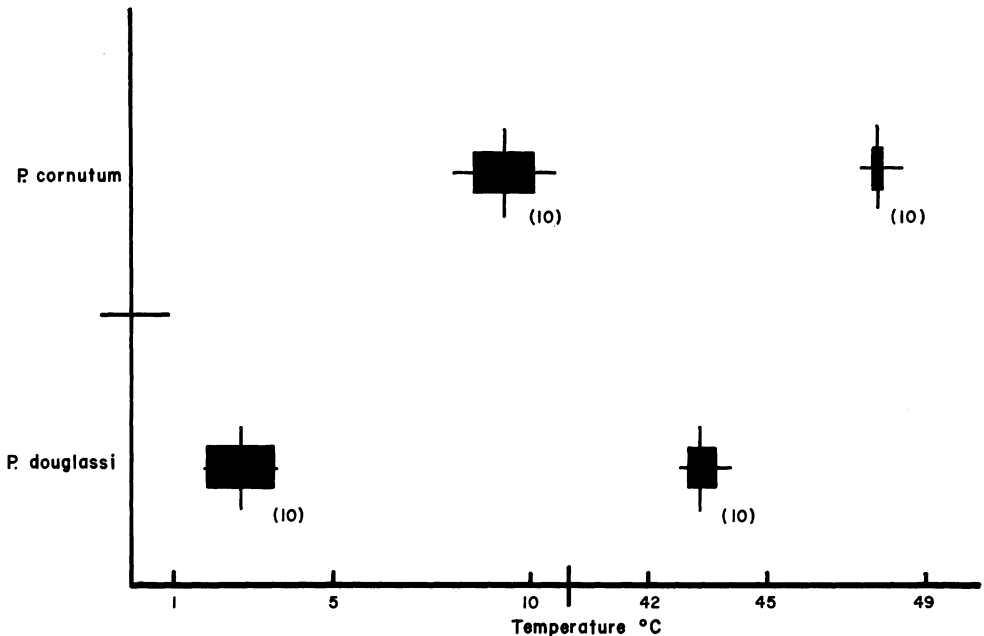
Fig. 1. Comparison of critical thermal maxima and minima of *Phrynosoma cornutum* and *Phrynosoma douglassii*. Vertical line represents mean, and horizontal line represents range and dark rectangle on each side of mean, the 95% confidence interval. Sample sizes in parentheses.

2.75° C, which was significantly lower (P < 0.01) than that of *P. cornutum* with a mean CTMin of 9.46° C (Fig. 1). When the body temperature of *P. cornutum* dropped to 24° C, the animals attempted to burrow in the sand by movements of the head and swimming movements of the body. At body temperatures below 20° C, *P. cornutum* remained still with their eyes closed until the CTMin was reached. In contrast, *P. douglassi* never attempted to burrow and actively moved at body temperatures as low as 6° C. Below this temperature, they remained motionless until the righting response was lost.

The mean CTMax of *P. cornutum* was 47.91° C, or significantly higher (P < 0.01) than the mean CTMax of 43.5° C in *P. douglassii* (Fig. 1). *P. cornutum* remained motionless until body temperatures reached 41–43° C, when they began to move rapidly. Panting was initiated at body temperatures between 44–46° C, and continued until the CTMax was reached. *P. douglassii* began rapid movement and panting at lower body temperatures (38–39° C) and continued until the CTMax was reached.

Subtraction of the CTMin from the CTMax gives the range in degrees C in which

a lizard has the capacity for coordinated movement. This may be considered the thermal tolerance range. The thermal tolerance range for *P. douglassii* was 40.75° C; 2.30 degrees C greater than that of *P. cornutum* which had a range of 38.45° C.

Preferred temperature.—The mean preferred body temperature for the *P. douglassii* in the laboratory was 35° C (33–36° C) or significantly lower (P < 0.05) than *P. cornutum* with a mean preferred body temperature of 38.5° C (37.5–39° C) *P. douglassii* moved around in the gradient, remaining at one body temperature for only brief periods.

