SHIFT IN BEHAVIOUR RELATED TO PREGNANCY IN *LACERTA VIVIPARA*

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Pregnancy is considered as a critical period for females of live-bearing reptiles (Vitt and Congdon, 1978 ; Shine, 1980 ; Vitt and Price, 1982). Maximal locomotor ability of gravid females is seriously impaired during this period in species with large brood size (Bauwens and Thoen, 1981 ; Garland, 1985 ; Seigel *et al.,* 1987 ; Brodie, 1989 ; Cooper *et al.,* 1990). As a consequence, species in which escape relies on flight may experience a cost of reproduction if reduced speed entails a greater risk of predation during pregnancy (Shine, 1980 ; Andren, 1985 ; Madsen, 1987).

Generally, live-bearing females show a reduction in activity during pregnancy (Vitt and Congdon, 1978 ; Bauwens and Thoen, 1981 ; Vitt and Price, 1982). This is usually interpreted as a predator avoidance behaviour (Brodie, 1989). Similar conclusions were reached for *Lacerta vivipara :* gravid females showed reduced maximal speed and a shift from flight to crypsis to escape from predators (Bauwens and Thoen, 1981 ; Van Damme *et al.,* 1990). This may also explain why mortality does not increase during gestation in this species (Bauwens, 1985).

Activity in ectotherms is influenced by thermal requirements (Huey, 1974 ; Porter and Tracy, 1983 ; Grant and Dunham, 1988). Temperature influences anti-predator behaviour (Christian and Tracy, 1981 ; Hertz *et al.,* 1982 ; Crowley and Pietruska, 1983 ; Greene, 1988 ; Losos, 1988), locomotor performances (Avery and Bond, 1989 ; Brodie, 1989 ; Van Damme *et al.,* 1989) and reproduction (Pilorge and Barbault, 1981 ; Duvall *et al.,* 1982 ; Ellner and Beuchat, 1984). Moreover, viviparity imposes physiological constraints (Tinkle and Gibbons, 1977 ; Shine and Bull, 1979 ; Shine, 1985) in which temperature may play an important role, in particular for embryonic development (Garrick, 1973 ; Stewart, 1984 ; Beuchat and Ellner, 1987).

In this paper, we compared the behaviour of gravid and post-gravid females of *Lacerta vivipara* in the absence of predators and their reaction to a threatening stimulus. In particular, we looked incidentally for the influence of temperature on behaviour.

MATERIAL AND METHODS

Lacerta vivipara is a small live-bearing Lacertid lizard. Gestation lasts from June to mid-August (for a more detailed description, see Bauwens and Verheyen,

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1985, 1987; Pilorge, 1987). It is commonly found in peatbogs, heathlands and meadows, where the ground is covered with a dense vegetation (Arnold *et al.,* 1978). Such an entangled vegetation impairs rapid movement (Avery and Bond, 1989), so that the lizard relies partly on flight and partly on crypsis to escape predators. While it is not a very fast lizard, females become even slower during gestation (Bauwens and Thoen, 1981; Van Damme *et al.,* 1989).

Two separate experiments were conducted at the end of the gestation period (end of July) with gravid and post-gravid females. This period was chosen : 1) to ensure that gravid females were roughly at the same stage of pregnancy, that is to say at the end of the gestation and before the peak of parturition ; 2) to allow us to compare gravid and post-gravid females.

DAILY ACTIVITY

On July 26, 1989, 6 gravid and 6 post-gravid females were collected in a peatbog, located on Mont Lozère (France, see Pilorge, 1987 for a more detailed description). Females were kept for one night indoors in individual terraria. The next day, they were randomly assigned to one of 12 experimental units of an enclosure built in the peatbog. Each unit (1.5 m × 1.5 m) was delimited by vertical opaque plates (0.8 m high). The 12 units were set in two juxtaposed rows on a roughly North-South axis. The habitat in each unit was standardized as much as possible: a small granitic rock and a branch of broom (*Sarothamnus scoparius*) were placed on a background of mixed species of herbaceous plants (*Nardus stricta, Molinia caerulea, Sphagnum pallustre*) and heather (*Calluna vulgaris*). This environment provided the lizards with sites for foraging, thermoregulating and hiding. Observations of the daily activity of the females began one day after release in the enclosure and lasted for 5 days. Temperature was recorded four times a day in the herbaceous layer (where females are mostly found at this period, Lecomte *unpubl. data*) with a probe thermometer. The daily mean value of these temperatures was then used to make comparisons between days, the weather conditions being as similar as possible within each day (uniformly sunny and windy). This was true for four of the five days of the experiment. Accordingly, the one cloudy day was excluded from the analysis. Each lizard was observed several times a day. The sequence of observations within each half day started with a randomly chosen lizard. Activity of the Common lizard begins at about 9 a.m. and finishes around 7 p.m. This enabled us to observe each of the twelve females during 1 to 3 periods of 15 mns each half day. Behaviour was classified according to 5 general patterns: basking and resting in the shade (BRS), foraging (F), walking (W), alert and running (AR) and hiding (H). The behaviour BRS is composed of thermoregulatory behaviours involving movements (shuttling) and immobilizations in the sun and in the shade (Huey, 1974). The duration of a pattern was the time a female spent performing this behaviour during each period of observation.

