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Shifts in body temperature and escape behaviour of female Podarcis muralis during pregnancy

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Average field body temperatures of pregnant female *Podarcis muralis* (32.62°C) were significantly lower than that of males and non-pregnant females (overall average: 33.74°C). However, when tested in terrarium with a strong thermal gradient in a limited space, which represents a low-cost environment for thermoregulation, neither body temperature nor position in the thermal gradient differed among groups of sex and reproductive condition. Body temperatures selected in thermal gradient (overall average: 33.77°C) was similar to those exhibited in the field by males and non-pregnant females. This means that low body temperature exhibited by pregnant females in the field is not a consequence of a change of the thermal preferences at this stage, but might be explained on the basis of constraints related to their reproductive condition. Pregnant females stay closer to the refuge and allow approach to a shorter distance than do males and non-pregnant females. Approach distance was partially explained by the distance to refuge, but even when the effects of the distance to refuge were removed by applying the residuals of the regression, the approach distance for pregnant females was significantly lower than for other individuals. This reflects the existence of a behavioural component of motion-less in addition to the tendency to remain closer to a shelter, and means a shift in the predator-avoidance tactic from flight to crypsis, presumably because effectiveness of the flight tactic would be reduced during pregnancy. The behavioural changes associated with pregnancy may preclude careful thermoregulation, as this requires frequent movements to exploit the variability of the thermal environment.

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Most diurnal lizards spend a large proportion of their time in activities related to thermoregulation, and this allows them to regulate body temperature within a relatively narrow range during the active period (Avery 1982). In many reptiles, the rate at which physiological functions operate varies with body temperature and a great number of studies conducted on different species have documented a general agreement between species-specific body temperatures (selected in thermal gradients or measured on animals active in the field) and optimal temperatures for physiological functions (Huey 1982, Bradshaw 1986). However, this statement may be insidious, because the "optimal" temperature is not a fixed trait, but can vary with season or geographical location within species (Huey et al. 1977, Grant and Dunham 1990, Sinervo 1990). Moreover, there is not strictly a single optimal temperature for all functions (Huey 1982) and, in particular, differences can exist between optimal temperatures for the embryonic development and that for most physiological functions of the pregnant female (Beuchat 1986). Maintenance of an appropriate body temperature is specially important for pregnant females, because temperature affects many aspects of the embryonic development, from incubation or gestation time (Saint Girons 1985, Muth 1990) to sex ratio of the offspring (Bull 1980, Janzen and Paukstis 1991), survivorship or frequency of morphological abnormalities (Vinegar 1974, Gutzke and Packard 1987).

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Furthermore, in some squamate reptiles incubation temperature can influence size at birth (Beuchat 1988, Phillips et al. 1990), and the subsequent behaviour and performance of the hatchlings (Burger 1990, 1991, Van Damme et al. 1992), even with long-term effects (Burger 1989), suggesting that incubation temperature acts as a set point for the lifetime (Burger 1990).

Thermoregulation involves a multiple adjustment of associated costs and benefits to maximize net gain, so that the optimal physiological temperature and the optimal ecological temperature are not always coincident (Huey and Slatkin 1976, Withers and Campbell 1985). In this context, a change in the equilibrium of the cost-benefit balance is likely to exist for pregnant females, because pregnancy implies a rise in the costs associated with thermoregulation (Huey and Slatkin 1976, Shine 1980) so, in fact, changes in body temperature and thermoregulatory behaviour during gestation are not unusual among squamate reptiles (see, e.g., Beuchat 1986). On the other hand, pregnant females have reduced locomotor performance and increased vulnerability to predation (Shine 1980, Seigel et al. 1987), which may result in less careful thermoregulation (Huey and Slatkin 1976), and changes in the predator-avoidance tactics (Bauwens and Thoen 1981, Brodie 1989).

The aim of this work is to examine possible modifications in body temperature, thermoregulatory behaviour and escape tactic of female *Podarcis muralis* during pregnancy, as suggested by preliminary data indicating lower field body temperature for pregnant females than for males and nonpregnant females (Van Damme et al. 1992). In addition, Van Damme et al. (1992) showed, for the same population as in this study, that hatchlings from eggs incubated at low temperatures (relative to field body temperatures) are larger and have better growth rate and higher sprint speed, providing a further concern to this research.