Unlike *P. douglassii*, *P. cornutum* thermoregulated by flattening its body directly below the lamps until their body temperatures rose to approximately 41° C. They maintained this body temperature for several minutes then moved away and situated themselves at varying distances from the heat source. Individuals would then maintain temperatures of 37–39° C for as long as 30 min.

Oxygen consumption and heart rate.—Oxygen consumption and heart rate increased as a function of temperature (Figs. 2, 3). The following equations describe the relationship
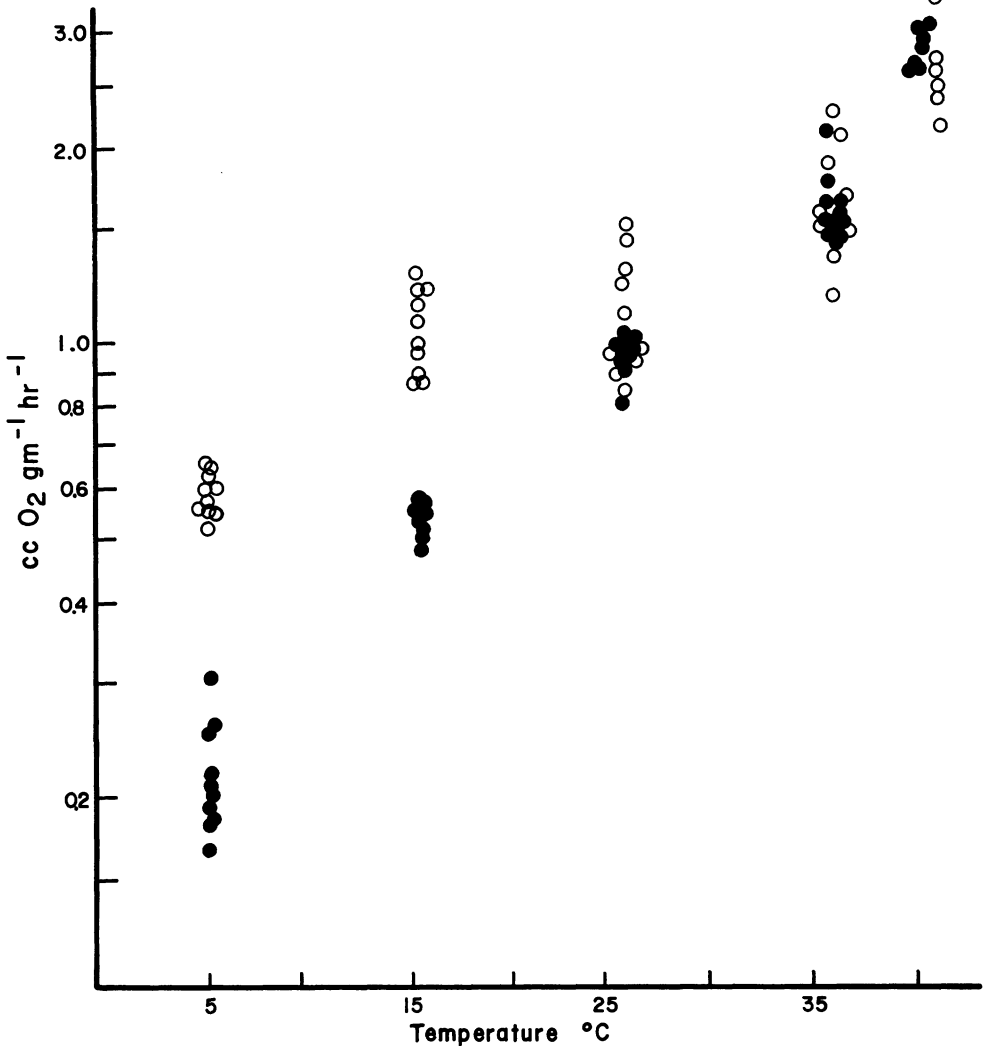
Fig. 2. Effects of temperature on oxygen consumption in *Phrynosoma cornutum* and *Phrynosoma douglassii*. The open circles represent oxygen consumption values for individual *P. douglassii*, solid circles values for *P. cornutum*.

between oxygen consumption in cc per gm⁻¹ per hr⁻¹, temperature in °C and heart rate in beats per hr⁻¹ and temperature in °C in *P. cornutum* and *P. douglassii*.

