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SELECTED BODY TEMPERATURES IN THE LIZARD *LACERTA VIVIPARA*: VARIATION WITHIN AND BETWEEN POPULATIONS

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Abstract—1. Selected body temperatures (SBT) of adult male, female and subadult *Lacerta vivipara* from a Belgian population, were measured monthly in a laboratory thermogradient.

2. Monthly mean SBTs varied between 29.9 and 34.0°C and differed significantly among months in all three lizard groups, and among lizard groups in 4 out of 6 months.

3. Evidence for a positive relationship between monthly SBT and air temperature was found in the subadults, but not in the adult lizards.

4. Monthly mean SBTs measured in this study were consistently higher (mean difference = 2.0°C) than those obtained by Patterson and Davies (1978) in a similar study on *Lacerta vivipara* from southern England.

Key Word Index—Selected body temperature; behavioural thermoregulation; *Lacerta vivipara*; intraspecific variation in body temperature

INTRODUCTION

Behavioural thermoregulation is a conspicuous aspect of the biology of many lizards, and has been the subject of numerous studies (reviews in Avery, 1982; Huey, 1982; Tracy, 1982). Although studies differ considerably in scope and completeness, the vast majority of the available data consists of temperature measurements of active lizards in the field. This data base indicates that most lizards maintain their body temperature around characteristic levels. However, since it has been realised that body temperatures maintained in the field are merely the result of a compromise between an animal's physiology and ecology (Licht *et al.*, 1966; De Witt, 1967; Huey and Slatkin, 1976; Huey, 1982), the relevance of field records to comparative and conceptual analyses of thermoregulation has been questioned. Inherent thermal preferences of lizards are probably best established in environments such as laboratory thermal gradients, where an ectotherm can regulate its temperature with a minimum of associated costs (Licht *et al.*, 1966). These so-called "preferred" or selected body temperatures [following the recommendation of Gans and Pough (1982), we will use the latter term] can be used for studying inter- and intraspecific variation in activity temperatures. They also provide a yardstick against which field records can be compared, and the impact of environmental conditions on the thermal performances of unrestrained lizards can be evaluated. The selected body temperature (SBT) can however not be considered as a fixed physiological trait as it has been shown to be affected by numerous factors (Huey, 1982).

We herein report a study of the intraspecific variation in SBTs in the lizard *Lacerta vivipara*. Throughout its geographic range, this lizard is subject to a strong seasonal and cool temperate climate. Patterson and Davies (1978) hypothesised that this lizard might shift its SBT in order to match environmental seasonality. These authors demonstrated that both season and sex indeed have a considerable influence on SBTs in this lizard (Patterson and Davies, 1978). However, the observed variation seemed not to be related to temporal differences in climatic conditions. Instead, these authors suggested that the observed variation reflects sexual and seasonal differences in the lizards' reproductive state. The objectives of the present study therefore were: (1) to provide a replica of Patterson and Davies' (1978) study and to indirectly test their suggestion by including non-reproductive animals in our analyses; (2) to compare SBTs in two geographically separated populations of this lizard and (3) to establish inherent activity temperatures against which body temperature in the field, recorded during an accompanying study (Van Damme *et al.*, MS), could be compared.

MATERIALS AND METHODS

Lacerta vivipara is a small (adult body length: 50–60 mm; weight: 3–4 g), ground-dwelling lizard that behaves like a typical heliotherm (Avery, 1976). This live-bearing lizard has a yearly reproductive cycle: mating and ovulation occur in April and May respectively, and the young are born during the last week of July and the first half of August (Bauwens and Verheyen, 1985). Lizards hibernate from October to the end of February (adult males) or the onset of April (adult females and immature lizards). Three age classes can be distinguished by body length: juveniles (born in the current activity season), subadults (born during the previous year) and adults (who are in at

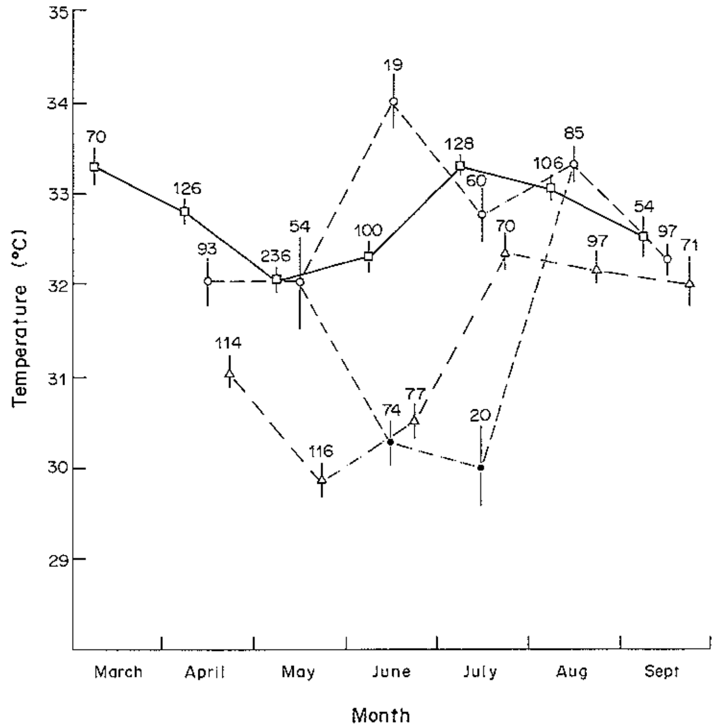

Fig. 1. Mean (±1 SE) selected body temperature for male (square), female (open circle: non-gravid; bullet; gravid) and subadult (triangle) *Lacerta vivipara* during different months. The numbers above each symbol indicate the number of measurements for each lizard group and month.

least their third activity season). Only adults are potentially reproductive.

