

THE INFLUENCE OF TEMPERATURE AND ACTIVITY ON AEROBIC AND ANAEROBIC METABOLISM IN THE VIVIPAROUS LIZARD, *LACERTA VIVIPARA* (JACQUIN).

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ABSTRACT

Aerobic and anaerobic metabolic rates were determined at temperatures between 20°C and 35°C for the viviparous lizard, *Lacerta vivipara*. Both parameters were found to be maximal around the preferred body temperature (30°C) with a low thermal temperature dependence above PBT. It is noted that *L. vivipara* does not need a large rate of anaerobic support and aerobic metabolism could supply the energy needed for activity.

INTRODUCTION

The active oxygen consumption of reptiles, particularly lizards, exceeds the resting (standard) oxygen consumption rate and the aerobic scope (the difference between the resting and active oxygen consumption rates) is maximal around the preferred body temperature (PBT) with a low thermal temperature dependence above this level (Bennett and Dawson, 1976; Bennett, 1982; Al-Sadoon, 1983). Maximal aerobic scope tends to be strictly temperature dependent in reptiles with the exception of iguanid and agamid lizards that can maximise this scope at the PBT (Bennett, 1982). It is also known that reptiles employ anaerobic metabolic scope (which is derived from the difference in lactate concentration levels between active and resting lizards) as a major energy source during the initial stages of forced activity (Bennett and Licht, 1972; Al-Sadoon, 1986) and the total metabolic scope (aerobic and anaerobic) is greatest at the PBT (Bennett and Dawson, 1972; Al-Sadoon, 1986).

The present study examines the aerobic and anaerobic metabolism of the viviparous lizard, *Lacerta vivipara* (Jacquin) to determine their contributions to the metabolic scope of this species.

MATERIALS AND METHODS

Common lizards, *L. vivipara*, were collected from the New Forest, Hampshire (Southern England) and housed in large tanks in the laboratory with food and water *ad lib*. The lizards remained in good condition throughout the experimental period despite the fact that they were fasted for at least 5-6 days preceding use. They were divided into two groups, one for the aerobic measurements and the other for anaerobic measurements.

Aerobic measurement

Oxygen consumption rate for resting and active lizards was determined using ten lizards at 20°C, 25°C, 30°C and 35°C in a double-chamber volumetric system (Al-Sadoon and Spellerberg, 1985, a,b). Estimations of

active metabolism were obtained from lizards subjected to electrical stimulation. Each individual was weighed placed into the sealed animal chamber of the volumetric system and were subjected to electrical shocks (10-14 volts) for at least five minutes via small stainless steel pin electrodes connected to a stimulator. These reached the animal through the top of the chamber and were implanted subdermally into its belly anterior to the hind limbs to stimulate rapid movement (period of stimulation). Thereafter, oxygen consumption determinations were taken every minute during the maximal activity period (a period of five minutes). Then the lizard was left to rest for another five minutes (recovery period) and oxygen consumption was recorded every minute during this postactive recovery period. The data were expressed as ml O₂/g body weight/hr and corrected to STP (see Fig. 2).

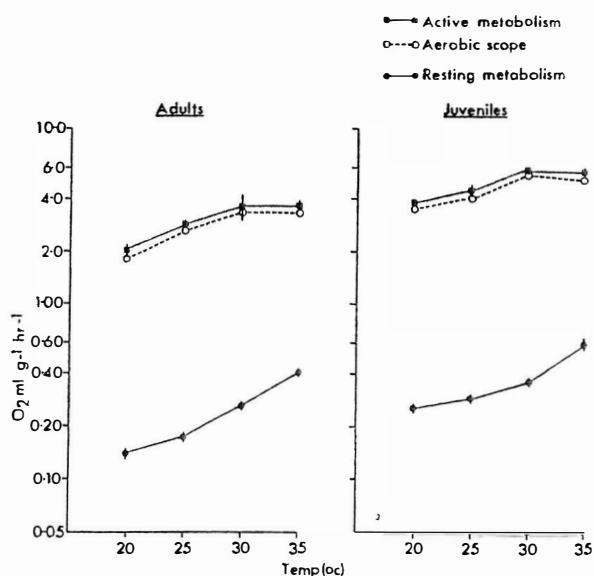


Fig. 1 Resting, active metabolism and aerobic scope of adult and juvenile *L. vivipara* determined at various temperatures. Each point represents the mean oxygen consumption of a number of lizards. Vertical lines represent \pm standard errors.

