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SEASONAL CHANGES IN METABOLISM OF THE LIZARD *LACERTA VIVIPARA*

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ABSTRACT

Acute oxygen consumption determinations for both adults and sub-adults of *L. vivipara* were made over the temperature range 5-30°C during summer and winter. During winter dormancy, both adults and sub-adults were found to have a metabolic rate lower than the metabolic rate of summer animals at each experimental temperature. This reduction of oxygen consumption in winter lizards can be interpreted as an "inverse compensation" (Precht's Type 5 pattern of response). It is concluded that this adjustment can reduce energy costs during the winter period and is a pre-requisite for survival during winter dormancy.

INTRODUCTION

Some reptiles have evolved a number of ways by which they can tolerate low winter temperatures. For example, some species of reptiles which inhabit cool, temperate zones and high altitudes have low critical minimum temperatures, compared to their summer critical minimum temperature (Spellerberg, 1976). Instantaneous shifts in the metabolic rate-temperature curves (Aleksiuk, 1971; 1976a) of cool-temperature species has been reported to be an adaptation to winter conditions. Many reptiles raise their metabolic rate after exposure to low temperature acclimation (Bennett and Dawson, 1976). In addition, a depression of body temperature below freezing point without internal ice formation, has been observed in few species (Lowe *et al*, 1971).

Winter dormancy in ectotherms has sometimes been called "brummation" to distinguish it from hibernation in endotherms, but it has not found universal acceptance (Gregory, 1982). In this research the term winter dormancy has therefore been used. Gilles-Baillien, (1974) has suggested that hibernation in small mammals differs from that of the winter dormancy in reptiles, particularly with regard to two aspects. Firstly, winter dormancy in reptiles does not involve adaptive hypothermia and secondly, reptiles do not regulate the dormancy state by internal means. The latter difference has been questioned since some reptiles do undergo some physiological adjustments in their metabolic rate during the winter dormancy period (Moberly, 1963; Bennett and Dawson, 1976; Gatten, 1978; Patterson and Davies, 1978a and Johansen and Lykkeboe, 1979).

The objective of this investigation was to measure levels of oxygen consumption during winter dormancy (adults and sub-adults) and to compare the results with the metabolic rate of *L. vivipara* during the summer.

MATERIALS AND METHODS

Six male adult *L. vivipara* (mean weight 3.8 gm) and six sub-adult *L. vivipara* (mean weight 2.6 gm) were used for the measurement of summer oxygen consumption. These two groups of lizards were obtained near the New Forest in Southern England. Metabolic rates (0_2 ml g^{-1} h^{-1}) were measured at various temperatures (5-30°C) during early September. These results are referred to as the "summer" levels of oxygen consumption.

A further two groups of six lizards each (adults, 3.9 gm; sub-adults, 2.7 gm) were used for the winter metabolic studies. These lizards were placed in a small tank (40 cm x 25 cm) and on 15th November 1980, the entire tank was buried at 35 cm depth in an outdoor vivarium. The tank was half filled with moist hay to maintain a high humidity. Ground temperatures inside the tank were recorded daily. The lizards were left for four months under these conditions which simulated natural conditions for winter dormancy of *L. vivipara*. The first measurements of oxygen consumption were made on 3rd February 1981, following 80 days winter dormancy. The lizards were removed from the holding tank and placed in the animal chambers and their oxygen consumption was measured at different temperatures between 5-30°C. After taking the oxygen measurements, the lizards were returned to the outdoor vivarium for further measurements of oxygen consumption during winter dormancy. The second determinations of oxygen consumption on the adults only were made on 2nd March 1981 (total of 100 days winter dormancy).