REACTION TO A STIMULUS

The reaction to a threatening stimulus was measured in a different subset of 7 gravid and 7 post-gravid females in homogeneous conditions of temperature of 25 °C. Each lizard was placed successively in an empty ring 2.92 m in circumference and was stimulated by touching the base of the tail with a stick each time it stopped walking for more than 3 s. This was assumed to simulate a tentative act of predation. We recorded the duration (T) for a female to complete a round in the ring. Each female was given 4 trials. After each trial, the ring was cleaned with water to eliminate odor cues for possible re-use. We computed the speed (S) at which each round (L) was completed, subtracting the time spent in pauses that required a new simulation : $S = L/(T - (3 * i))$ where i is the number of stimulations during the round. The mean distance between two stimulations (D) was computed as follows : $D = L/(i + 1)$.

DATA ANALYSIS

Statistical analyses including ANOVA, nested ANOVA, and non-parametric tests were performed using SPSS/PC+ (Norusis, 1986).

RESULTS

Since body size may influence locomotor ability, we first examined the homogeneity in body size among the different kind of females. There was no significant difference in snout-vent length between gravid and post-gravid females, both in the sample used for measuring behaviours (gravid females : SVL (snout-vent length) = 57.5 mm, *sd* = 2.6 ; post-gravid females : SVL = 59.4 mm, *sd* = 3.4 ; t-test, $P = 0.358$) and in the sample used for measuring the reaction to a stimulus (gravid females : LMA = 61.0 mm, *sd* = 3.74 ; post-gravid females : LMA = 61.0 mm, *sd* = 3.41 ; t-test, $P = 1.00$).

COMPARISONS OF THE DURATION OF EACH TYPE OF BEHAVIOUR

The duration of each type of behaviour was analysed by a three-way nested-ANOVA without repetition. The factors taken into account were the day of observation, the female reproductive status and the individuals nested within female reproductive status. In three types of behaviour (BRS, H and F) there was a significant individual component (Table I). Days of observation did not influence the duration of behavioural patterns. Most of the time, females did not spend much time in alert or walking (respectively 5 % of their activity) and this may explain our inability of detect any difference in these behaviours. However, female reproductive status had a significant effect on BRS and on the amount of time spent hidden (H). Note that the difference between the two categories of females was largely dependent on the day of observation (Table I), and more specifically on the daily average temperature (Fig. 1a). Gravid females appeared to adjust their thermoregulatory activity to ambient temperature with a peak of BRS around 18 °C. Concomitantly, they spent less time hidden at that temperature (Fig. 1b). Post-gravid females were less influenced by temperature.

REACTION TO A THREATENING STIMULUS

The mean distance between two stimulations (D) was normally distributed. A two-way ANOVA (with individuals and trials as factors) did not reveal any

TABLE I

Analysis of the variation in duration of different types of behaviours with respect to individuals (I), female reproductive status (R) and day of observation (Day). Results of a three-way nested (I within R) ANOVA (SPSS-PC+) without replicates.

For each behaviour are given the probabilities of the day and R main effects, of the Day * R interaction and of the effect of I nested within R.

Behaviours	Day effect	R effect	Day * R interaction	I within R
Df	3,30	1,30	3,30	10,30
Basking and resting in the shade	.167	< .001	< .001	< .001
Hidden	.349	.002	.036	< .001
Foraging	.873	.999	.274	.007
Walking	.392	.783	.932	.239
Alarming	.416	.854	.893	.823

significant difference between trials in gravid females (mean D = 38.03 cm; $F_{3,18} = 1.83$, $P = 0.178$) nor in post-gravid females (mean D = 40.66 cm; $F_{3,17} = 1.91$, $P = 0.168$). Assuming that there was no interaction between female and trial effects, we used each trial as independent repetitions. A nested-ANOVA (female effect nested within reproductive status effect) revealed a strong difference between females ($F_{12,41} = 12.66$, $P < 0.001$), but no effect of reproductive status ($F_{1,41} = 1.61$, $P = 0.211$).

No transformation of variable (see Sokal and Rohlf, 1981) could account for the level of heteroscedasticity of speed. A non-parametric analysis of variance did not show any difference between trials (Kruskal-Wallis test: gravid females $\chi^2_3 = 1.06$, $P = 0.787$, post-gravid females: $\chi^2_3 = 1.71$, $P = 0.634$). As in the case of the mean distance, there was a strong difference between females ($\chi^2_{13} = 35.28$, $P < 0.001$), but no difference with reproductive status ($\chi^2 = 1{,}51$, $P = 0.219$).

