

ENERGY EXPENDITURE AND METABOLIC ADAPTATION DURING WINTER DORMANCY IN THE LIZARD *LACERTA* *VIVIPARA* JACQUIN

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Abstract—1. *Lacerta vivipara* were hibernated from October to March. Respiration rates were measured at various times during this period and compared with respiration rates of lizards at the same temperatures in July.

2. Rates of respiration at 10°C soon after entry into hibernation and towards the end of the dormant period did not differ significantly from rates at 10°C in July.

3. After several weeks in hibernation at 10°C a depression of metabolism occurred which produced acclimated respiration rates significantly lower than 10°C rates measured at other times of year. This is interpreted as a probable case of negative metabolic compensation to temperature (inverse acclimation).

4. No difference in respiration rates at 5°C could be detected between dormant and summer lizards.

5. Energy expenditure during winter dormancy accounts for approximately 5% of the energy assimilated annually from food. Inverse acclimation at 10°C effects an energy saving amounting to about 35% of the total dormancy expenditure.

INTRODUCTION

MOST work on the physiology of winter dormancy in animals has been performed on mammals, in which there is a marked and measurable reduction in the rate of oxygen consumption associated with the onset of hibernation (see Altman & Dittmer, 1974; Kayser, 1965; and Spector, 1956, for data on several species). Despite the fact that many species of temperate reptiles are dormant in winter, little is known about the metabolic physiology of hibernation in these animals, although a few studies have demonstrated some depression in metabolism during hibernation (Aleksuik, 1976; Mayhew, 1965; Moberly, 1963). Part of the reason for this deficiency in our knowledge is the difficulty with terrestrial ectotherms—particularly those which thermoregulate behaviourally—in distinguishing between conforming and compensating metabolic responses to ambient temperature. Only if the low temperature metabolic rate of an ectotherm in winter dormancy exhibits a pattern of negative compensation (Prosser, 1958) or Precht Type 5 response (Precht, 1958) can winter dormancy be regarded as true hibernation rather than cold-induced torpor.

In the study reported here, which is part of a series of studies of energy allocation in cool and warm temperate lizards, the low temperature metabolic rates of dormant and non-dormant British Common Lizards, *Lacerta vivipara*, are compared. Data are presented which support the view that this lizard undergoes true hibernation in the sense defined above. In addition, the energetic cost of hibernation, in both

absolute and food-relative terms, has been calculated and an estimate made of the energy saving effected by the observed negative metabolic compensation to temperature. *Lacerta vivipara* is of particular interest in connection with the study of low temperature adaptations in reptiles because its distribution extends further from the equator than that of any other living reptile (Andersen, 1971).

MATERIALS AND METHODS

All *Lacerta vivipara* used in this study were caught at two localities in the south of England, and were maintained in an outside vivarium at Nottingham until required for experimentation. During this period they were fed on *Tenebrio molitor* larvae. Prior to their transfer to laboratory conditions, food was withheld from the lizards for one week in the case of winter lizards, and for between three and seven days in the case of summer lizards.

Winter metabolism

In mid-October, lizards of both sexes were taken from the outside vivarium and placed in a glass aquarium measuring 92 cm × 31 cm × 31 cm high. The glass sides of the aquarium were covered with black paper, the top was closed with a wooden, ventilated lid, and the entire tank was placed in a constant temperature room in which ambient temperature could be varied. The aquarium was half filled with damp hay, and several bowls of water were placed on the floor of the aquarium to help maintain a high relative humidity.

The following ambient temperature regime was used during the winter period: for the first nine weeks (until mid-December), ambient temperature was held at 10°C; for the next 11 weeks (until early March) it was lowered to 5°C; finally, it was raised once more to 10°C. We consider that this temperature regime, combined with conditions of constant darkness and high relative humidity, provided a reasonable simulation of the environmental condi-

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tions encountered naturally by hibernating *Lacerta vivipara* in England.

The rate of respiration of selected lizards was measured, at the same temperature as that of the constant temperature room, at the following times during the dormant period (the experimental temperature, time of year and code number assigned to each lizard group, are given in parentheses):

1. One to two weeks after being placed in the constant temperature room (10°C, late October, 10A).
2. Seven to eight weeks after being placed in the constant temperature room (10°C, early December, 10B).
3. Four to six weeks after the temperature was lowered to 5°C (5°C, mid January, 5A).
4. Ten to eleven weeks after the temperature was lowered to 5°C (5°C, late February, 5B).
5. Two to five days after the temperature was raised to 10°C (10°C, early March, 10C).

