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LACK OF METABOLIC ACCLIMATION TO DIFFERENT THERMAL HISTORIES BY TADPOLES OF LIMNODYNASTES PERONI (ANURA: LEPTODACTYLIDAE)¹

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Tadpoles of *Limnodynastes peroni* show no evidence of any ability to undergo thermal metabolic acclimation when kept at 15 C and 25 C for periods up to 75 days. When kept for 90–120 days, small differences were seen between rate-temperature curves of 15 C and 25 C history tadpoles. The reality of these differences as evidence for thermal metabolic acclimation is difficult to assess. An overall equation to describe the effect of temperature (T , C) and weight (W , grams) on oxygen consumption (Q_{O_2} , ml g⁻¹ h⁻¹) is $\log_{10} Q_{O_2} = -2.13 + 0.05T - 0.48 \log_{10} W$, for which $r^2 = 0.86$ (no. = 360). Q_{10} is 3.16 and in the relationship $M \propto W^b$ (where M = oxygen consumption, ml h⁻¹), the exponent $b = 0.52$. The results suggest that in tadpoles of *L. peroni* any adaptations to fluctuating temperatures may be behavioral rather than physiological or biochemical.

INTRODUCTION

Aquatic ectotherms are well known to adopt various behavioral, biochemical, and physiological strategies to minimize the effect of varying ambient temperature on the rate at which their life functions proceed.

Metabolic compensation is one such homeostatic mechanism. Bullock (1955) pointed out that the acutely measured rate-temperature (R-T) curve of temperature-dependent rate functions in ectotherms may be modified by the animal's previous thermal history. It has long been recognized that ectothermic animals reared at cool temperatures may have higher metabolic rates at a given temperature than animals with a warmer thermal history (Prosser and Brown 1961; Precht et al. 1973). The translational and rotational changes in the R-T

curve which are seen as evidence of thermal acclimation have been categorized and discussed by Precht et al. (1973). Hochachka and Somero (1973) provide a useful discussion of the biochemical mechanisms by which metabolic acclimation occurs. Observations on thermal metabolic acclimation are usually extrapolated to and interpreted in terms of acclimatization to field conditions. Most work has been done on fish (see reviews by Fry 1958, 1964). In habitats subject to long-term seasonal fluctuations, the fish tend to show good acclimatory ability, whereas those from habitats subject to rapid short-term fluctuations in environmental temperature show little, if any, compensation (Morris 1965). Extrapolating this observation to terrestrial ectothermic vertebrates, one would predict that terrestrial amphibia and reptiles, living in habitats which are not buffered by the high specific heat of water against diurnal temperature fluctuations, would show minimal thermal metabolic acclimation.

In reptiles, metabolic acclimation does

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occur but is usually incomplete and often absent (Bennett and Dawson 1976), and the major thermal strategies in reptiles are certainly those behavioral and physiological mechanisms directed toward the regulation of core temperature (see review by Templeton 1970). Adult anura appear to undergo little or no compensatory thermal metabolic acclimation (see Discussion), and, like reptiles, they are known to select suitable temperatures by behavioral means (Fitch 1956; Brattstrom 1963). Living in water, however, the larvae of amphibians are more likely to show metabolic compensation than are adult frogs, especially those which may overwinter between hatching and metamorphosis. In tadpoles, few studies have examined possible modification of the R-T curve by previous thermal history. Lucas and Reynolds (1960) showed that thermal preferenda in *Rana catesbiana* and *R. pipiens* are dependent on previous thermal history. Brown (1969) showed that heat resistance of four species of tadpoles could be increased by warm thermal history. These observations suggest compensatory abilities. However, Parker (1965) concluded that tadpoles of *R. pipiens* are unable to adjust their metabolic rate in compensation for ambient temperature, and further investigation seemed warranted.

Metabolic acclimatory abilities may confer little advantage to tadpoles where larval life span is short and contained within a single season. Accordingly, in the present study a species was chosen whose tadpoles are long lived and may overwinter.

The study was undertaken to determine whether or not the tadpoles of *Limnodynastes peroni* (Leptodactylidae) undergo thermal metabolic acclimation.

