SHORT NOTE

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VARIATION IN PREFERRED BODY TEMPERATURE IN AN OVIPAROUS POPULATION OF *LACERTA* (*ZOOTOCA*) *VIVIPARA*

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The intraspecific variation of preferred temperatures (Tp) was analysed in an oviparous population of *Lacerta vivipara* and compared with viviparous populations. Lizards collected in central Pyrenees were exposed to a thermal gradient and Tp was measured at four time intervals. Tp was strongly dependent on lizard condition (males > non-pregnant females > pregnant females = immatures) and more weakly with time of day (early morning > mid-day). Individual females increased their Tp after egg-laying. Class-by-class comparisons did not reveal substantial differences with viviparous populations as expected for the thermal rigidity hypothesis. Nevertheless, on a short time scale, Tp should be interpreted as a compromise between different selective pressures including not only thermal environment but also reproductive condition and energy allocation.

Key words: behaviour, lizard, thermoregulation

The temperature selected in the absence of thermoregulatory constraints (preferred body temperature, Tp) is a relevant trait highly correlated with optima for many physiological processes in lizards (Huey & Bennet, 1987; Bauwens *et al*., 1995). Two kinds of variability in Tp should be considered: among populations/species and within a population. At the population/species level, evidence for both rigidity and flexibility on an evolutionary scale has been found in many lizard groups (i.e. Hertz *et al*., 1983; Bennet & John-Alder, 1986; Christian & Weavers, 1996; Castilla *et al*., 1999). These discrepancies probably stem from different rates of response to directional selection for this trait across evolutionary lineages (Labra, 1998). Studies on lacertids seem to support the thermal rigidity hypothesis within this family (Van Damme *et al*., 1989*a*, 1990; Gvozdík & Castilla, 2001; but see Scheers & Van Damme, 2002). Independently of this, Tp can also change within a population on a short time scale in response to temporal variation within an individual lizard's life (e.g. seasonal changes, reproductive condition and feeding status, see Castilla *et al*., 1999 for a revision in lacertids).

The common lizard *Lacerta* (*Zootoca*) *vivipara* (for taxonomic aspects, see Harris & Carretero, 2003) is the only lacertid exhibiting reproductive bimodality. Whereas viviparism is the reproductive mode throughout most of its range, oviparous populations have been recorded in two disjunct areas: the Cantabrian Mountains, the Pyrenees and Aquitaine, and Austria, Slovenia and N Italy (Bea, 1978; Braña & Bea, 1987; Heulin *et al*., 2000; Mayer *et al*., 2000; Suget-Groba *et al*., 2002). Oviparism is considered plesiomorphic within this species but oviparous populations of SW Europe and those from Central Europe, described as subespecies *carniolica* (Mayer *et al*., 2000), are not directly related (Surget-Groba *et al*., 2001). Recently, a study carried out on viviparous populations (Gvozdík & Castilla, 2001) confirmed thermal rigidity of Tp in populations living under different climate regimes but also detected intraspecific variation within the same population (see also Patterson & Davies, 1978, Van Damme *et al*., 1986, 1987). These findings suggest that, although Tp is evolutionary conservative at population/species level, within one particular population physiological optima may conflict and selective pressures vary with the lizard's condition (i.e. sex, reproductive status, size). Thus, overall Tp for one species would be an oversimplification. On the other hand, viviparity in squamates is considered a response to cold since embryo development can be completed under more favourable thermal environment inside the mother (see for instance Shine, 1985; Andrews & Rose, 1994; Qualls *et al*., 1997). If this is the case in *L* (*Z.*) *vivipara*, a shift in Tp would be expected (at least in females) between oviparous and viviparous forms.

This note aims to determine the extent of intraspecific variation for Tp using an oviparous population of *L.* (*Z.*) *vivipara* as a model. Furthermore, the results are compared with those reported for some viviparous populations.