DISCUSSION

Females spent over 80 % of their time hiding and thermoregulating (hiding can mostly be interpreted as a thermoregulation activity, a mean for avoiding low and high temperatures under the soil (see Huey *et al.,* 1989). On average, gravid females spent more time hiding, and consequently less time basking and resting in the shade, than post-gravid females. This result is largely dependent on daily ambient temperature. Gravid females showed a peak of BRS activity when the mean ambient temperature averaged 18 °C (temperature measured in the shade and outside the enclosure). In contrast, post-gravid females spent more time basking than gravid females during days when the ambient temperature was lower. Garrick (1973) reported similar results for *Sceloporus cyanogenis.* These differences are difficult to explain by the anti-predator hypothesis.

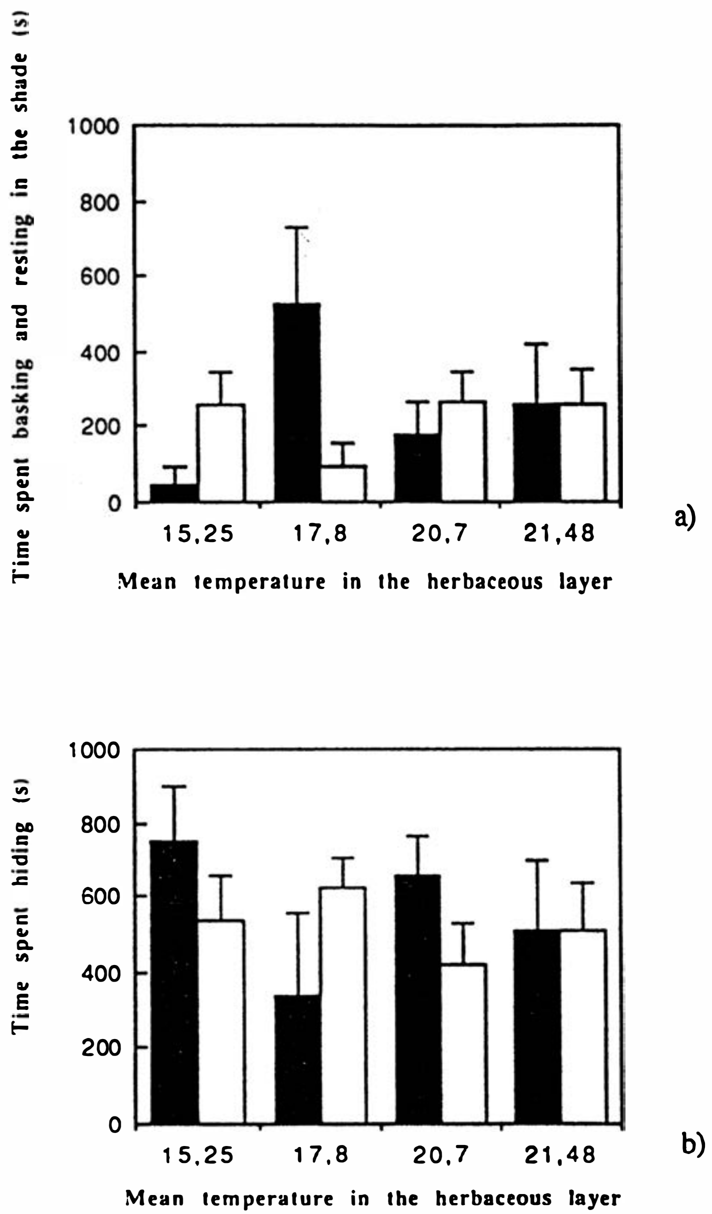

Figure 1. — Influence of the daily average temperature on a) basking and resting in the shade, and b) hiding, according to reproductive status (gravid females : solid bars, post-gravid females : open bars). Vertical lines : 95 % confidence interval.

An alternative explanation based on embryonic development requirement can be proposed. In *Sceloporus jarrovi* (Beuchat and Ellner, 1987) and in *Lacerta* *vivipara* (Avery, 1975 ; Patterson and Davies, 1978), the preferred body temperature is lower in gravid females than in non gravid ones, and the rate of embryonic development and the viability of the clutch are strongly affected by temperature (Beuchat and Ellner, 1987). The temperature (27 °C) at which broods of *Lacerta vivipara* exhibit the highest hatching success *in vitro* (Maderson and Bellairs, 1962) corresponds fairly well to the preferred body temperature (PBT) of females carrying embryos (Patterson and Davies, 1978). As we have no detailed information on the temperature in the enclosure with respect to the behavior displayed by the females, the results recorded here cannot constitute a serious proof of this theory. Moreover the temperature was recorded outside the enclosure. However, after the experiment, we simultaneously measured temperature at this place and inside the enclosure : the maximum temperatures recorded in the enclosure were 5 °C higher in the shade and 10 °C higher in the sun than outside the enclosure. So, 18 °C in the shade and outside the enclosure would correspond to a natural range of 23 °C-28 °C inside the enclosure (wind screen effect of the enclosure). Therefore, the array of temperature which pregnant females experienced when they displayed their daily activity corresponds to the temperature which maximises the success of embryonic development. Nevertheless, this gives some limited support to the embryonic development theory. More precise data on ambient and body temperatures are necessary to test this alternative hypothesis further.