MATERIAL AND METHODS

Limnodynastes peroni is a large (to 65 mm) widespread Leptodactylid frog

which occurs on the coastal plains and in the ranges of eastern Australia. In suburban areas it frequently makes use of fish ponds and similar artificial ponds for breeding, and it seems tolerant of polluted water (Barker and Grigg 1977). Its distribution from 18° to 42°S lat suggests that it is a eurythermal species. Its tadpoles are long lived, often overwintering.

Egg masses of *L. peroni* were collected from the Sydney suburb of Sylvania and transported to the laboratory in water from the site of collection. After hatching at room temperature (ca. 20 C), the tadpoles were divided into groups and subjected to a series of different time and temperature combinations as shown graphically in figure 1. This gave groups of tadpoles with short, intermediate, and long-term thermal history at cold (15 C) and warm (25 C) temperatures. These temperatures were chosen because they are close to mean winter and summer water temperatures encountered by tadpoles in the Sydney area. Three time periods of exposure were decided on because of the potential this gave for comparison between them. Lengthy periods were chosen with reference to similar work described elsewhere for fish and

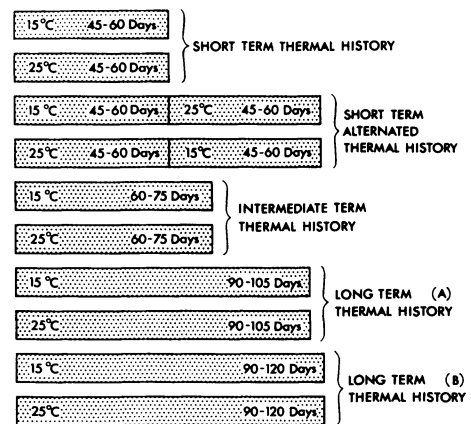


FIG. 1.—Graphic representation of the 10 different time and temperature regimes to which tadpoles were subjected.

because previous work on amphibians has allowed only brief periods for acclimation to occur (see Discussion). Since differential growth rates between tadpoles at high and low temperatures could have a substantial effect on the results, we established also two groups which were exposed first to one temperature and then to the other. Tadpoles were fed frozen lettuce every second day and the water was changed weekly with water at the required temperature. Tadpoles were kept under constant illumination. Measurements of oxygen consumption were made on 15 C and 25 C tadpoles alternately to minimize any likelihood of a time bias being introduced within a group.

Oxygen consumption was measured in six respirometers, each a 25-ml Erlenmeyer flask sealed with a rubber stopper and mounted within a water bath maintained at the required measurement temperature. One tadpole was placed in each of five vessels for 20 min prior to commencement of a measurement period. The sixth vessel served as a control. No air spaces were present. Water samples for analysis were withdrawn through a narrow-gauge polyethylene tube passing through the rubber stopper and fitted with a tap. Water removed at sampling was replaced automatically through a second polyethylene tube which drew on an aerated supply of fresh water in a 1-liter flask mounted within the water bath. Water samples of 2 ml were drawn at the beginning of the measurement period and at half-hour intervals thereafter for 2 h. The first milliliter was taken to flush the dead space, and the oxygen partial pressure of the second was measured using a Radiometer oxygen electrode and PHM-71 gas analyzer. Calculations of oxygen consumption were based on the rate of decline in oxygen content within the flasks, corrected for the 2 ml of fresh aerated water intro-

duced at each sampling. Oxygen partial pressure did not fall below two-thirds saturation, preventing any possibility of a depression of metabolism due to oxygen lack (Helf and Stubblefield 1931; Norris, Grandy, and Davis 1963). The possibility that diel or seasonal cycles in oxygen consumption influenced the results was minimized by the experiments being conducted within as short a period as practicable, and measurements were always made during the normal working day. Furthermore, Hutchinson and Kohl (1971) found no diel cycling of oxygen consumption in frogs kept under constant illumination. At the end of each measurement period, the tadpoles were weighed and the results converted to $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at STPD (standard temperature and pressure, dry).

Thirty individuals from each of the 10 subgroups were tested at both 15 C and 25 C. No tadpole was tested more than once. Statistical procedures were based on Snedecor and Cochran (1973), and the 5% level of probability was accepted as significant.