A total of 31 common lizards (6 adult males, 19 adult females and 6 subadults) belonging to an oviparous Pyrenean population were collected by hand in a subalpine meadow at 1800 m (Plan de Beret, Naut Aran UTM grid 31T CH3434: see Roig *et al*. (2000) for a detailed description of the study site) between the second half of June and the first half of July in 1997 and 1998. This interval corresponds to the egg-laying period of this population (Roig *et al*., 2000). Lizards were kept in individual 0.5 × 0.4 × 0.3 m terraria for less than two weeks with food and water provided *ad libitum,* and then released after the experiments. Each lizard was individually exposed to a photothermal gradient (~ 20-45ºC, 0.5 × 0.5 × 1.5 m length) produced by a 100 W reflector bulb fixed 15 cm above the substrate maintaining natural photoperiod. Humidity (90%) was kept uniform along the gradient by using a pebble base covered by moss which was periodically sprayed and provided sufficient shelter. Tp was measured by insert-

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TABLE 1. Descriptive statistics of Tp considering the different classes and time intervals. In order to prevent pseudoreplication, totals are calculated with the means of each individual for the four time intervals (8:45-14:45).

Class	Time	*n*	Mean	SE	Min.	Max.
Males	8:45	6	33.90	0.86	30.2	36.5
	10:45	6	33.12	0.30	32.3	34.3
	12:45	6	33.37	0.66	30.5	35.0
	14:45	6	33.22	0.59	31.8	35.5
	total	6	33.40	0.90	30.2	36.5
Pregnant females	8:45	12	29.60	0.46	26.7	32.2
	10:45	12	27.98	0.39	26.4	30.0
	12:45	12	28.19	0.55	26.1	31.9
	14:45	12	28.18	0.38	25.7	30.2
	total	12	28.49	0.45	25.7	32.2
Non-preg. females	8:45	18	31.92	0.35	28.7	34.6
	10:45	18	31.77	0.33	28.9	34.2
	12:45	18	32.31	0.40	29.7	35.5
	14:45	18	31.61	0.51	27.3	34.8
	total	18	31.90	0.40	27.3	35.5
Subadults	8:45	6	29.90	0.21	29.2	30.5
	10:45	6	29.67	0.70	27.7	32.3
	12:45	6	29.40	0.49	27.8	31.4
	14:45	6	28.12	0.83	25.5	30.8
	total	6	29.27	0.56	25.5	32.3

TABLE 2. Results of the general ANOVAR of Tp considering class and time, and separate ANOVAR for females considering time. When significant, results of *post-hoc* Schffée's test are provided.

2-way ANOVAR	*F*	df	*P*
Class	43.73	3, 38	2.11×10^{-12}
Time	3.14	3, 114	0.03
Class x time	1.07	9, 114	0.39

Scheffé Tests

Class	Mean	Males	Non-preg. fem.	Preg. fem.
Males	33.40			
Non-preg. fem.	31.90	0.04		
Preg. fem.	28.49	4×10^{-10}	2×10^{-9}	
Subadults	29.27	4×10^{-7}	7×10^{-5}	0.52

Time	Mean	8:45	10:45	12:45
08:45	31.33			
10:45	30.63	0.18		
12:45	30.82	0.45	0.95	
14:45	30.28	0.01	0.73	0.40

Nested ANOVAR for females	*F*	df	*P*
Pregnancy	51.34	1, 10	3.05×10^{-5}
Time [pregnancy]	1.73	6, 60	0.12

ing a k-thermocouple probe associated with a digital thermometer (Digitron 3208K, accuracy 0.01ºC) in the cloaca. Body temperatures were recorded only for active lizards during a single day at four consecutive intervals of 2 hrs (8:45-12:45, Table 1) distributed throughout the period of diel activity observed in the field; the photothermal gradient was connected one hour before the first measurement. When possible (n=11), individual females were analysed before and after egg-laying in terraria.

Data were not transformed since distributions did not deviate from normality (Komogorov-Smirnov tests, $P>0.05$ in all cases), were homocedastic (univariate Levene tests and multivariate Box M, $P>0.05$ in all cases) and variances and means were uncorrelated. Since measurements were repeated for the same individual (for each interval and, in most females, before and after egg-laying), statistical analysis was based on Analysis of Variance for Repeated Measures (ANOVAR) of Tp with class (males, pregnant females, non-pregnant females, subadults) as between subject factor and time interval as within subject factor. Sphericity assumption was not rejected prior to non-nested analysis (Mauchley's sphericity tests $W=0.89$, $\chi^2=4.34$, $P=0.50$ and $W=0.89$, $\chi^2=4.34$, $P=0.50$). Sequential Bonferroni correction (Rice, 1989) was used when multiple tests were evaluated simultaneously.