P. douglassii
log heart rate = 0.76 + .03T
log oxygen consumption = –1.28 + .015T

P. cornutum
log oxygen consumption = –1.78 + .03T
log heart rate = 0.86 + 0.27T
(beats/min)

There were no significant differences between the heart rates of *P. douglassii* and *P. cornutum* at various temperatures. Oxygen consumption in *P. douglassii* was significantly higher $(P < 0.05)$ than *P. cornutum* at 5° and 15° C. This was also reflected in the higher oxygen pulse in *P. douglassii* at these temperatures (Table 1). Temperature coefficient (Q_{10}) values indicate marked increases in metabolic rates at the high and low extremes (Table 1). There were no marked changes in activity correlated with
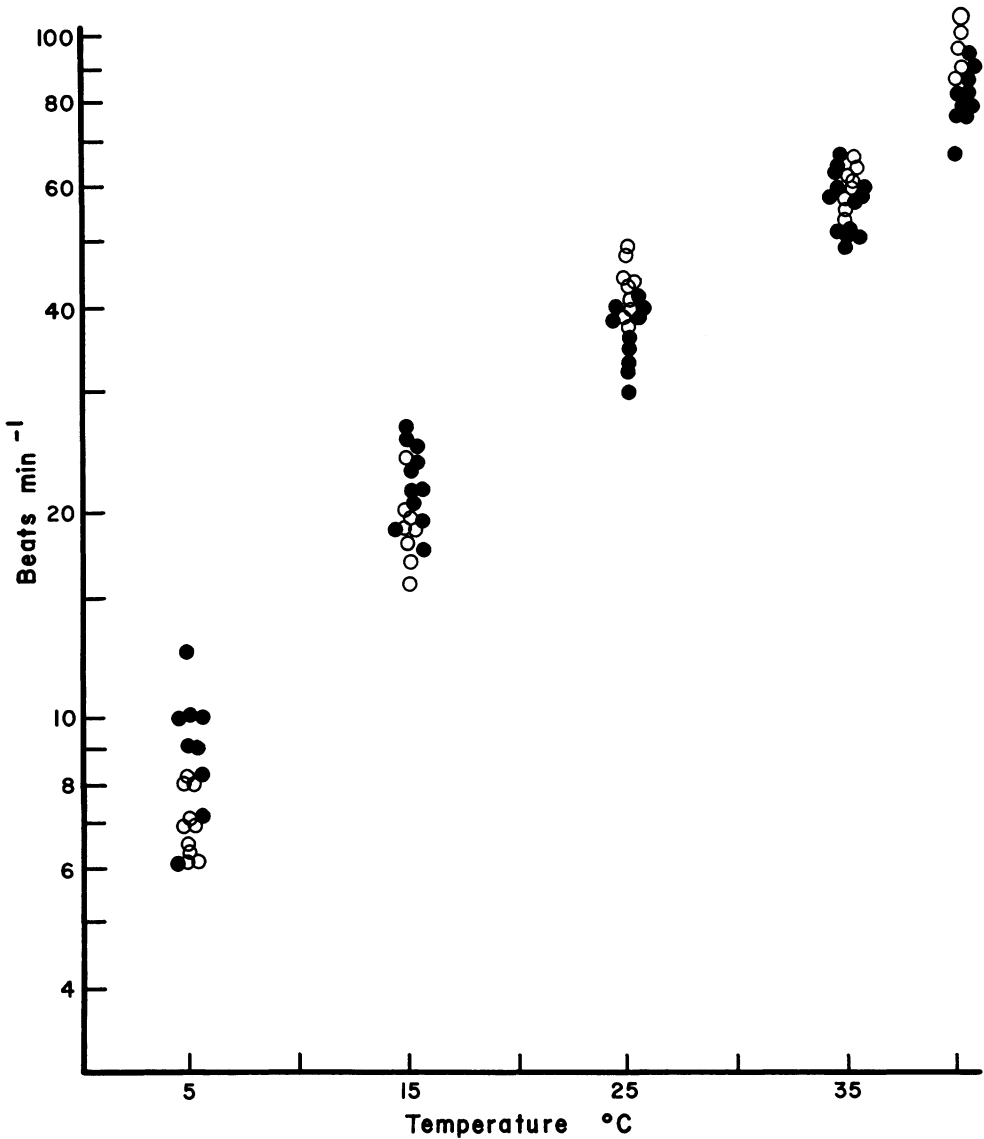
Fig. 3. Effects of temperature on heart rates of *Phrynosoma cornutum* and *Phrynosoma douglassii*. Presentation same as in Fig. 2.