RESULTS

Summary results for each of the 20 measurement groups are given in table 1.

A multiple regression equation was generated for each of the five time groups, using the method of least squares: $\log Y = a + b_1 X_1 + b_2 X_2 + b_3 \log X_3$; where Y = oxygen consumption ($\text{ml g}^{-1} \text{ h}^{-1}$), X_1 = thermal history (C), X_2 = measurement temperature (C), X_3 = tadpole weight (g), and b_1, b_2, b_3 = respective partial regression coefficients.

The following equations and the statistics of comparisons within groups are given in table 2. Note the high values of coefficients of determination (r^2) in each case. Short-term thermal history: $\log Y = -2.11 - 0.0023 X_1 + 0.0563 X_2 - 0.4247 \log X_3$. Short-term alternated thermal history: $\log Y = -2.14 +$

0.0007 $X_1 + 0.0511 X_2 - 0.4097 \log X_3$. Intermediate-term thermal history: $\log Y = -2.08 + 0.0019 X_1 + 0.0427 X_2 - 0.4785 \log X_3$. Long-term thermal history, A: $\log Y = -2.14 - 0.0050 X_1 + 0.0597 X_2 - 0.4104 \log X_3$. Long-term

thermal history, B: $\log Y = -1.98 - 0.0090 X_1 + 0.0517 X_2 - 0.4617 \log X_3$. The results, standardized to a weight of 0.25 g, are plotted in figure 2 to enable visual comparisons.

Weight and measurement temperature exerted a significant effect on oxygen consumption, but only after more than 75 days experience of a cold or warm thermal history did the previous thermal history exert any effect. The exponent of weight, b , in the relationship $M \propto W^b$ (where M = oxygen consumption, in ml h⁻¹ and W = weight in grams) ranged from 0.52 to 0.59. The slope of the acutely measured R-T curve was steep in all groups; $Q_{10} = 2.67 - 3.96$ (fig. 2). Comparisons of Q_{10} within time groups showed no differences between tadpoles kept at different temperatures, although there were differences between groups. At either measurement temperature, significant differences in the performance of cold- and warm-history tadpoles were seen only in tadpoles kept longer than 75 days prior to measurement. A small but significant effect of treatment was seen in each of the long-term groups, and they are different from each other.

TABLE 1

MEAN OXYGEN CONSUMPTION AND MEAN WEIGHT OF TADPOLES IN EACH OF THE 20 MEASUREMENT GROUPS (No. = 30 in each case)

Term and T (°C, History)	T (°C, Measurement)	Weight (g) ±SE	O ₂ Consumption (ml g ⁻¹ h ⁻¹) ±SE
Short:			
15.....	15	.27 ± .010	.090 ± .002
15.....	25	.26 ± .010	.336 ± .009
25.....	25	.25 ± .011	.325 ± .013
25.....	15	.36 ± .017	.070 ± .003
Short (alternated):			
15.....	15	.23 ± .012	.076 ± .002
15.....	25	.23 ± .013	.278 ± .008
25.....	25	.18 ± .010	.276 ± .007
25.....	15	.20 ± .009	.092 ± .003
Intermediate:			
15.....	15	.28 ± .008	.083 ± .002
15.....	25	.24 ± .008	.293 ± .007
25.....	25	.21 ± .012	.261 ± .009
25.....	15	.23 ± .013	.077 ± .004
Long (A):			
15.....	15	.22 ± .014	.091 ± .004
15.....	25	.22 ± .012	.366 ± .013
25.....	25	.25 ± .014	.311 ± .014
25.....	15	.26 ± .015	.080 ± .005
Long (B):			
15.....	15	.26 ± .016	.075 ± .003
15.....	25	.25 ± .012	.218 ± .012
25.....	25	.38 ± .018	.184 ± .014
25.....	15	.36 ± .017	.070 ± .003

NOTE.—What appear to be significant differences between acclimation groups at the same measurement temperature derive from effects of weight, not thermal history (see table 2).