Predation may affect other aspects of behaviour than thermoregulatory activity, in particular escape tactics and foraging mode. We have shown that when artificially stimulated, gravid females did not respond differently than post-gravid females both in number of stimuli needed to complete a certain distance and in the speed at which they ran. By contrast, Bauwens and Thoen (1981) showed that gravid females were slower than post gravid ones in a Belgian population. This discrepancy might be due to differences in the design of the experiments, in the variables measured (e.g. the substraction of time spent in pauses that required a new stimulation in our study while the latter authors did not) in their interpretation or in the sample size involved. Furthemore, Bauwens and Thoen (1981) observed that in the field gravid females tolerated shorter approach distances by a human predator than non gravid ones. However, Heulin (1984) showed that, in a Breton population, gravid females had a smaller home range than post-gravid ones, and as a consequence are likely to be nearer to a shelter than post-gravid females. Bauwens and Thoen (1981) discarded this explanation because flight distances were not related to approach distances in gravid females in contrast to post-gravid ones. On this basis, they concluded that facing a predator, whatever the distance from a shelter is, gravid females shift from flight to crypsis. However, the variance of flight distances values of pregnant females was much smaller than that of non gravid ones. This reduced variation might explain why no significant relationship between approach and flight distances could be found in gravid females, while there is a significant relationship in non gravid females ($r^2 = 0.05$; $N = 223$, Bauwens and Thoen, 1981). However, it is also possible that the stimulus chosen in our study does not adequately simulate the approach of a predator. These considerations call for much caution in interpreting the results in terms of an anti-predator hypothesis.

The data we have gathered are still preliminary, in particular because the way we have measured temperature was quite crude. However, our first results are not contradictory to the hypothesis that the acquisition of viviparity in this species would be a recent event : 1) some populations still show an oviparous mode of reproduction (Heulin, 1988), 2) the two types of individuals still interbreed and their progeny is fertile (Heulin, 1989). The optimal temperature of egg development (under rocks or grass) is equal to, or lower, than that of the embryo *in utero* and is much lower than the preferred body temperature of females. Therefore, one possible cost of the acquisition of viviparity would be for the females to tune their activities to the temperature requirements of egg development. In this scheme, predation could still play a role as a factor of reinforcement : gravid females being less active predation is reduced and consequently survival increases. In addition, predation may also influence other types of behaviour (i.e. distances from a shelter). Further studies are still needed to clarify the respective roles of predation and embryonic development in the behavioural changes during pregnancy in live-bearing lizard species.

SUMMARY

The reduction of activity during pregnancy in live-bearing females of reptiles is mostly interpreted in the literature as a predator avoidance behaviour. We compared the daily behaviour in the absence of predators and the reaction to a threatening stimulus in gravid and post-gravid female *Lacerta vivipara.* Some results seem to indicate that thermoregulatory activity did not show a similar pattern in gravid and post-gravid females. As for the reaction to a threatening stimulus there were no differences between the two types of females. Although only indicative, these data are difficult to explain by the anti-predator hypothesis but could be better understood if the physiological requirements of the embryonic development were taken into account. The relationship between thermoregulatory behaviour and viviparity is also discussed from an evolutionary point of view.

RÉSUMÉ

Dans la littérature, la réduction d'activité pendant la gestation des femelles de reptiles vivipares est la plupart du temps interprétée comme un comportement d'évitement des prédateurs. Nous avons comparé le comportement journalier de *Lacerta vivipara* gestantes et post-parturientes et la réaction de ces deux types de femelles face à un stimulus simulant un prédateur. L'activité de thermorégulation n'est pas de même type, en fonction de la température, chez les femelles gestantes et post-parturientes. Aucune différence n'est mise en évidence pour les deux types de femelles quant à la réaction à un stimulus menaçant. Bien que seulement indicatifs, ces résultats sont difficilement explicables si on envisage seulement l'hypothèse d'un comportement anti-prédateur ; ils pourraient être en partie induits par les besoins physiologiques du développement embryonnaire. Les relations entre le comportement de thermorégulation et la viviparité sont discutés d'un point de vue évolutif.

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