Summer metabolism

The metabolic rates of 'summer lizards' were measured in July. These lizards were maintained in the outside vivarium and fed on *Tenebrio molitor* larvae until required for respirometry. During this period they were exposed to natural photothermal conditions and thus able to thermoregulate behaviourally. Night time temperatures occasionally fell as low as 10°C. Mean preferred body temperature for male *Lacerta vivipara* at this time of year is 30.5°C (Patterson & Davies, 1978). Between three and seven days prior to respirometry, male lizards were transferred to the constant temperature room, where photothermal conditions were similar to those outside but controlled, with ambient temperature set at 10°C and cage lights (under which the lizards could bask and thereby raise their body temperatures to preferred levels) switched on for 14 h per day. Thus the July lizards were in as near a natural physiological condition as possible at the time their respiration rates were measured. These rates were measured at 5°C and 10°C. Only male lizards were used in the July experiments because *Lacerta vivipara* is an ovoviviparous species whose females are carrying developing embryos in July. The respiration of these embryos contributes significantly to the total oxygen consumption of the female (Patterson & Davies, unpublished results).

Measurement of oxygen consumption

Oxygen consumption was measured in small constant pressure respirometers having animal and compensation chambers connected by a U-tube containing Dixon's manometer fluid. Carbon dioxide was absorbed by small bags of soda lime placed in the animal chamber.

Only lizards with complete tails were used. In the evening, lizards were placed in the respirometers and the respirometers

were placed in a constant temperature water bath at the required experimental temperature (5°C or 10°C). The water bath was covered with a black cloth so that the lizards were in constant darkness. The following morning, the taps of the respirometer were closed and readings taken at regular intervals for 3 to 8 h.

Oxygen consumption values were converted to standard conditions according to the method of Scholander *et al.* (1952), and expressed as microlitres per gram per hour ($\mu\text{g}^{-1} \text{h}^{-1}$). Since the lizards were quiescent and fasted, these values can be assumed to approximate to standard metabolic rate in all cases. Where necessary, they were converted to energy units (J) by multiplying by 0.0202 ($1 \mu\text{l O}_2 \equiv 0.0202\text{J}$).

Statistical analysis

Differences in oxygen consumption rates between treatment groups were analysed by means of the *t*-test (Bailey, 1959). These differences were considered significant when $P \leq 0.05$.

RESULTS

Oxygen consumption rates for *Lacerta vivipara* at various times during the period of dormancy are shown in Table 1. The rates of the 10B group are significantly lower and considerably less variable than those of the 10A group, despite no change in ambient temperature. The observed sex differences in metabolic rate are significant in the case of the 10B group, but not in the case of the 10A group. Lowering the temperature of the constant temperature room to 5°C resulted in a further significant reduction of metabolic rate. The 5A and 5B rates are not significantly different from one another. Raising the temperature again to 10°C induced a rise in respiration rate to a level (10C) not significantly different from the mean 10A rate, but significantly higher than the mean 10B rate.

Table 2 shows the rates of respiration of male *Lacerta vivipara* measured in July. The 10°C rate of summer animals is not significantly different from either the 10A or the 10C rates of dormant animals, but is significantly greater than the 10B rate. The 5°C rate of summer animals is not significantly different from either the 5A or 5B rates of dormant animals.

Table 1 also shows the metabolic rates of dormant animals expressed in energetic terms. If a close correspondence between the conditions of simulated and natural dormancy is assumed, it is possible to estimate from these metabolic data the energy cost of

Table 1. Metabolic rates of male and female *Lacerta vivipara* during winter dormancy

Temperature (°C)	Group*	Sex	N	Mean weight (g)	Mean metabolic rates		
					($\mu\text{l O}_2 \text{g}^{-1} \text{h}^{-1}$) ($\bar{x} \pm \text{S.D.}$)	(J day ⁻¹) (per gram)	(per individual)
10	10A	♂	10	3.362	50.85 ± 34.86	24.65	82.87
		♀	10	3.472	44.44 ± 27.59	21.54	74.80
	10B	♂	10	3.476	17.58 ± 1.24	8.523	29.63
		♀	10	3.455	20.78 ± 3.11	10.07	34.81
5	5A	♂	10	3.476	11.89 ± 2.86	5.764	20.04
		♀	10	3.472	13.48 ± 2.84	6.535	22.69
	5B	♂	5	3.304	13.25 ± 6.74	6.424	21.22
		♀	5	3.264	12.30 ± 2.24	5.963	19.46
10	10C	♂	5	3.348	37.55 ± 20.50	18.20	60.95
		♀	5	3.345	37.56 ± 9.73	18.21	60.91

* See Materials and Methods for definition of these groups.

Table 2. Respiration rates of male *Lacerta vivipara* at 5°C and 10°C during July

Temperature (°C)	N	Mean Weight (g)	Respiration rate ($\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) ($\bar{x} \pm \text{S.D.}$)
10	5	3.333	37.63 \pm 12.26
5	5	3.290	12.46 \pm 1.75

winter dormancy in adult *Lacerta vivipara*. For this purpose we have assumed that dormant lizards respire for two weeks at rate 10A, for seven weeks at rate 10B, for eleven weeks at rate 5AB, and for three weeks at rate 10C. The total energy expended during the dormant period was calculated as shown below and corresponds to the expenditure of a lizard becoming dormant in mid-October and emerging from dormancy in late March. It was assumed that the lizards respire at the 10A rate for a much shorter period than the 10B rate because some of the 10A group lizards were already respiring at the same rate as the 10B group lizards when their rate of oxygen consumption was measured a few days after they were placed in the constant temperature room. Thus it is likely that the 10A respiration rate is of short duration.