DISCUSSION

The data show that the tadpoles of *Limnodynastes peroni* are aquatic ectotherms whose ability to undergo thermal

TABLE 2

MULTIPLE REGRESSION ANALYSIS OF THE DEPENDENCE OF OXYGEN CONSUMPTION (ml g⁻¹ h⁻¹) OF TADPOLES OF "LIMNODYNASTES PERONI" ON PREVIOUS THERMAL HISTORY, MEASUREMENT TEMPERATURE, AND BODY WEIGHT

TERM	TADPOLES (No.)	COEFFICIENT OF DETERMINATION	SIGNIFICANCE OF REGRESSION COEFFICIENTS		
			b ₁ (Thermal History)	b ₂ (Measurement Temperature)	b ₃ (Weight)
Short.....	120	.98	NS	< .005	< .005
Short (alternated).....	120	.98	NS	< .005	< .005
Intermediate.....	120	.88	NS	< .005	< .005
Long (A).....	120	.96	< .005	< .005	< .005
Long (B).....	120	.98	< .005	< .005	< .005

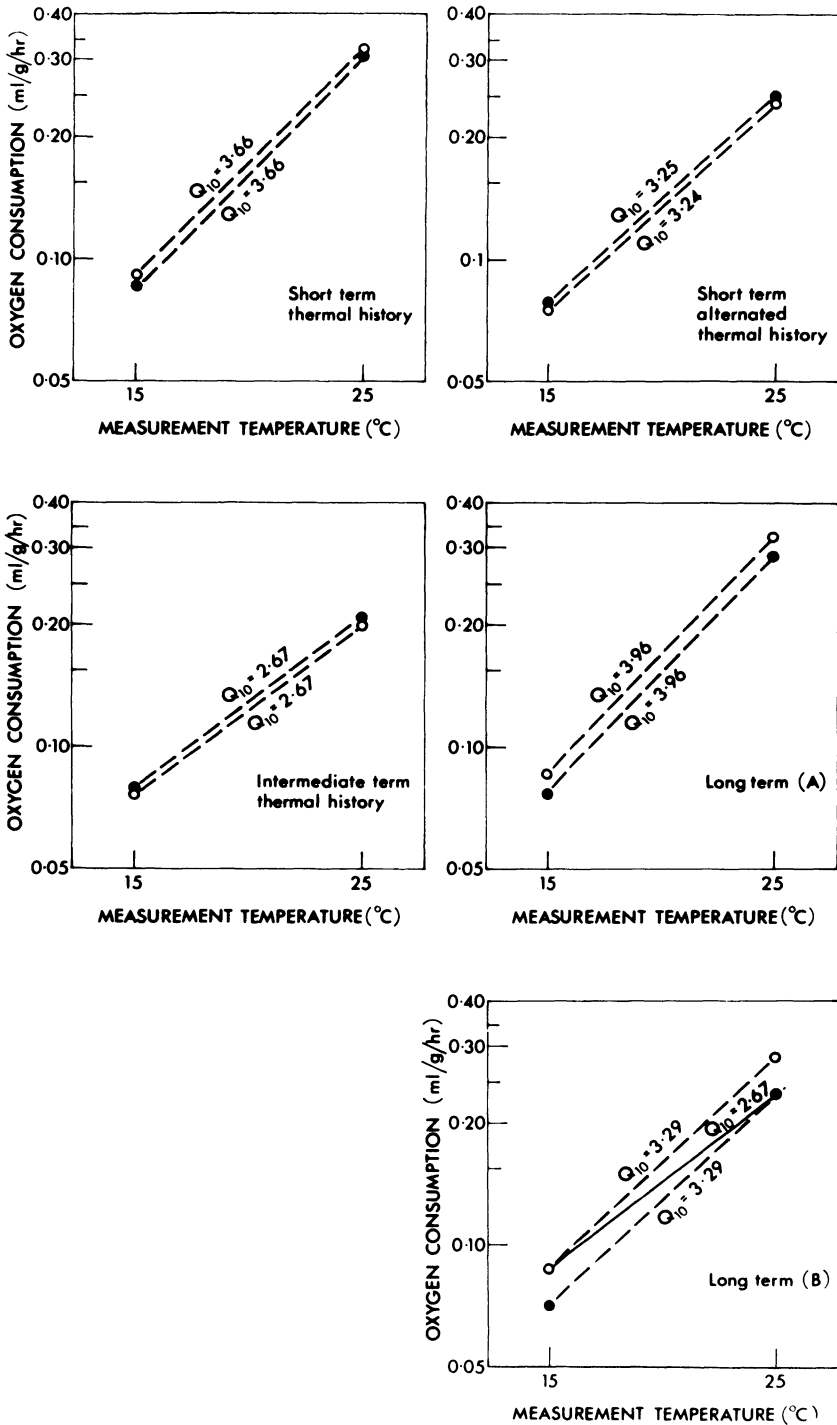


FIG. 2.—Acutely determined rate-temperature functions in each of the 10 different regimes of time and temperature (open circles = 15 C history, closed circles = 25 C history). Values have been calculated for tadpoles at a mean weight of 0.25 g.

metabolic acclimation is either nonexistent or very limited. Two-months exposure to cold or warm conditions showed no thermal history-dependent shift or rotation in the R-T curve. The difference between groups exposed in excess of 90 days, though statistically significant, is small, and it is doubtful whether it can be interpreted as metabolic compensation. That the difference is real is emphasized by its being present in both long-term groups. The time course of acclimation is much less than 75 days in other animals (see Precht et al. 1973), and it would seem much more likely that the observed differences in the long-term groups can be interpreted in terms of factors unrelated to thermal metabolic acclimation. Similar factors may account for the observed differences between the performance of different groups, for example, differences in Q_{10} and in absolute overall oxygen consumption, particularly between long-term A and B. Each group consisted of siblings from the one eggmass, so genetic homogeneity was higher within than between groups. This, combined with differences in maturity, could account for some of the observed variability.

The results agree with the conclusion of Parker (1965) that tadpoles of *Rana pipiens* do not undergo thermal metabolic acclimation. In tadpoles of *L. peroni*, behavior may be the main strategy by which the effects of environmental temperature fluctuations could be minimized.