A double chamber volumetric system was used for measurements of oxygen consumption. Animals were not allowed to acclimate to the test temperature i.e. acute M-T curves were obtained. Six to eight small respirometers were used. Each respirometer consisted of two 500 ml flasks joined by a vertical glass manometer filled with manometer fluid. One of the flasks served as the animal chamber and the other as a compensating chamber (thermobarometer). Small bags of soda lime (carbon dioxide absorbent) and silicagel (water absorbent) were placed in each flask. Each respirometer was placed in a water bath to maintain a constant experimental temperature to +0.5°C. The animals were fasted for two days then placed in the flasks at a given temperature (experimental temperature) for 1-4 hours. During this time no readings were taken in order to ensure that the effects of handling were reduced and that the respiration reached standard levels. After this resting period the animal's resting metabolism (standard metabolism) was measured by closing the animal chamber to the atmosphere and then adjusting the thermobarometer so that it was also closed to the atmosphere. The manometer fluid rises as oxygen is consumed in the animal chamber. A syringe (1 ml) of pure oxygen was attached to the animal chamber and direct readings from the syringes could then be taken indicating the volume of oxygen necessary to re-adjust the manometer fluid to its previous level. This process was repeated and readings were taken every 10-15 minutes for at least two hours. Further readings over shorter intervals (e.g. 5 minutes) were taken at higher temperatures because of the high metabolic rate associated with higher temperatures. Between four and six values of oxygen consumption (at each temperature level for each animal) were selected from the lowest but consistent readings. The procedure was repeated for temperatures ranging from 5-30°C intervals. The oxygen consumption values obtained were converted to standard conditions and expressed in mls oxygen consumed per g body weight per hour. All experiments were made at a time when the lizards would normally be active. Full details of the methods may be found in Al-Sadoon (1983) or Al-Sadoon and Spellerberg (1985b).

Comparisons of mean oxygen consumption between experimental groups were made using two tail t-tests. The rejection level of statistical significance adopted in this research was $P>0.05$. Most of these statistical analyses were made with the aid of computer (ICL 2900) at Southampton University.

RESULTS

Rates of oxygen consumption of adult and sub-adult *L. vivipara* for both summer and winter groups are given in Table 1. Statistical analysis revealed no significant difference ($P>0.05$ between the two winter groups of adult lizards at any of the six temperatures. However statistical analysis did show that mean oxygen consumption values for both adults and sub-adults were significantly higher for the summer lizards compared to the winter lizards at all temperatures. Data for the two winter samples for the adult lizards were combined when the summer and winter samples were compared (Table 1). At all temperatures the oxygen consumption of sub-adults was found to be higher than that of adults and this may be explained by using specific metabolism which varies inversely with body weight (Al-Sadoon and Spellerberg, 1985a).

The M-T curves for adults and sub-adults were obtained by plotting (semi-log) the mean oxygen consumption values against the appropriate temperatures. A comparison of the M-T curves for both summer and winter samples is shown in Fig. 1.

	Adults				Sub-adults		
Temp.	Oxygen consumption						
(°C)	Summer	80 days winter dormancy	100 days winter dormancy	P (Data for winter combined)	Summer	80 days winter dormancy	P
5	.037	.016	.017	<.010	.082	.030	<.002
10	.051	.023	.021	<.005	.150	.051	<.001
15	.068	.045	.049	<.010	.183	.089	<.020
20	.131	.063	.064	<.020	.206	.126	<.050
25	.160	.101	.128	<.001	.263	,164	<.050
30	.292	.145	.141	1.001	.385	.252	<.010

TABLE 1. Mean oxygen consumption values (0_2 ml g^{-1} hr^{-1}) for adults and sub-adults of *L. vivipara*. Summer and winter samples were examined at various temperatures.

From these data it is possible to calculate Q_{10} values which are presented in Table 2. The "overall" Q_{10} values for the winter groups are higher than the "overall" Q_{10} values for the summer groups.