Table 1 shows the descriptive statistics of Tp for the four classes and the four time intervals. Data have not been pooled due to the high degree of heterogeneity in the results. In fact, ANOVAR revealed variation of Tp with time and class (Table 2). Lizards tended to select higher temperatures in the early morning and lower in the early afternoon. Moreover, significant class variation was detected. Males attained higher Tp than non-pregnant females; both classes exhibited higher values than pregnant females and subadults which did not show significant differences between them. A separate analysis performed for those females analysed before and after

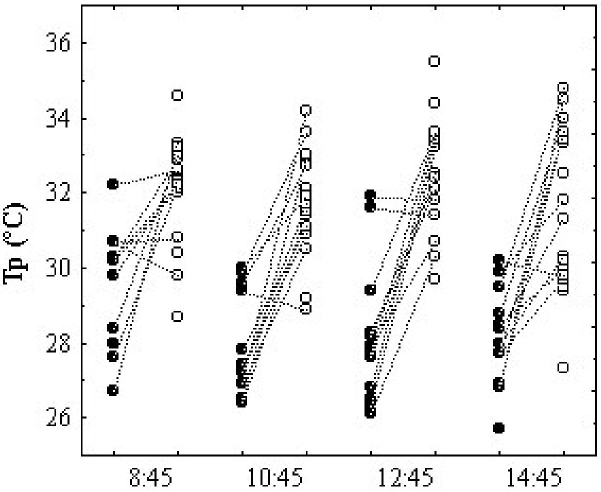

FIG. 1. Diel variation of Tp in females showing individual variation after egg-laying. Lines connect dots belonging to the same individual. Black circles, pregnant females; open circles, non-pregnant females.

TABLE 3. Comparative statistics of Tp in adult *Lacerta (Zootoca) vivipara* from different European populations. Homologous comparisons are performed between Pyrenees and the other localities (samples from the literature) by means of *t*-tests. Pooled calculations excluded pregnant females. n.p., non-pregnant; p., pregnant. * significant after sequential Bonferroni correction .

Area (groups compared)	Reproductive mode	Reference	*n*	Tp mean±S.D.	Compared to Pyrenees		
					t	df	*P*
Great Britain (pooled)	viviparous	Patterson & Davies (1978)	12	31.0±0.9	2.34	34	0.02
Austrian Alps (pooled)	viviparous	Van Damme *et al.* (1990)	92	32.1±2.9	0.32	114	0.75
Belgium (pooled)	viviparous	Van Damme *et al.* (1990)	151	32.3±2.5	<0.0001	173	>0.99
Czech Republic (pooled)	viviparous	Gvozdík & Castilla (2001)	24	31.4±1.3	1.99	46	0.05
Pyrenees (pooled)	oviparous	This study	24	32.3±1.8	-	-	-
Belgium (males, June)	viviparous	Van Damme *et al.* (1986)	100	32.3±2.0	1.32	104	0.19
Belgium (males, July)	viviparous	Van Damme *et al.* (1986)	128	33.3±1.1	0.21	132	0.83
Czech Republic (males)	viviparous	Gvozdík & Castilla (2001)	12	31.5±1.4	2.63	16	0.02
Pyrenees (males)	oviparous	This study	6	33.4±1.5	-	-	-
Belgium (n.p. females, June)	viviparous	Van Damme *et al.* (1986)	19	34.0±1.3	4.23	35	0.0001*
Belgium (n.p. females, July)	viviparous	Van Damme *et al.* (1986)	60	32.7±2.3	1.39	76	0.16
Czech Republic (n.p. females)	viviparous	Gvozdík and Castilla (2001)	12	31.3±1.4	1.01	28	0.32
Pyrenees (n.p. females)	oviparous	This study	18	31.9±1.7	-	-	-
Belgium (p. females June)	viviparous	Van Damme *et al.* (1986)	74	30.3±2.6	2.33	84	0.02
Belgium (p. females July)	viviparous	Van Damme *et al.* (1986)	10	30.0±1.3	4.79	20	0.0001*
Czech Republic (p. females)	viviparous	Gvozdík & Castilla (2001)	7	29.5±0.5	1.61	17	0.10
Pyrenees (p. females)	oviparous	This study	12	28.5±1.5	-	-	-

egg-laying (Table 2) showed a clear increase of Tp for the same individuals (Fig. 1). Time differences were not significant when this group was analysed separately.