All lizards used in this study were caught in the Belgian national nature reserve 'de Kalmthoutse Heide' [Kalmthout (51°25′ N–4°25′ E), province of Antwerp, Belgium]. Lizards were freshly caught in the field and were not maintained in the lab for longer than 14 days to avoid acclimation to laboratory conditions Individually marked (toe-clipped) lizards were housed in a thermal gradient which consisted of a rectangular terrarium (100 × 50 cm), with a 150 W bulb suspended above one end. Air temperatures in the gradient ranged from 18 to 55°C. Active lizards were taken from the test tank once an hour, for 6–8 times daily and their cloacal (= body) temperature was measured (to the nearest 0 1°C) within 15 s by inserting a thermocouple connected to an electronic thermometer. To avoid physical damage, body temperatures of juvenile lizards (body size: 20–30 mm) were not recorded and this age group will not be considered.

RESULTS

Monthly measurements of SBTs in adult males, females and subadults are summarized in Fig 1. Preliminary analyses revealed no significant differences in SBT among individual lizards in any of the age/sex groups and months (ANOVA, all $P > 0.05$). Different measurements of an individual were therefore considered to be independent. Selected temperatures were subject to a highly significant seasonal variation in all three age/sex groups (ANOVA, all $P < 0.001$; Fig. 1). In addition to the seasonal variation, SBTs differed significantly among lizard groups in 4 out of 6 months. Adult males generally selected the highest temperatures, whereas subadults preferred remarkable low temperatures, especially during spring. Selected temperatures were lower in gravid than in non-gravid females (lumped data for June and July samples: t-test, $P < 0.001$.

We attempted to relate the observed seasonal variation in SBTs in the distinct lizard groups to the monthly mean air temperatures for the period 1954–1984 as measured in a nearby weather station (Essen, 2 km NNE) (source: Maandberichten van het K.M.I.). We found no evidence for a positive relationship in the adult lizards (Spearman rank correlation, $P > 0.10$) In the subadults, a marginally non-significant positive relationship [$r_s = 0.714$, $P = 0.055$ (one-tailed test)] was found between monthly mean SBTs and ambient temperatures. Upon discarding the April-sample, the correlation for the remaining months is highly significant [$r_s = 0.900$, $P = 0.02$ (one-tailed test)]

We compared our estimates of monthly SBTs in adult lizards during April–September with those of Patterson and Davies (1978) Monthly mean SBTs measured in our study were higher than the corresponding values of Patterson and Davies (1978) in all 12 samples (Binomial test, $P = 0.0002$). The mean value of the difference in all pairs of monthly estimates was 2.04°C (range: 0.1–4.8°C)

DISCUSSION

The observed pattern of seasonal variation in SBTs in the adult lizards agrees reasonably well with and confirms that found by Patterson and Davies (1978). In neither of both data sets a positive relationship between monthly SBTs and ambient temperatures was apparent In contrast, SBTs of the adults were generally higher during the cooler months These results force us to reject the hypothesis that the seasonal shift in SBTs in the adult lizards is an adaptation to environmental seasonality. In the subadults, monthly SBTs tended to increase with environmental temperatures, except for the period immediately after termination of hibernation This might indicate some degree of physiological acclimatisation to environmental seasonality

The differences in SBTs between the non-reproductive subadults and the adult lizards provides some support to the suggestion of Patterson and Davies (1978), namely that the variation in SBTs of the adults reflects, at least to some extent, sexual and seasonal differences in physiological state. We adopt their suggestion, and provide some additional documentation on the apparent relation between variation in SBT and this lizard's reproductive cycle The selection of relatively high body temperatures by adult males in late summer (July–August) and early spring (March) coincides with the occurence of respectively spermatocyto- and spermiogenesis during these periods (Courty and Dufaure, 1979). Although the optimal temperature of spermatogenesis has yet to be established in *L. vivipara*, evidence for the temperature dependence of the rate of sperm development has been provided in this species and some of its close relatives (Joly and Saint Girons, 1975, 1981; Licht *et al*, 1969). The adoption of high SBTs by reproducing adult females during August–September and April–May coincides with respectively the early development and maturation of the ova (Morat, 1969; Avery, 1975; Xavier, 1982). Numerous studies have shown that high temperatures stimulate follicular growth in a variety of lizard species (review in Duvall *et al*, 1982). The rather low SBT of gravid females can be related to the low thermal optimum (27°C) of the *in vitro* development of *L. vivipara* embryos (Maderson and Bellairs, 1962) In this context, the difference in SBTs during June–July between gravid and non-gravid females (which include non-reproducing and post-parturient adult individuals) is noteworthy It should however be noted that these interpretations imply acceptance of the hypothesis that different physiological processes have different optimal temperatures. Detailed data which allow a test of this hypothesis are scarce for lizards in general (Huey, 1982), and completely lacking for the species studied. Therefore, our suggestions necessarily remain speculative.

The monthly mean SBTs in our lizards were consistently higher than the corresponding estimates obtained by Patterson and Davies (1978) on *L. vivipara* from southern England. Assuming that this result is not an artifact due to differences in experimental procedure or equipment, it would constitute the first demonstration of variation in SBTs among populations of a lizard species This result encourages further study of the variation among populations in SBTs and examination of a possible relation between eventual differences in thermal characteristics and environmental variables. *L vivipara* would constitute an ideal organism for such a study, as it occurs over a wide range in Europe and Central Asia, where it lives in a variety of habitats.

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