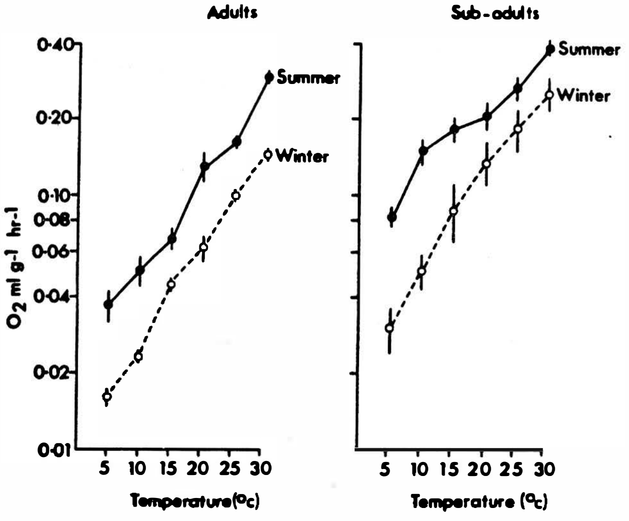

Fig. 1. Acutely measured M-T curves of *L. vivipara* (adults and juveniles) determined at different temperatures in summer and winter seasons. Each point represents the mean oxygen consumption of several lizards. Vertical lines represent ± standard errors.

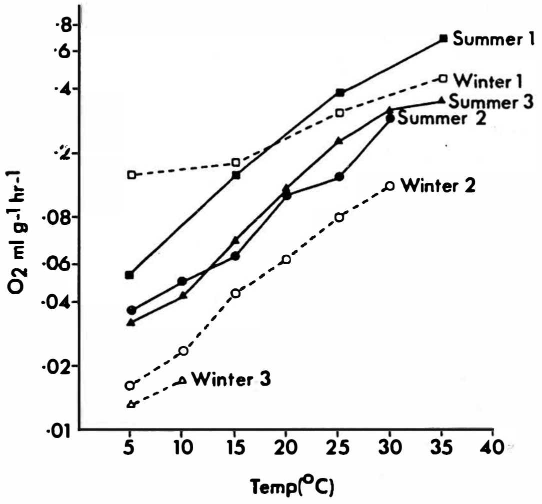

Fig. 2. Comparison between the M-T curves of different populations of *L. vivipara* (adults) during winter and summer seasons. (1) Sveegaard and Hansen (1979); (2) Present study (1983); (3) Patterson and Davies (1978a, 1978b).

In Fig. 2 the oxygen consumption values recorded in this research are compared with the results from two other studies on *L. vivipara*. It is interesting to note that the M-T curves for *L. vivipara* from Denmark are higher than the M-T curves for *L. vivipara* collected in England. Whereas results in the present study showed

	Adults			Sub-adults	
Temp. interval (°C)	Summer	80 days winter dormancy	100 days winter dormancy	Summer	80 days winter dormancy
5-10	1.90	2.06	1.52	3.34	2.89
10-15	1.77	3.82	5.44	1.48	3.04
15-20	3.71	1.96	1.87	1.26	2.00
24-25	1.49	2.57	3.59	1.63	1.69
25-30	3.33	2.06	1.23	2.14	2.36
"Overall" (5-30)	2.28	2.41	2.33	1.85	2.34

TABLE 2. Q^{10} values for oxygen consumption of adults and sub-adults of *L. vivipara*.

that summer levels of oxygen consumption of summer lizards were always higher than those of winter, this is not the case for the *L. vivipara* from Denmark. That is, Sveegaard and Hansen (1979) reported higher levels of oxygen consumption for winter animals at 5°C and 15°C compared with results for the summer animals. At higher temperatures the reverse was true.

DISCUSSION

The acute M-T curves for the summer and winter groups of adult and sub-adult lizards (Fig. 1) shows that there is a reduction in the metabolic rate of winter lizards. This observed reduced level of resting oxygen consumption in the winter lizards may be regarded as "inverse" or "undercompensation" as suggested by patterns of responses described by Precht (1958). Energy conservation in *L. vivipara* during their dormancy period (early October to early March) is obviously important since at that time food could not be obtained nor could it be digested efficiently at such low body temperatures (Spellerberg, 1982).