It seems that both larval and adult anurans do not conform to typical patterns of compensatory thermal metabolic acclimation seen in fish and many invertebrates. Packard and Bahr (1969) found no differences between metabolic rates of montane and piedmont populations of *Pseudacris triseriata* acclimated (for 3.5 days) at 10 and 20 C and measured at the acclimation temperature only. Holzman and McManus (1973)

kept *R. vergatipes* at 5, 15, and 25 C (for 4–6 days). They found no differences between R-T curves of any of the groups over the 5–15 C range, whereas at 25 C the frogs acclimated at 25 C had a higher metabolic rate than those kept at either 5 or 15 C, an inverse effect. Likewise, Weathers (1976) found inverse metabolic “compensation” in bullfrogs kept for several weeks at 5, 12.5, and 20 C. Packard (1972), measuring tissue metabolism in two species of toads, found conflicting results between the responses of liver and skeletal muscle, whereas a study of skeletal muscle from *R. temporaria* showed thermal metabolic acclimation in “winter” frogs but not in “summer” frogs (Lagerspetz, Harri, and Okslahti 1974).

Although anura appear to undergo little or no thermal metabolic acclimation, there is no doubt that other physiological parameters may correlate strongly with previous thermal history. Work by Brattstrom and Regal (1965), Brattstrom (1968, 1970), and Holzman and McManus (1973) has demonstrated acclimation of LD₅₀, CTM, and OS (onset of spasms) temperatures in many species of amphibia. Dramatic changes in these values may occur very rapidly, even in only 2 or 3 days, yet these changes are not necessarily related to metabolic compensation and are not an index of it. The short exposure times allowed by some experimenters attempting to evaluate the extent of thermal metabolic acclimation in adult frogs suggest that these workers are using the time course of changes in CTM or LD₅₀ as indicators of the time course of any metabolic acclimation that may occur. Allowing such short periods for acclimation is in sharp contrast to results from studies on the time course of metabolic acclimation in fish (Fry 1964), and this may account for some of the negative and confusing results from amphibia.

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