Given these assumptions, a tentative estimate of the total energy cost of winter dormancy in adult *Lacerta vivipara* can be computed as follows:

For a male weighing 3.4 g, the total energy expended during the period of dormancy is (data from Table 1):

$$(82.87 \times 14) + (29.63 \times 49) + \left(\frac{20.04 + 21.22}{2} \times 77 \right) + (60.95 \times 21) = 5481 \text{ J per lizard}$$

For a female weighing 3.4 g, the total energy expended is:

$$(74.80 \times 14) + (34.81 \times 49) + \left(\frac{22.69 + 19.46}{2} \times 77 \right) + (60.91 \times 21) = 5655 \text{ J per lizard}$$

DISCUSSION

Some of the rates of oxygen consumption presented in this paper were obtained from lizards which had been allowed to thermoregulate, and which had therefore been subjected every day to a range of temperatures between the body temperature attained by basking (about 30°C; see Avery, 1971 and Patterson & Davies, 1978) and the temperature of the constant temperature room (the temperature to which the lizards' bodies fall at night). Therefore it is necessary to be cautious when applying classical acclimation terminology to these respiration rates, for classical studies of thermal acclimation in ectotherms have typically used animals which had been exposed to a constant rather than a fluctuating temperature regime (Precht, 1958; Prosser, 1958).

However, the 10B rate of respiration was measured when the lizards had been in hibernation at 10°C for several weeks, so this can be regarded as an acclimated rate. Since the 10B rate of respiration is less

than respiration at 10°C at any other time, it is likely that this is a case of "inverse thermal compensation", Precht's Type 5 pattern of response (Precht, 1958). If this is so, the observed depression is acclimatory and therefore the term "hibernation" to describe the winter dormancy of *Lacerta vivipara* is justified. Negative adjustments of this kind have been reported for a number of hibernating reptiles and amphibians (Fitzpatrick *et al.*, 1971, 1972; Fitzpatrick & Brown, 1975; Hazel & Prosser, 1974; Hoskins & Alekskiuk, 1973; Mayhew, 1965; Moberly, 1963), and are usually interpreted as a device for effecting energy economies during prolonged periods of enforced fasting. Our own calculations, based on estimates of the overall energetic cost of hibernation and various measurements of metabolism at 10°C, lend strong support to this view, for they suggest that the 50% depression of metabolism in the 10B group of lizards can achieve savings of 35–40 J per 3.4 g lizards per day. This metabolic depression, even when sustained for a relatively short period (seven out of 23 weeks in the experimental case), is equivalent to approximately 35% of the total quantity of energy expended during hibernation.

The fact that no negative compensation occurs at 5°C, which may seem odd at first sight, can also be accounted for (partly, at least) in energetic terms. A 50% reduction of 5°C metabolism would save about 10 J per 3.4 g lizard per day, which even over a longer period of time (11 weeks in this case) amounts to a total energy saving of only 14% of the total quantity expended during hibernation, considerably less than the saving effected by a 50% reduction of 10°C metabolism.

The respiration rate of *Lacerta vivipara* in early March (10C group), just after the ambient temperature had been raised from 5°C to 10°C, was not significantly different from the 10A or the 10°C July groups, but markedly higher than the 10B group. In other words, the rise in temperature induced non-hibernation type rather than hibernation type 10°C respiration rates. Moberly (1963) and Viitanen (1967) have demonstrated a correlation between rise in soil temperature and termination of hibernation in reptiles. The present work provides some physiological evidence that a rise in temperature may, by itself, induce reptiles to terminate hibernation.

Using data reported by Avery (1971, 1975), it is possible to calculate that assimilated food provides a typical 3.4 g adult *Lacerta vivipara* with between 96 kJ and 126 kJ per year. On the assumption that the cost of hibernation is 5.4–5.7 kJ for a lizard of this size, it is evident that survival through a period of hibernation equal to 44% of the year (23 weeks) requires approximately 5% of the total annual food-energy budget. There are few other studies of this type, but by using data reported by Fitzpatrick (1973), it is possible to compare *Lacerta vivipara* with the salamander *Desmognathus ochrophaeus*. Individuals of both species expend very similar quantities of energy, in weight relative terms, during hibernation (1.6 kJ·g⁻¹ for *L. vivipara*, 1.9 kJ·g⁻¹ for *D. ochrophaeus*). However, because the annual food-energy income of *D. ochrophaeus* is much less than that of *L. vivipara*, this expenditure amounts to a considerably higher proportion of the total annual energy budget

in the case of the salamander (17% as against 5% in the lizard). Since the absolute quantities of energy allocated to reproduction are also approximately the same in the two species and growth has ceased in both cases, the much greater total energy budget of *Lacerta vivipara* presumably reflects greater activity during that part of the year when it is not in hibernation.

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