That winter oxygen consumption rates at each experimental temperature are lower than might be expected for summer measurements at the same temperature has been reported for many species of reptiles. Moberly (1963) for example observed a reduction in winter metabolism at higher temperatures in the desert lizard, *Dipsosaurus dorsalis*. Acclimation to cold resulted in reduction of active and standard metabolism of *Chelydra serpentina* (Gatten, 1978). Other studies (Mayhew, 1965; Fitzpatrick *et al*, 1971, 1972; Hoskins and Aleksuik, 1973; Fitzpatrick and Brown, 1975; Sveegaard and Hansen, 1979 and Johansen and Lykkeboe, 1979) have also demonstrated a reduction in the oxygen consumption rates following exposure to low temperatures.

The overall Q_{10} of winter lizards is higher than that of summer lizards for both adults and sub-adults (Table 2). This observation emphasises the comparatively large differences in oxygen consumption between summer and winter animals at low temperatures whereas at higher temperatures the difference diminishes. Previous research has shown that in some other species of reptiles the Q_{10} is higher in dormant than in non-dormant or active animals (Aleksiuk, 1976a; Aleksiuk, 1976b; Gatten, 1978; Johansen and Lykkeboe, 1979).

The present results are similar to those reported by Patterson and Davies (1978a, 1978b). Comparison of the present results with those obtained by Sveegaard and Hansen (1979) strongly suggest that there may be latitudinal and temperature based adjustment in the M-T curve of *L. vivipara* (from Denmark). That is, those lizards obtained from areas near the New Forest have, during both winter and summer, a lower metabolic rate compared to those lizards studied in Denmark over the same temperature range. This effect seems to indicate that the lizards are adapted to local temperature conditions. Assuming that, an average, daily summer temperature in Denmark is lower than that in England (15°C and 23°C respectively) the following hypothesis could be presented: a comparison between the oxygen consumption rate of an English *L. vivipara* at an average summer day temperature of 23°C (0.150 0_2 ml g^{-1} hr^{-1}) and a Danish *L. vivipara* at 15°C an average Danish summer day temperature (0.160 0_2 ml g^{-1} hr^{-1}) shows a close similarity of the oxygen consumption rates. These results may support evidence of metabolic adjustments to climate and thus provide insights into the capability of reptiles to adapt to cold environments.

The higher levels of oxygen consumption at 5°C and 15°C (results from Sveegaard and Hansen (1979) in Fig. 2) for winter animals, compared to the summer animals are particularly interesting. This elevation in the lower part of the M-T curve in respect to the upper part of the curve for the winter *L. vivipara* from Denmark suggests the presence of a temperature dependent shift which has previously been reported by Tromp and Avery (1977).

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SHORT NOTE:

OPTIMAL TEMPERATURE FOR INNER-EAR PERFORMANCE AGREES WITH FIELD BODY TEMPERATURE IN *PHELSUMA* (REPTILIA: GEKKONINAE)

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The performance of the vertebrate inner ear is often assessed by the electrical AC output of the hair cells: the alternating potentials of the cochlear duct, commonly nicknamed "cochlear microphonics", or CM. The shape of the audiogram (displaying sound intensity required for a standard CM response, against a scale of sound frequencies) is affected by temperature. In reptiles, at least, one can define for each species an optimal temperature which yields an optimal audiogram (Werner, 1972, 1976).

In a recent review I showed good overall correlation among lizards between these specific optimal temperatures for cochlear performance, and variously defined ecological, whole body, optimal or preferred body temperatures (Werner, 1983). This is part of the well-known phenomenon that many physiological processes of reptiles tend to have their temperature optima at or near the ecologically preferred body temperature (Huey, 1982).

For *Phelsuma madagascariensis* my limited data (Werner, 1976, 1983) had suggested a cochlear optimum around 30°C, and an overall preference in captivity of 26-29°C (Fig. 1). Unfortunately, at the time I overlooked the paper by Crawford and Thorpe (1979) who found that in the field (on Praslin, Seychelles, in August) *Phelsuma madagascariensis*