Anaerobic measurement

Total lactate production at different temperatures was determined in the whole body homogenates of resting and active lizards according to the method of Bennett and Licht (1972) and the data were expressed as mg lactate/g body weight.

Statistical analyses of differences between mean values of various groups at each temperature were performed using one-way analysis of variance (ANOVA) and were considered significant at $P < 0.05$.

RESULTS

Resting and active oxygen consumption rates

Mean values of resting oxygen consumption expressed as ($\text{ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$) were observed to increase with rising temperature from 20-35°C in both adult and juvenile lizards (Fig. 1). During the first 1-2 minutes of stimulation, the lizards were continuously moving around the animal chamber and the amounts of oxygen consumed during this period were considered to represent the active oxygen consumption.

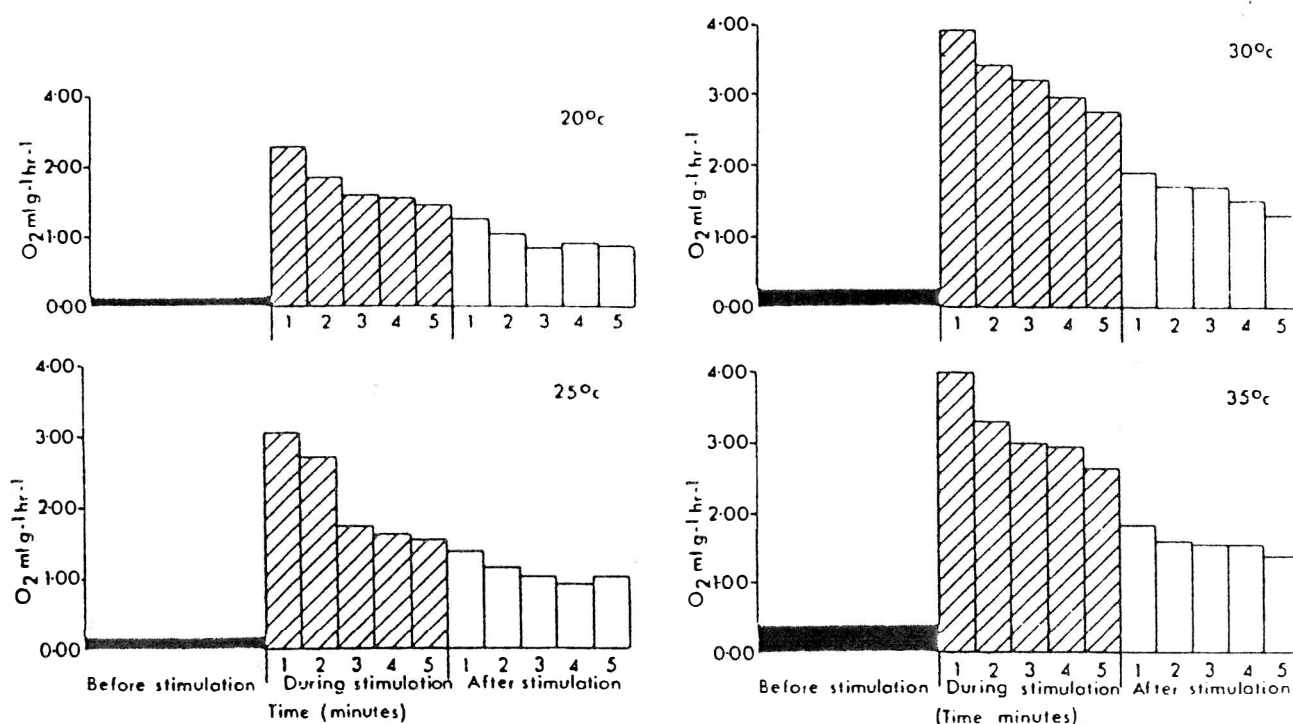


Fig. 2 Oxygen consumption rate of six male adult *L. vivipara* prior to stimulation and at one minute intervals, during 5 minute of stimulation and 5 minute of recovery. ■ resting O_2

This was also observed to increase with rising temperature from 20-30°C, but remained almost constant ($Q_{10} \approx 1$) at 30-35°C in both adult and juvenile lizards. The overall Q_{10} values of active lizards were lower than those of resting ones (Table 1) and so were the total means for active oxygen consumption during five minutes of post-activity ($P < 0.05$) at all temperature levels tested (Fig. 2). On the other hand, the aerobic scope increased with rising temperature from 20-30°C but dropped between 30°C and 35°C in both adult and juvenile lizards (Fig. 1).

