

PREFERRED BODY TEMPERATURE: SEASONAL AND SEXUAL DIFFERENCES IN THE LIZARD *LACERTA VIVIPARA*

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(Received 20 December 1976; accepted 26 June 1977)

Abstract—1. Mean preferred body temperatures (PBT) of thermoregulating *Lacerta vivipara* were measured monthly in the laboratory between April and October.

2. Mean PBT varied between 27.3°C and 32.4°C.

3. Male lizards usually had higher PBT than females.

4. In general, PBT were higher in spring and autumn than in summer, although the PBT of females was very low early in the spring.

INTRODUCTION

MOST LIZARDS, when allowed to thermoregulate behaviourally, are able to maintain their body temperature at or near a level typical of their species, the so-called "eccentric" or "preferred body temperature" (PBT) (Licht *et al.*, 1966; Templeton, 1970). While there are certain problems associated with the use of these terms (Licht *et al.*, 1966; De Witt, 1967; Brattstrom, 1970; Heath, 1970; Templeton, 1970), their practical value as descriptions of empirically determined body temperatures in thermoregulating ectotherms justifies their continued use at the present time.

Small, temperate, diurnal lizards usually utilise incident solar radiation directly as their primary means of acquiring the heat necessary for thermoregulation (Templeton, 1970). Since maximum levels of solar radiation vary considerably with season in temperate regions, it is not unreasonable to suppose that the PBT of temperate lizards might also vary seasonally as part of a general physiological strategy of compensation for changing levels of ambient radiation. However, evidence in support of this hypothesis is currently lacking, for although field studies have demonstrated that the body temperatures during activity of some warm temperate lizards are lower in winter than in summer (Mayhew, 1963; McGinnis, 1966), laboratory studies under standardised conditions have so far failed to reveal any signs of a seasonal influence on PBT (Stebbins, 1963; McGinnis, 1966; Licht, 1968). Field observations of seasonal differences in body temperature are not in themselves evidence of PBT differences since they could equally well be accounted for by supposing that at certain times of year lizards are unable to reach their species-typical PBT (McGinnis, 1966; Licht, 1968; Templeton, 1970).

It is probable that cool temperate and warm temperate lizards show considerable differences in their physiological adaptations to climate (Patterson & Davies, unpublished data). Consequently, as part of our studies of energy allocation in lizards, we have used *Lacerta vivipara* (a cool temperate, ovoviparous species) to re-examine the possibility that cer-

tain lizards undergo seasonal changes in PBT. Since males and females might be expected to have different thermal requirements in an ovoviparous species, we have also investigated the influence of sexual differences on PBT in this species.

MATERIALS AND METHODS

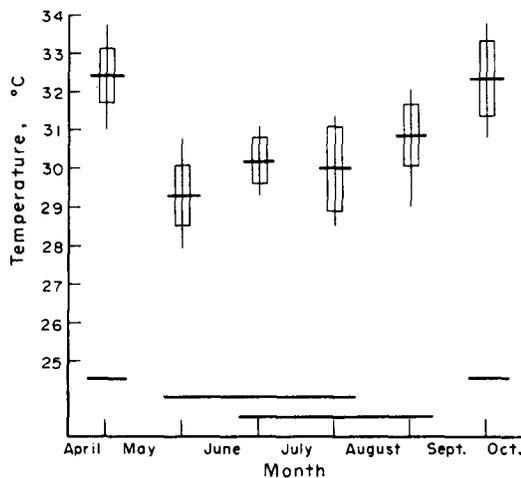
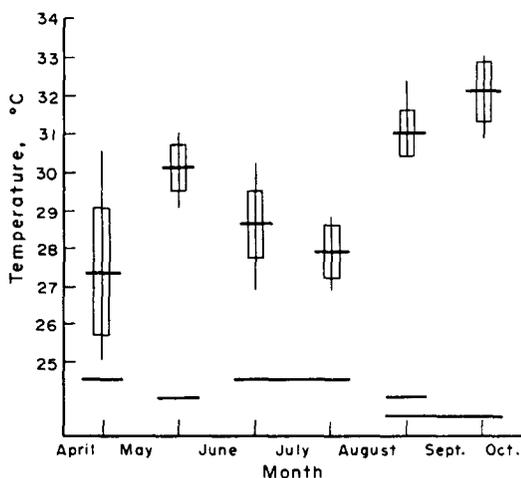
The *Lacerta vivipara* used in this study were caught at two localities in the south of England. At the time of the experiments all lizards were either freshly caught or had been maintained since capture in an uncovered outdoor vivarium measuring 3 m by 5 m. Insects suitable for food were freely available in this enclosure and were supplemented by the provision of mealworms, maggots and first and second instar locusts. All the lizards had therefore been exposed to natural photothermal and feeding conditions prior to the experiments.

The evening before body temperature observations were to be made, lizards were placed in the test tank, a glass aquarium measuring 41 cm × 26 cm × 26 cm high fitted with a wooded lid. Cover, water and food (mealworms) were continuously available, and a 60 W light bulb attached to the underside of the lid served as a source of both light and heat. The test tank was kept in a constant temperature room maintained at 10°C. When the 60 W light bulb was on, the shade temperature in the tank rose to 16°C, which is considerably below the PBT of *Lacerta vivipara*.