Materials and methods

Field work was conducted at two sites (Noreña and Caleao) in central Asturias (Northern Spain), during the reproductive season in the years 1990 and 1991. Data on summer activity patterns and thermoregulation have been previously reported for the same population (Braña 1991). Lizards were captured by noose and handled taking care to minimize heat flow. Field body (cloacal), air (10 cm above ground), and substrate temperatures were taken with a Schultheis quick-reading thermometer within 10 s of capture. The data used in this study were from sunny days in May-July, avoiding records from lizards which were warming in the early morning or thermoregulating under suboptimal climatic conditions.

To study selected body temperature and position in a thermal gradient, lizards were caught in late June and early July, and housed in terraria without refuges (40 × 50 cm) in which a 150 W lightbulb created a gradient of air temperatures (measured at 1 cm above the ground) from ambient temperature (18–21°C) to 42°C. Lizards were subjected to natural photoperiod and accustomed to terraria from 1 to 3 d before initiating trials. Records of selected body temperatures were taken with Schultheis thermometers at three intervals, from one to three h after the heat source was set. Lizard's position at the same hourly intervals was assigned to one of the following three zones: A) the warmest zone, with air temperature higher than 35°C, B) intermediate zone, from 30 to 35°C, which lies in the range of the mean ± 1 sd of body temperatures of lizards taken in the field (Braña 1991), and C) the zone of air temperature under 30°C, below the usual field body temperature of active lizards in summer. No more than one record of body temperature was taken every day for the same individual, and lizard's positions were also recorded on different days than body temperatures.

To examine possible changes in the predator-avoidance tactic, I assessed the distance to which a lizard allows approach of a potential predator (for further considerations, see Rand 1964, Heatwole 1968, Bauwens and Thoen 1981). Approach distance was determined by walking at a slow and fairly constant step towards an animal previously sighted until it attemps to escape. When the lizard hides into a distinct shelter, I also measured the distance from the initial position to the refuge. Both the approach distance and the distance to the refuge were measured to the nearest 1 cm.

In this work, the term pregnant or gravid designates females with oviductal eggs. This condition was actually confirmed by palpation on lizards handled to obtain data on field body temperature and for those subjected to laboratory trials. However, sex and reproductive condition of the lizards from which I recorded approach distance and refuge distance were ascribed by eye, because most of them were not caught later. Mistakes in the assignment affected only 7.5% of the lizards captured after such records were taken ($n = 53$), most of them involving females with advanced vitellogenic follicles.

Differences among groups of sex and reproductive condition in continuous variables (body temperatures, approach distance, distance to shelter) were tested using t-tests (for paired comparisons) or Analysis of Variance (ANOVA) followed, if significant, by Scheffé multiple comparison test ($p < 0.05$). To examine whether body temperature selected in thermal gradient was different among groups of sex and reproductive condition in successive time intervals, I used two-way ANOVA with group and time as factors. As advised by Underwood (1981), the use of the same individual organisms in different time intervals will lead to non-independent data. To approach independence, random samples of 15 data were obtained from the whole available data-set from each group/time combination (containing

Table 1. Field body temperatures and environmental temperatures for groups of sex and reproductive condition of the lizard *Podarcis muralis*. Statistics for linear regressions of body temperature (y) on environmental temperatures (x) are given for both air and substrate temperature (y = a + bx).

	Body temperature	Air temperature				Substrate temperature				sample size
	mean±1 sd	mean±1 sd	b	a	F	mean±1 sd	b	a	F	
Pregnant females	32.62±1.58	20.48±4.12	0.24	27.66	27.23*	27.68±4.44	0.24	25.95	34.32*	43
Non-pregnant females	34.04±1.74	22.32±4.34	0.26	28.16	19.61*	28.95±4.14	0.29	25.64	23.65*	28
Males	33.58±1.79	21.43±4.31	0.21	29.13	15.10*	28.47±4.55	0.23	26.94	24.37*	48

All temperatures in °C. *P < 0.001.

from 25 to 51 data). Slopes of the regressions of air and substrate temperatures on body temperature were compared by Analysis of Covariance (ANCOVA). The three-dimensional contingency table reporting position of lizards in the thermal gradient by sex-stage and time interval was analysed by means of χ^2 following Zar (1984). Results throughout the text are reported as mean ± one standard deviation, and the level of statistical significance was set at $\alpha = 0.05$.