Resting and active lactate production

Mean values whole-body lactate concentration expressed as mg lactate per gram body weight at different temperatures (20-35°C) for juvenile and adult lizards are shown in Fig. 3. There was no significant difference ($P > 0.05$) in these values between resting adult or juvenile lizards over the entire temperature range, but they increased in active ones at 20-30°C and dropped between 30-35°C (Fig. 3). The Q_{10} values for resting and active lactate concentrations are given in Table 1.

Temperature interval (°C)	Q ₁₀ values for oxygen consumption						Q ₁₀ values for lactate production					
	Resting		Active		Aerobic scope		Resting		Active		Anaerobic scope	
	juv.	adults	juv.	adults	juv.	adults	juv.	adults	juv.	adults	juv.	adults
20-25	1.33	1.45	1.33	2.00	1.33	2.04	1.50	1.05	1.40	1.35	1.35	1.65
25-30	1.50	2.40	1.76	1.64	1.78	1.59	1.00	1.52	1.06	1.40	1.09	1.32
30-35	2.75	2.40	0.93	0.97	0.84	0.92	1.16	0.68	0.94	0.59	0.83	0.52
Overall Q ₁₀ (20-35)	1.78	2.03	1.30	1.47	1.26	1.44	1.20	1.03	1.12	1.04	1.07	1.04

TABLE 1: Q₁₀ values for aerobic and anaerobic metabolism of resting and active lizards of *L. vivipara* at various temperatures.

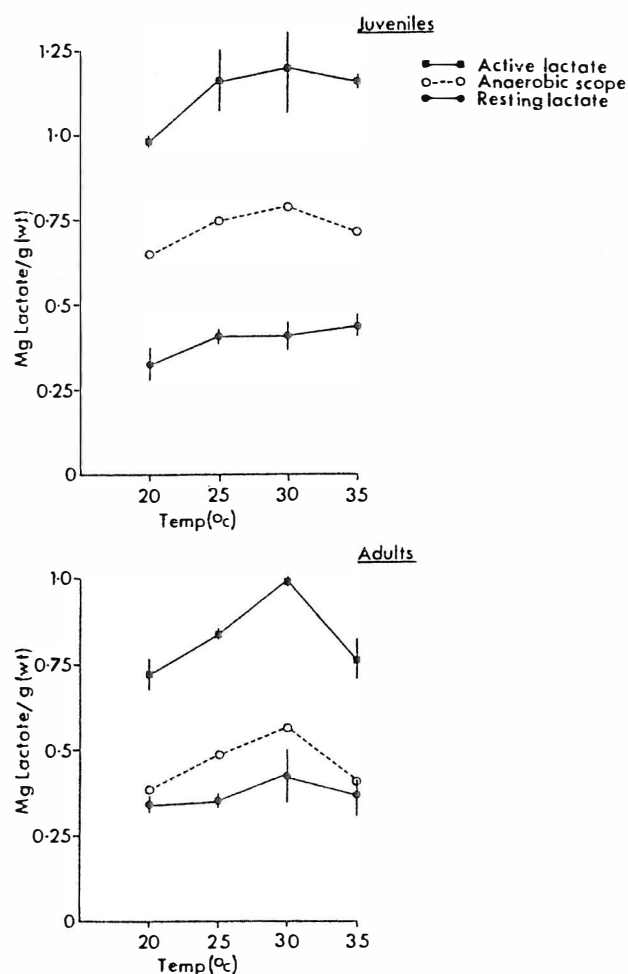


Fig. 3 Whole-body lactate concentration of resting, active (stimulated) lizards and the anaerobic scope of juvenile and adult *L. vivipara* determined at various temperatures. Each point represents the mean of several animals. Vertical lines represent \pm standard errors.

The highest Q_{10} values for active juvenile lizards were between 20–25°C and between 25–30°C for active adults and the lowest were between 30–35°C for both of them. The anaerobic scope values for both increased with rising temperature from 20°C to 30°C and decreased at 35°C (Fig. 3). There was no significant difference ($P > 0.05$) in the overall Q_{10} values between active and resting lactate production in either juvenile or adult lizards (Table 1).

DISCUSSION

The results indicate that the metabolism-temperature curves of both juvenile and adult *L. vivipara* are similar in shape but those of the resting and active juveniles are above those of the adults. This may be explained by the weight-specific metabolism which varies inversely with body weight (mean weights of the adults and juveniles were 3.8 and 1.4g respectively). Similar observations were made by Al-Sadoon (1983) for the desert skink, *Chalcides ocellatus*.