The test lizards were left in the dark overnight and then at 10.00 a.m. the following morning, the light in the test tank was switched on and left on until 6.00 p.m. During this 8 h period, the lizards were able to thermoregulate by basking, utilising the heat emitted by the light bulb. Apart from an initial period of 15–45 min when the lizards emerged and warmed up, their body temperatures remained relatively constant during the period when the light was on. Therefore, after this warming-up phase, the body temperature of each lizard was measured 5 or 6 times during the course of the day by inserting the bulb of a Schultheis fast-registering mercury thermometer (Bogert,

Table 1. Mean PBT of thermoregulating *Lacerta vivipara* maintained individually or in groups of six in the test tank

Time of year	Sex	Number of lizards in test tank at one time	N	Mean PBT (°C)	SD	t	P
June-July	♂	1	6	30.7	0.69	1.084	>0.1
	♂	6	6	30.2	0.77		
	♀	1	6	28.6	0.73		
	♀	6	6	28.5	1.15		
August-September	♂	1	6	31.3	0.75	0.695	>0.1
	♂	6	6	30.9	1.05		
	♀	1	6	30.7	0.81		
	♀	6	6	31.0	0.77		

Fig. 1A. Mean PBT of male *Lacerta vivipara* at different times of the year. Thick horizontal lines are means, vertical rectangles are 95% confidence limits and vertical lines are ranges. Means not underscored by a common line or by lines at the same level are significantly different from each other.Fig. 1B. Mean PBT of female *Lacerta vivipara* at different times of year. Symbols as for 1A.

1949) into its cloaca. The PBT of individual lizards was computed as the mean of these measurements. A number of tests were conducted with just one lizard at a time in the test tank. However, since no significant difference in mean PBT was detected between lizards tested on their own and those tested in groups (see below under Results), for convenience groups of six lizards were used for most of the test. When more than one lizard was present in the test tank, each lizard was marked on the flank with coloured nail varnish to aid individual recognition.

The PBT of both sexes was measured in this way at monthly intervals from the end of April to the beginning of October, a different (i.e. previously untested) group of lizards being used on each occasion. Thus measurements were made over most of the period when both sexes of *Lacerta vivipara* are naturally active.

Differences in mean PBT between treatment groups were analysed by means of *t*-tests (Bailey, 1959). Differences were considered significant when $P \leq 0.05$.

RESULTS

Table 1 compares the mean PBT of lizards tested either singly or in groups of six in the test tank. In no case is there a significant difference between lizards tested singly and lizards tested in groups of six. Thus the presence of other lizards does not appear to affect the body temperature maintained by thermoregulating *Lacerta vivipara*. Both Verbeek (1972) and Avery (1976) have noted that there is little interaction between individuals of this species. In view of these findings it was considered that mean PBT data could be obtained equally well from lizards tested singly and lizards tested in groups. All subsequent figures presented here were obtained from lizards maintained in groups of six in the test tank.

The monthly PBT data for each sex of *Lacerta vivipara* are summarised in Fig. 1. Evidently both sex and season have considerable influence on PBT. Only for the May-June, the August-September and the September-October figures is there no significant difference between the PBT of male and female lizards. At other times males have significantly higher PBT than females ($P < 0.01$, *t*-test).

Seasonal variations of mean PBT within each sex are different in the two sexes. Males have a high mean

PBT (32.4°C) early in the season. By late spring, this has decreased and the mean PBT remains between 29.3 and 30.9°C for the whole summer. In the autumn it rises again.

In female *Lacerta vivipara*, the mean PBT is low early in the year (27.3°C). There is a brief rise in late spring, but thereafter the mean PBT falls and stays low (between 27.9 and 28.5°C) during the summer. In autumn, the females' mean PBT rises to its highest level (32.1°C).

DISCUSSION

It is tempting to try and correlate these observed PBT differences with other seasonal and sexual differences in the animals' physiology. For example, the high PBT of males in spring coincides with spermiogenesis (Herlant, 1933; Saint Girons, 1963); the ova are approaching maximum size at the time of the late spring PBT increase in females (Avery, 1975); and the PBT of females is low in the summer for the whole of the period that embryos are developing in the oviducts (Avery, 1975). Furthermore, the PBT of females carrying embryos (27.9–28.6°C) corresponds fairly well with the temperature (27°C) at which *Lacerta vivipara* embryos develop most successfully *in vitro* (Maderon & Bellairs, 1962).

However, it is probably unwise to speculate at this stage about the causal relationship underlying these correlations because some aspects of the PBT differences do not seem to be related to any known feature of the lizards' way of life. For instance, it is not immediately obvious why both sexes should show an increase in PBT in the autumn or why males should have generally higher PBT than females, or indeed why the PBT of females should be higher during the maturation of ova than during pregnancy.

The differences in seasonal pattern of PBT change between the two sexes may be related to the later spring emergence of female *Lacerta vivipara*, for at the time of the April–May results (when the females have a very low PBT) the females have only recently emerged from hibernation while the males have been active for over a month. If the April–May PBT of the female is ignored, the seasonal patterns of the two sexes look much the same, although the males still have generally higher PBTs.

It may be relevant to point out that under the rather low levels of solar radiation which often prevail in the British Isles, under natural conditions it is unlikely that an individual *Lacerta vivipara* will be able to reach its PBT each time it emerges. Consequently, the PBTs reported here may be more in the nature of "target temperatures" than temperatures which are inevitably achieved by basking lizards. Nevertheless, this study quite clearly demonstrates that under conditions where *Lacerta vivipara* is able to thermoregulate unrestrictedly, both sex and season have considerable influence on PBT.

Acknowledgements—This work was supported by a grant from the Science Research Council.

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Key Word Index—Preferred body temperature; behavioural thermoregulation; lizard; *Lacerta vivipara*; sexual and seasonal influences on body temperature.