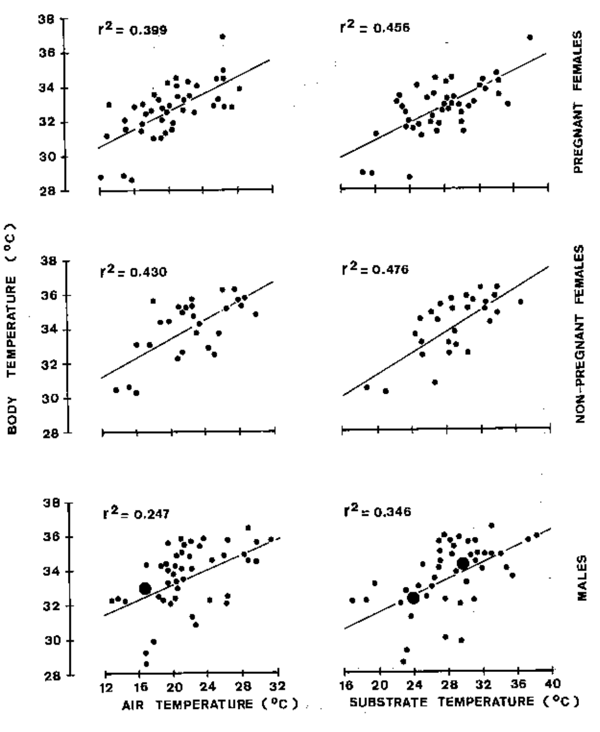

Fig. 1. Field body temperatures plotted against environment temperatures (air and substrate) for lizards grouped by sex and reproductive condition. Coefficients of determination (r^2) and regression lines (statistics for these lines are in Table 1) are given for each plot. Large dots include three data points.

Results

Field temperatures

Field body temperatures of mature lizards (minimum snout-vent length = 50 mm) during the reproductive season (Table 1) showed significant differences among groups of sex and reproductive condition (ANOVA, $F_{2,116} = 6.645$, $p < 0.01$). Body temperature of pregnant females (mean ± 1 sd = 32.62 ± 1.58°C; n = 43) was lower than those of mature males and non-pregnant females which, in turn, were homogeneous with respect to body temperature (Scheffé test a posteriori, $p < 0.05$; overall average body temperature for males and non-pregnant females: 33.74 ± 1.77°C; n = 76).

Among-group differences in air and substrate temperature at the point of capture were not significant (ANOVA, $F_{2,116} = 1.635$ for air temperature, and $F_{2,116} = 0.762$ for substrate temperature; $p > 0.1$ in both cases). For all lizard groups body temperature significantly increased both with air and substrate temperature (Fig. 1). Rates of increase of body temperature with environment temperatures were similar for all three groups, as the slopes of the regression lines were homogeneous (ANCOVA, $F_{2,115} = 0.280$, $p = 0.759$, for the regression of body temperature on air temperature, and $F_{2,115} = 0.314$, $p = 0.737$, for that on substrate temperature).

Selected body temperature and position in the thermal gradient

Body temperatures selected in the thermal gradient showed no significant effects of time or group of sex and reproductive condition (two-way ANOVA, $F_{2,126} = 1.851$, $p = 0.161$ for time; $F_{2,126} = 0.104$, $p = 0.901$ for group) nor significant interaction effects among them ($F_{4,126} = 0.144$, $p = 0.965$). Overall average body temperature selected in the terraria (33.77 ± 1.79°C, n = 135) was similar to those exhibited in the field by males and nonpregnant females ($t = 0.151$, $p > 0.1$; see Field temperatures), and also to previously published data for postreproductive individuals of the same populations (Braña 1991).