The resting oxygen consumption values of juvenile and adult *L. vivipara* are in line with values reported for lizards of comparable size (see Andrews and

Pough, 1985). However, the active oxygen consumption data obtained in the present study are the first for any lizard of the size of *L. vivipara*.

The aerobic metabolic scope for juvenile and adult *L. vivipara* was observed in the present study to increase with rising the temperature from 20°C to 30°C and the lizard appears to maximise this scope at its PBT which thereafter became independent of temperature. The maximisation of the aerobic scope at the PBT is understandable as, under natural conditions, most reptiles are known to be capable of thermoregulation. At temperatures exceeding the PBT, the aerobic scopes of several lizard species were shown to be temperature independent (Bennett and Dawson, 1972; Wilson, 1974; Bennett *et al.*, 1975; Bennett and Gleeson, 1976; Al-Sadoon, 1986).

As in the observations of Bennett and Licht (1972) on six species of lizards of comparable size to *L. vivipara*, the present results show little variation in resting lactate production between juveniles and adults. On the other hand the anaerobic scope values of adult *L. vivipara* reported in the present study are lower than those reported for lizards of similar size. However, comparison between the anaerobic scope values of juvenile *L. vivipara* (wt \bar{x} 1.2g) with those lizards of similar size show little variation (values for *Xantusia vigilis* (wt \bar{x} 1.2g) were 1.19, 1.32mg lact./g (wt) at 20°C and 30°C respectively, and scope values of for *Scincella lateralis* (wt \bar{x} 1.7g) were 0.94, 0.88mg lact./g (wt) at 20°C and 30°C respectively, Bennett and Licht, 1972). This variation in the anaerobic metabolism between *L. vivipara* and other lizards of similar size could be due to the method of measuring the anaerobic metabolism in these lizards. The previous anaerobic values (Bennett and Licht, 1972) were calculated as the amount of lactate produced during activity to exhaustion by stimulating the animal for a longer period of time (4–6 minutes). These values were termed the 'anaerobic capacity' whereas the present values for *L. vivipara* are taken from stimulating the animals for a shorter period of time (2 minutes). Unlike the aerobic scope, the anaerobic scope and the anaerobic capacity are less temperature dependent and are less than predicted for biological reaction rates in general. The Q_{10} ranges from 1.09 to 1.35 and from 1.32 to 1.65 above 20°C in *L. vivipara* adults and juveniles respectively (Table 1). However, the anaerobic scope has very low temperature dependence (Q_{10} less than 1) above the PBT. This temperature dependence in the anaerobic metabolism may be of great importance for these animals during activity, particularly when avoiding predators and when the lizard's temperature is below the preferred levels. Similar observations were made by Al-Sadoon (1986) on *C. ocellatus*.

The data obtained for *L. vivipara* (adults and juveniles) during the initial stages of forced activity in the present study might indicate that the animals rely mainly on the aerobic contribution of ATP (Table 2) as a major source of energy at the voluntary body temperature (20°C to 35°C) and that the ATP produced by aerobic, anaerobic and total metabolic scope for the animal increases with rising temperature till reaching maximal levels at 30°C (PBT for

Exper. Temp. (°C)	Aerobic scope ATP ($\mu\text{mole/g/2 min}$)				Anaerobic scope ATP ($\mu\text{mole/g/2 min}$)				Total metabolic scope ATP ($\mu\text{mole/g/2 min}$)	
	juv.	(%)	adults	(%)	juv.	(%)	adults	(%)	juv.	adults
20	34.80	76	18.17	74	10.83	23	6.34	26	45.63	24.51
25	40.21	76	26.00	76	12.59	24	8.17	24	52.80	34.17
30	53.75	80	32.86	78	13.15	19	9.38	22	66.89	42.24
35	49.49	80	31.03	82	12.01	19	6.80	18	61.50	37.83

TABLE 2: Aerobic and anaerobic contribution to the total metabolic scope during 2 min. of activity in juveniles and adults of *L. vivipara*.