Comparative Tp values for different populations of *L.* (*Z.*) *vivipara* are shown in Table 3. Overall differences found with the viviparous populations of Britain and the Czech Republic were not significant after sequential Bofferoni correction. Available results allowed separate comparisons with Belgium and the Czech Republic. Pyrenean pregnant and non-pregnant females showed higher temperatures than their Belgian equivalents in June and in July, respectively. No differences were found for males when results were Bonferroni-corrected.

The results indicate that, within the population studied, Tp is strongly dependent on lizard condition and more weakly on time of day (Castilla *et al*., 1999 and references therein, Rismiller & Heldmaier, 1982). Interpopulation analysis should then avoid using pooled data but perform at least class-by-class comparisons. When comparing in such a way, however, present results mostly agree with the results obtained for viviparous populations.

During the long gestation period, selected body temperatures of females seem to reflect the optimum for embryonic development (~27°C for *in vitro* development in viviparous populations, Maderson & Bellairs, 1962), rather than the optimum for physiological processes of the female itself. This seems to be true for both reproductive modes (Heulin, 1987; Van Damme *et al*., 1987; Gvozdík & Castilla, 2001; this study). Alternatively, lower Tp in gravid females could reflect decreased basking intensity, associated with changes in antipredatory behaviour. Gravid (viviparous) females of this species tend to be slower (Van Damme *et al*., 1989*b*) and therefore may be more sensitive to predation when basking in the open (Bauwens & Thoen, 1981). In any case, individual monitoring of females in this study demonstrates that, once released from embryos after egg-laying, females immediately raise their Tp. This confirms that selective pressure for decreasing Tp is linked (directly or indirectly) to pregnancy. Nevertheless, differences between males and non-pregnant females still persist. This result, not detected for the viviparous populations (Gvozdík & Castilla, 2001), needs additional testing with pre-reproductive females in order to distinguish between possible residual effects of pregnancy in females and active selection of higher temperatures by males due to other selective pressures, especially the spermatogenic cycle (Patterson & Davies, 1978; Van Damme *et al*., 1986).

Subadult lizards preferred lower temperatures than adults (except pregnant females). It has been suggested (Carretero & Llorente, 1995) that this opportunistic thermal behaviour allows immature lacertids to remain active for a longer period (both daily and annually) than adults, thus increasing their opportunities for food consumption and, hence, for growing. Alternatively or additionally, evaporative loss is important in this species (Reichling, 1957) and probably more acute for small lizards due to their high surface/volume ratio (Bowker, 1993; Lorenzon *et al.*, 1999).

Diel variation of Tp observed was weak but significant. In general, lacertids tend to raise their Tp when environmental temperatures are low, i.e. when the thermal environment is more unfavourable and thermoregulation become a priority in relation to other requirements (Rismiller & Heldmaier, 1982; Tosini & Avery, 1994). Excluding the effect of reproductive activity, the seasonal variation reported for this species seems to follow a similar pattern (Patterson & Davies, 1978; Rismiller & Heldmaier, 1982; Van Damme *et al.*, 1987).

Finally, concerning the Tp variation found between populations, marginal differences between oviparous (Pyrenean) and viviparous populations can be easily attributed to differences in laboratory methods (see Gvozdík & Castilla, 2001) and/or in the numbers of lizards of each class composing the total samples. However, procedures were essentially the same for Pyrenean, Belgian and Czech populations and Tp variation between members of the same class was still recorded in some cases. However, such differences do not show a clear pattern of divergence between oviparous and viviparous forms, but may well arise secondarily from seasonal variation (Van Damme *et al.*, 1986) since experiments were not simultaneous and the reproductive cycle changes with environmental conditions. For instance, the strong increase of Tp observed in Pyrenean males after the breeding season may be tentatively associated with rapid spermatogenesis observed in this high mountain population due to climatic constraints (Roig *et al.*, 2000).

In conclusion, the present results did not differ from those expected for thermal rigidity at species/population level, extending the confirmation of this hypothesis to both reproductive modes within *L.* (*Z.*) *vivipara*. Nevertheless, within a population, Tp is a complex trait that should be interpreted as a compromise between different selective pressures including not only thermal environment but also energy allocation and, obviously, reproductive condition. Other possible factors should also not be excluded, among them social behaviour and parasites (Castilla *et al.*, 1999). Future research should try to generalize these findings to other lacertid species (i.e. Tosini & Avery, 1996).

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