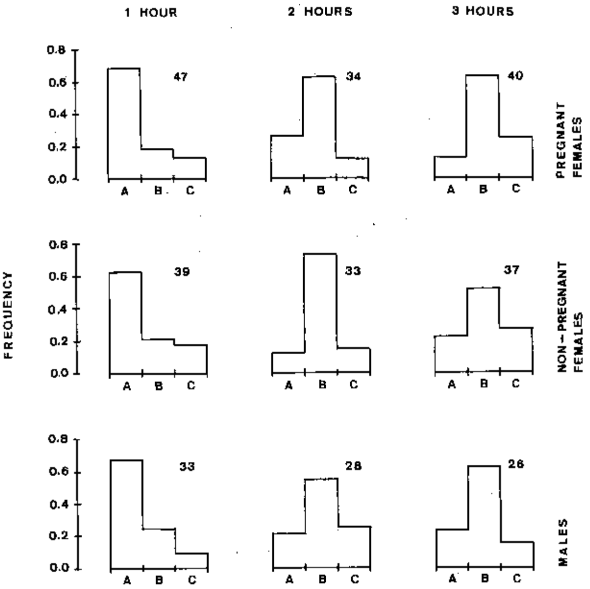

Fig. 2. Position of lizards in relation to zones of the thermal gradient at successive time intervals. Sample sizes are given on each histogram.

Fig. 2 shows the situation of lizards in the thermal gradient at successive time intervals. At the first hour interval lizards of all three groups stand mainly in the warmest zone (A), whereas in subsequent intervals most of them move to zone B, and, also, there was an increase in frequency of animals in the cool zone (C). Distribution of lizards in the thermal gradient at time intervals showed that the three variables in the analysis were not independent ($\chi^2 = 81.93$, d.f. 20, $p < 0.001$), but there were no significant differences among pregnant females, nonpregnant females and males (test for partial independence; Zar, 1984; $\chi^2 = 8.84$; d.f. 16; $p > 0.5$).

Approach distance and refuge distance

The basic data about approach and refuge distance for the three groups of sex and reproductive condition are represented in Fig. 3. No significant differences existed in distance to shelter between males (mean ± 1 sd: 28.47 ± 19.39 cm, n = 76) and non-pregnant females (25.08 ± 10.58, n = 37), but pregnant females hide at a shorter distance (19.00 ± 8.99, n = 42; ANOVA, $F_{2,153} = 5.15$, $p<0.01$; Scheffé test).

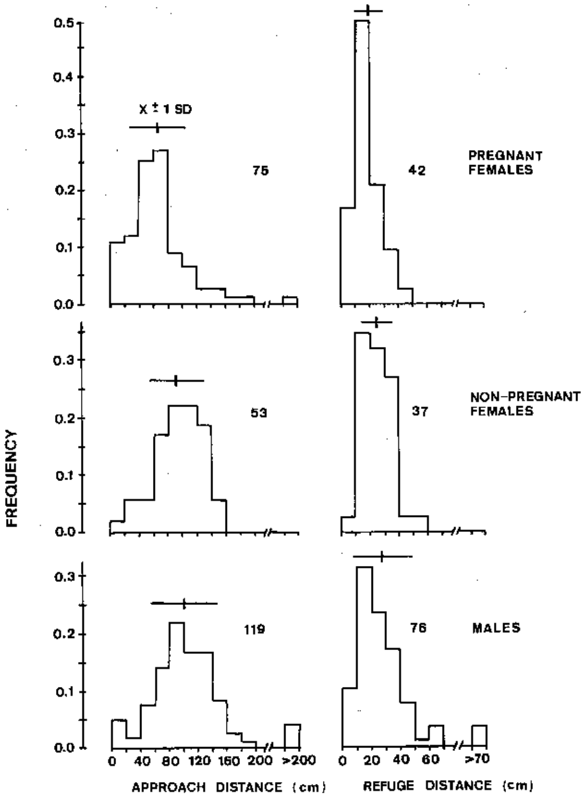

Fig. 3. Frequency distributions for approach distance and refuge distance of males, gravid females and non-gravid females. Sample sizes and position of the mean (± one standard deviation) are shown on each histogram.