these increases. At 40° C *P. cornutum* showed no signs of ill effects or panting, but *P. douglassii* behaved as described when subjected to extremely high temperatures in the CTMax measurements. They had to be removed from the respirometers after 2 hr at 40° C. In this period they had lost an average of 0.1 g in body weight (apparently due to panting or respiratory water loss) and were in danger of expiring.

DISCUSSION

The variety of habitats which *P. douglassii* is capable of inhabiting is partially a function of its wide range of thermal tolerance and in particular its low CTMin. Although its CTMax is lower than *P. cornutum*, it is probably sufficiently high to allow *P. douglassii* to inhabit most environments inhabited by *P. cornutum*. The only other lizard that has been reported active at temperatures as

TABLE 1. OXYGEN PULSE AND Q_{10} IN *Phrynosoma cornutum* AND *Phrynosoma douglassii*.

Species	Temp (°C)	$\bar{x}$ O_2 Consumption cc gm^{-1} hr^{-1}	$\bar{x}$ Heart Rate Beats hr^{-1}	O_2 Pulse cc $beat^{-1}$ gm^{-1}	Q_{10}-O_2
P. cornutum	5	.0220	510.0	4.1×10^{-5}	
	15	.0540	1320.0	4.2×10^{-5}	2.45
	25	.0968	2202.0	4.3×10^{-5}	
	35	.1661	3426.0	4.8×10^{-5}	1.79
	40	.2835	4956.0	5.4×10^{-5}	2.95
P. douglassii	5	.0592	1420.0	1.4×10^{-5}	
	15	.0959	1146.0	9.2×10^{-5}	1.61
	25	.1157	2550.0	4.5×10^{-5}	1.20
	35	.1706	3618.0	4.6×10^{-5}	1.47
	40	.2653	5956.0	4.5×10^{-5}	2.43

low as *P. douglassii* is the iguanid *Liolaemus multiformis*, of the high Andes of southern Peru, which is capable of coordinated movement at a body temperature of 1.5° C (Pearson, 1954). Thus *P. douglassii* is capable of movement at body temperatures nearly as low as those tolerated by a species living at 4575 m. Undoubtedly the ability of *P. douglassii* to be active at low temperatures is an important factor in the adaptation of this species to high elevation. *P. douglassii* can emerge and bask at the low ambient temperatures that prevail at elevations greater than 2500 m.

Kour and Hutchison (1970) provided comparative information on CTMax and CTMin in lizards. For *P. cornutum* acclimated at 35° C their data are equivalent to ours. In their study the only species which had a CTMin nearly as low as *P. douglassii* was *Xantusia vigilis* (acclimated at 25° C). Since they found significant shifts in the CTMin after acclimation at lower temperatures, data on the CTMin of *P. douglassii* acclimated to similar temperatures will be necessary for accurate comparisons.

Along with the behavioral and ecological differences between *P. douglassii* and *P. cornutum*, several physiological differences are apparent. In *P. cornutum* the oxygen pulse increased gradually at higher temperatures, indicating either an increased stroke volume or the absorption of a greater volume of oxygen per volume of blood in the lungs or both. *P. cornutum* may be meeting the increased metabolic needs at high body temperatures by increasing cardiac output through the acceleration of heart rate alone. Q_{10} values for *P. cornutum* remained constant between 15° and 35° C and increased considerably between 5° and 15° C and 35° C and 40° C. This is an indication that metabolism increased markedly at these two extremes. At higher temperatures increased respiratory demands can be met by an increased oxygen consumption and cardiac output, however at lower temperatures, oxygen consumption is reduced sharply and the change in metabolic rate between 15° and 5° C is almost as great as between 35° and 40° C as indicated by the Q_{10} values. This may result from increased cardiac output or changes in oxygen binding capacities of the respiratory pigments at low temperatures.