L. vivipara, see Avery, 1979) before declining at temperatures above that level. At the PBT, aerobiosis was observed in the present study to provide 78 per cent and 80 per cent of the total scope during the two minutes of forced activity for adults and juvenile *L. vivipara* respectively (Fig. 4). A similar observations on other animals indicated that aerobic scope accounted for more than 80 per cent of total ATP produced during a 3 minute of activity in the Giant toad *Bufo marinus* (Miller and Hutchison, 1980). Bennett and Licht (1973) reported that *Bufo boreas* depend on aerobic metabolism to sustain activity. The larger values of the aerobic scope in *L. vivipara* could be related, to some extent, to the behaviour of this species in the field. In its natural habitat of heathland, field edges and wooded areas, *L. vivipara* is a shuttling heliotherm that emerges in sunny mornings to spend a considerable part of the day basking, foraging and feeding (Avery, 1971). If disturbed, its reaction is to seek refuge within seconds. Hence, such type of behaviour does not need a considerable rate of anaerobic support and aerobic metabolism alone is sufficient to supply the required energy.

Moreover, small lizard species had much greater aerobic scope levels than larger ones. This difference may be related to the greater pressure from predation for smaller animals, and also the capacity of larger lizards for defence against predators. Also, other physiological functions such as oxygen transfer across the lungs, could be the reason for this variation. These considerations would also suggest that juveniles of *L. vivipara* would have much higher aerobic scope than adult lizards.

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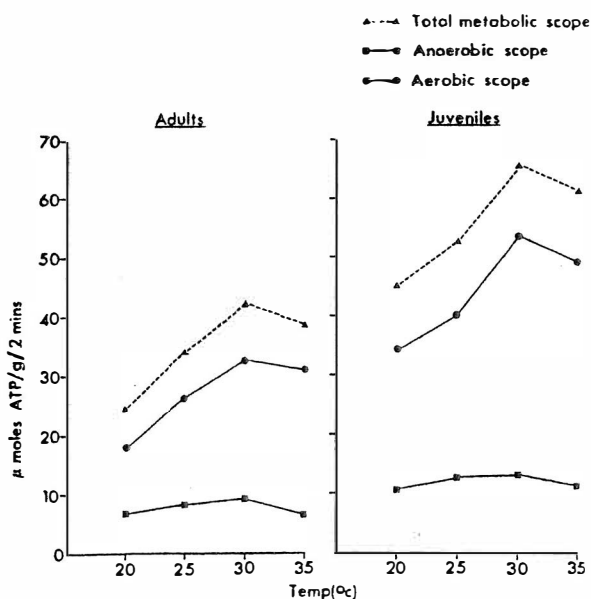


Fig. 4 Aerobic, anaerobic and total metabolic scope ATP generation during 2 minute of burst activity in *L. vivipara* (adults and juveniles). ATP was measured by the method of Bennett and Licht (1972).

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GROWTH, MOVEMENT AND POPULATION DYNAMICS OF *NATRIX MAURA* IN A DRYING RIVER

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ABSTRACT

Viperine water snakes were studied by mark-recapture in a small river in Eastern Spain from 1981 to 1983, a period of drought. Observed growth rates between captures were low and highly variable. Growth rings were counted in skull bones; narrow rings could not be found, and the observed rings were probably from periods of faster growth or normal growth before the drought. The rings predict that males and females reached maturity in their third and fifth years, respectively. The effect of drought was greater on growth than on reproduction. Movements of snakes captured several times at long intervals suggest that the home ranges of mature males and females were 170m and 250m of river, respectively, although some individuals moved 1km between years. A review of published data showed that widely foraging grass and garter snakes have greater displacements between captures than the more sedentary water snakes.

There were estimated to be 1060 and 390 adult males and females in the main study area, which was a 2km length of river which included most of the permanent unpolluted water in the river system. Annual survival of adult snakes remaining within the study area was estimated as 0.53 ± 0.16 and 0.71 ± 0.25 in males and females, respectively. A simple model of the dynamics of this population was developed from results on survival, recruitment, growth and fecundity, as a hypothesis for further study. The model suggested that: 1) There was dispersal of adult males but not adult females — this was supported by the population size structure in peripheral areas where mature females were scarce and which were probably stocked by dispersal. 2) The number of adult males and females was stable or increasing, and juvenile survival of about 0.65 year^{-1} would be necessary for total population stability.

INTRODUCTION

The dynamics of snake populations have proved difficult to study, as these animals are difficult to find or catch (especially juveniles), they have slow growth without external indicators of age, and often show long

seasonal movements. After surveying the available data (which suggested that those populations which had been studied were unable to maintain themselves), Turner (1977) concluded 'one is left with distinct reservations as to the suitability of snake populations for this sort of ecological endeavour'. After the