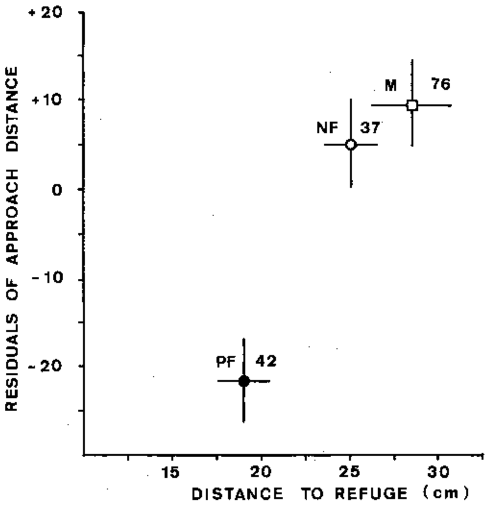

Fig. 4. Plot of the distance to refuge versus residuals of approach distance (from the regression on refuge distance), for males (M), pregnant females (PF), and nonpregnant females (NF). Mean values (± one standard error) and sample sizes are shown.

Approach distance showed a similar pattern among groups ($F_{2,242} = 17.27$, $p < 0.0001$; Scheffé test), being smaller in pregnant females (66.15 ± 40.29 cm, n = 74; 75% of cases below 80 cm) than in males (101.57 ± 45.28 cm, n = 119; 29% below 80 cm) and non-pregnant females (94.42 ± 32.68, n = 53; 30% below 80 cm). Distance to shelter explained 11.78% of the variance in the approach distance (least square regression line: $AD = 0.86\ RD + 72.00$; $F_{1,154} = 20.56$, $p < 0.0001$). Removing effects of refuge distance by applying residuals of the above regression, pregnant females also exhibited shorter approach distance than did males and non-pregnant females ($F_{2,153} = 11.68$, $p<0.0001$; Scheffé test; Fig. 4).

Discussion

In *Podarcis muralis*, females carrying eggs exhibit lower field body temperatures than do males and non-pregnant females. Shifts in body temperature during pregnancy have been reported for a number of squamate reptiles, including both higher and lower temperatures for pregnant females than for other individuals in the population (for reviews, see Shine 1980, Beuchat 1986, Beuchat and Ellner 1987). Since costs associated with thermoregulation may increase throughout the pregnancy (as do the weight and volume of clutches, Shine 1983), changes in body temperature and thermoregulatory behaviour during gestation seem more likely to occur in live-bearing species. In fact, most of the reported cases of shift in body temperature during pregnancy correspond to viviparous squamates (see, e.g., Stewart 1965, Patterson and Davies 1978, Stewart 1984, Beuchat 1986, 1988, Charland and Gregory 1990, Rosen 1991, and references therein; but see also Schall 1977, Shine 1980). However, many oviparous lizards exhibit advanced egg retention (Shine 1983), and specifically *Podarcis muralis* lay eggs with embryos in stages 25 to 29 in the Dufaure and Hubert's (1961) classification (Braña et al. 1991), which represents around half the total period of embryonic development. Therefore, most of the arguments established to account for shifts in body temperatures and behavioural modifications in gravid females of viviparous reptiles (Shine 1980, Bauwens and Thoen 1981, Ellner and Beuchat 1984, Beuchat 1986, 1988, Brodie 1989, Charland and Gregory 1990) can also apply to oviparous specis with prolonged egg retention.

Incubation (or gestation) in reptiles proceeds more rapidly at high temperatures (Muth 1980, Heulin et al. 1991, Van Damme et al. 1992). Therefore, the maintenance of higher temperatures by pregnant females would reduce the developmental time, providing a longer growth period for the young before wintering, which may improve overwinter survival and anticipate their reproductive maturity (Beuchat 1986). In addition, this may allow females to lay more clutches in the reproductive season, mainly in oviparous species with prolonged egg retention (Braña et el. 1991). However, embryonic mortality and frequency of abnormalities in neonates may also be higher than in incubations at intermediate or low temperatures (Maderson and Bellairs 1962, Vinegar 1974, Gutzke and Packard 1987). In addition, Gutzke and Packard (1987) showed for the bull snake (*Pituophis melanoleucus*) that young hatching from eggs incubated at intermediate or low temperatures are longer and have less residual yolk and less storage lipids than those from eggs at high temperature. For the same population of the lizard *Podarcis muralis* studied here, Van Damme et al. (1992) reported higher embryo survival, hatchling size, posthatch growth rate and performance (sprint speed of the hatchlings) for eggs incubated at temperatures lower than those that minimize the incubation time, close to temperatures maintained by adults in the field or selected in thermogradients (Avery 1978, Braña 1991, Van Damme et al. 1992, and this work). It is interesting to recall that larger size at birth and initial growth rate of the hatchlings incubated at low temperatures may compensate to some extent for differences in the time of emergence (Van Damme et al. 1992). In different viviparous populations of the lizard *Lacerta vivipara*, pregnant females consistently exhibit lower body temperatures than males or non-pregnant females (Patterson and Davies 1978, Van Damme et al. 1986, Heulin 1987). These authors pointed out the correspondence of the lowered body temperatures of pregnant females with the low thermal optimum for embryonic development in vitro for *Lacerta vivipara* (Maderson and Bellairs 1962).