Physiological studies on other lizards with thermal requirements similar to *P. cornutum* have produced results similar to those obtained in this study. The heart rate of *P. cornutum* between 5° and 40° C is nearly identical to that in *Dipsosaurus dorsalis* (Licht, 1965). Heart rate, oxygen consumption and oxygen pulse in *Crotaphytus collaris* (Dawson and Templeton, 1963) showed similar increases with temperature as in *P. cornutum*. Bartholomew and Tucker (1963) found similar increases in the oxygen pulse in *Amphibolurus barbatus*, but with a drop at elevated temperatures.

In *P. douglassii*, oxygen pulse values remained constant between 25° and 40° C, however; they were higher at 15° and 5° C. Oxygen consumption in *P. douglassii* at these temperatures was significantly higher than that for *P. cornutum* while their heart rates were essentially the same. Thus it appears that *P. douglassii* exhibits physiological changes opposite those found in *P. cornutum*. It is clear that *P. douglassii* cannot meet

oxygen demands at the higher temperatures by increasing cardiac output or rate of oxygen consumption as indicated by its oxygen pulse. However, at 5° and 15° C oxygen pulse increased (instead of decreasing) indicating that they were meeting their oxygen demands by either increased cardiac output or more efficient oxygen transport by the respiratory pigments of the blood or both. It may be that *P. douglassii* possesses respiratory pigments and enzymes that function at temperatures lower than those of *P. cornutum*.

LITERATURE CITED

BALLINGER, R. E. AND J. SCHRANK. 1970. Acclimation rate and variability of the critical thermal maximum in the Lizard *Phrynosoma cornutum*. Physiol. Zool. 43:19–22.

BARTHOLOMEW, G. A. AND V. A. TUCKER. 1963. Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. Physiol. Zool. 36:199–218.

DAWSON, W. R. 1967. Interspecific variation in physiological responses of lizards to temperature. *In*: Lizard ecology, a symposium. W. W. Milstead, ed., pp. 230–257. Univ. Missouri Press, Columbia, Mo.

——— AND J. R. TEMPLETON. 1963. Physiological responses to temperature in the lizard *Crotaphytus collaris*. Physiol. Zool. 36:219–236.

——— AND ———. 1966. Physiological responses to temperature in the alligator lizard, *Gerrhonotus multicarinatus*. Ecology 47:759–765.

HEATH, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. Univ. Calif. Pub. Zool. 64:97–129.

HUDSON, J. W. AND F. W. BERTRAM. 1966. Physiological responses to temperature in the ground skink, *Lygosoma laterale*. Physiol. Zool. 39:21–29.

KOUR, E. L. AND V. H. HUTCHISON. 1970. Critical thermal tolerances and heating and cooling rates of lizards from diverse habitats. Copeia 1970 (2):219–229.

LICHT, P. 1965. Effects of temperature on heart rate of lizards during rest and activity. Physiol. Zool. 38:129–137.

———, W. R. DAWSON AND V. H. SHOEMAKER. 1966. Heat resistance of some Australian lizards. Copeia 1966 (2):163–169.

LOWE, C. H. AND V. VANCE. 1955. Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*. Science 122:73–74.

PEARSON, O. P. 1954. Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Peru. Copeia 1954(2):111–116.

STEBBINS, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston.

TEMPLETON, J. R. 1964. Cardiovascular response to temperature in the lizard *Sauromalus obesus*. Physiol. Zool. 37:300–306.

WHITFORD, W. G. AND V. H. HUTCHISON. 1963. Cutaneous and pulmonary gas exchange in the spotted salamander, *Ambystoma maculatum*. Biol. Bull. 124:344–354.

DEPARTMENT OF BIOLOGY, NEW MEXICO STATE UNIVERSITY, LAS CRUCES, NEW MEXICO 88001. *Present address* (AAP): DEPARTMENT OF ZOOLOGY, UNIV. OF MISSOURI, COLUMBIA, MISSOURI 65201.