Therefore, it is plausible that, in some instances, optimal developmental temperature for embryos might be lower than that for most physiological functions of the pregnant female. Then, the low body temperature selected in thermal gradients by pregnant females of some reptile species (e.g., Patterson and Davies 1978, Van Damme et al. 1986) would be the one that maximizes fitness (reproductive success) by compromising between the optimal temperature for the adult lizard and that for the embryonic development (Beuchat and Ellner 1987). On the other hand, although mean activity temperatures and mean selected temperatures are strongly correlated for diurnal lizards (Huey 1982), environmental constraints (e.g., thermal environment) or costs associated with thermoregulation (e.g., risk of predation) may prevent lizards to achieve the preferred temperature. The shift in field body temperature of female *P. muralis* during pregnancy is not the consequence of a change of their thermal preferences at this stage, but may be a result of the increased cost of thermoregulation, precluding them to attain optimal temperature; when subjected to an environment in which thermoregulation has virtually no associated costs (in terrarium, without predator and with a strong thermal gradient in a few centimetres), pregnant females behave like males and non-pregnant females and exhibit the same body temperature. Furthermore, these temperatures are similar to those exhibited by males and non-pregnant females in the field, and also to the ones previously reported for postreproductive individuals of the same population (Braña 1991). This indicates that 1) the thermal environment in nature during the reproductive period is favourable enough to allow thermoregulation close to the preferred temperature, and 2) low temperatures exhibited by pregnant females in the field might be explained on the basis of constraints related to their reproductive condition. This means that, subjected to different environmental conditions, pregnant females would thermoregulate at different levels and, then, that field body temperatures can vary among populations.

Pregnant *P. muralis* stay closer to refuge and allow predators to approach to a shorter distance than do males and non-pregnant females. Approach distance was partially explained by the distance to the shelter, but values for pregnant females remained significantly lower when the effects of the distance to refuge were removed. Then, there is a behavioural component of motion-less independent of (in addition to) the tendency to remain closer to a refuge. This means a shift in the predator-avoidance tactic from flight to crypsis, presumably because effectiveness of the flight tactic would be reduced during pregnancy. The change in the escape tactics in females burdened by voluminous clutches (a mean relative clutch mass of 47.4% has been reported for *P. muralis* from Asturias , Braña et al. 1991) follows the same logic as the evolution of higher relative clutch mass in those lizard species whose predator escape tactic and foraging mode are "passive" (crypsis and sit-and-wait, respectively), as reported by Vitt and Congdon (1978) and Vitt and Price (1982).

Many thermoregulatory behaviours of reptiles involve movements that may increase conspicuousness and probability of encounter with predators (Huey 1982). In addition, gravid females are more vulnerable to predation than are non-gravid females, because of reduced mobility, endurance and running speed (Shine 1980, Bauwens and Thoen 1981, Gardland and Else 1987, Madsen 1987, Seigel et al. 1987, Brodie 1989). Then, shifts in the predator-avoidance tactic from flight to crypsis in pregnant females may compensate the loss of locomotor ability (Bauwens and Thoen 1981), but may also preclude accurate thermoregulation, as this requires frequent movements to exploit the variability of the thermal environmental (Adolph 1990). Then, low field body temperatures exhibited by females during gestation might be a byproduct of the change in the predator-avoidance behaviour, since it would restrict the scope and frequence of movements. As environmental temperatures at the point of capture (air and substrate) were not consistently different for pregnant females (although both mean and variance were slightly lower in all cases; see Table 1), an alternative (or simultaneous) possibility would be a decrease of the activity time or the basking frequency, as reported for pregnant females in some lizard species (Shine 1980).

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