

SHORT COMMUNICATION

INFLUENCE OF PREGNANCY ON BEHAVIORAL
THERMOREGULATION IN THE NORTHERN PACIFIC
RATTLESNAKE *CROTALUS VIRIDIS OREGANUS*

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Incubation within appropriate thermal limits is important for the normal development of the reptilian embryo (Maderson & Bellairs, 1962; Fox *et al.* 1966; Osgood, 1978; Burger *et al.* 1987). Among the viviparous reptiles in which the optimum temperature for embryonic development differs from the temperature of optimum activity in the adult, one would predict a shift in thermoregulatory behavior of the pregnant female. We have examined the influence of pregnancy on the thermoregulatory behavior of the northern Pacific rattlesnake (*Crotalus viridis oreganus*) to test this prediction.

Past studies have shown no consistent pattern for predicting thermoregulatory behavior by reptilian females during pregnancy. While some lizards lower body temperature (Garrick, 1974; Beuchat, 1986, 1988; Van Damme *et al.* 1986), other lizards and snakes elevate or do not change preferred body temperature during pregnancy (Stewart, 1965, 1984; Werner & Whitaker, 1978; Gibson & Falls, 1979; Gannon & Secoy, 1985; Hailey *et al.* 1987). Some data also suggest more precise behavioral temperature control in pregnant females (Stewart, 1984; Beuchat, 1986). One difficulty in interpreting the previous studies stems from the variety of conditions and experimental procedures used to obtain the data. Consequently, we conducted these studies in the laboratory utilizing as simple and well-defined an experimental design as possible.

Radiotelemetry was used to compare voluntary body temperatures of pregnant *versus* nonpregnant female as well as pregnant *versus post-partum* *C. v. oreganus* in a thermal gradient. Five pregnant and three nonpregnant snakes were collected in late May and June and two additional, nonpregnant females were collected in early August. All snakes were collected in Garfield and Whitman Counties, Washington, and Latah and Nez Perce Counties, Idaho. One apparently pregnant snake was discovered to be infertile; data from that animal were not included.

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Body temperatures were determined with temperature-sensitive transmitters (Model V-M, Mini-Mitter Co., Sunriver, Oregon), coated with 'parafin/elvax' (Mini-Mitter Co.), which were implanted into the peritoneal cavity following the procedure of Brown *et al.* (1982). Before implantation, the transmitters were calibrated at 5°C intervals from 15 to 40°C. Surgery was completed for the first group of eight snakes in mid-July and transmitters were implanted in the last two in early August. Testing of thermoregulatory behavior began no sooner than 1 week following surgery and was conducted in a long, narrow wooden cage divided into two halves, each 103 cm × 30 cm × 46 cm high. This enabled simultaneous testing of two snakes. The thermal gradient was established by positioning a 50-W GE infrared heat lamp (about 56 cm above the cage floor) at opposite ends of the cage. Within an hour, a stable gradient was established, ranging from 40°C directly beneath the lamp to ambient room temperature (about 20°C) near the divider. The test cage was positioned alongside a one-way mirror which was a wall of a small observation room. With this set-up, snakes could be observed closely without entering the room and without being disturbed by sight, sound or odor. Two snakes were placed in the testing cage in the afternoon and the lamps turned on. They were left overnight, and transmitter signals were recorded the next day at 30- to 60-min intervals, beginning at 08.00 h and ending by about 15.30 h. Two animals (nonpregnant females) were analyzed four times and the others were analyzed six or seven times between 20 July and 7 October, 1987. Data from pregnant/*post-partum* and nonpregnant snakes were analyzed for differences between mean, standard deviation, and range of body temperatures by a repeated-measures ANOVA. Simple repeated measures and contrast tests were used to analyze for similar temperature differences between pregnant and *post-partum* snakes.

All snakes regulated their body temperature by shuttling between the warmer and cooler portions of the enclosure, with most periods of inactivity being spent near the heat source. Most snakes maintained body temperatures that fluctuated around an overall mean of 29.5°C (all snakes, with the exception of the infertile female, all time periods). Individual variation is illustrated in Fig. 1.

Grand means for all pregnant/*post-partum* and all nonpregnant snakes are shown in Fig. 2. There were no significant differences between mean body temperature, standard deviation, and range of body temperature for pregnant/*post-partum* and nonpregnant snakes, whether before or after birth. However, body temperature for pregnant females changed significantly after birth, in mean ($P < 0.001$), standard deviation ($P = 0.024$) and range ($P = 0.044$). The prebirth mean was 30.7°C, standard deviation was 0.89°C and range was 26.9–34.6°C, whereas the postbirth mean was 28.5°C, standard deviation was 1.41°C and range was 23.3–32.0°C. Therefore, there was a tendency for pregnant snakes to thermoregulate higher, and with less variability, before than after birth. The results from this species suggest that the optimum temperature is higher, and the temperature range is narrower, for embryonic development than for the activities of the *post-partum* female. Also, the body temperature of the pregnant snakes

tended to decrease gradually throughout the duration of the study (Fig. 3). A similar decrease with the progression of pregnancy was noted by Patterson & Davies (1978) for *Lacerta vivipara*. This suggests a change in thermophilic behavior of the female caused by the course of pregnancy. Beuchat (1988) has

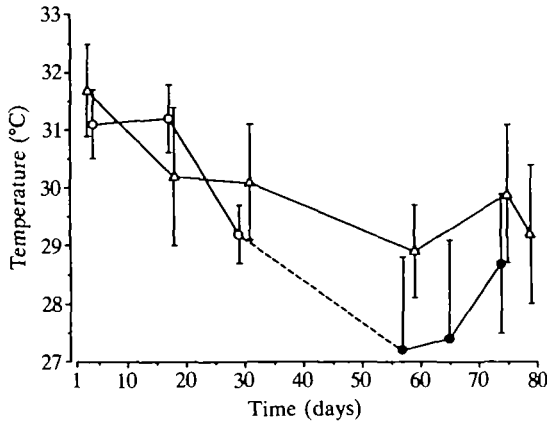


Fig. 1. Daily mean body temperature for a representative pregnant (○)/post-partum (●) and nonpregnant (Δ) *Crotalus viridis oreganus*. Each point is the mean and standard deviation ($N = 7-8$) of the body temperatures recorded on a given day for these snakes. Day 1 is 20 July, 1987. In this species, ovulation occurs from mid-May to mid-June and parturition generally occurs over a 30-day period beginning in early September (Diller & Wallace, 1984).

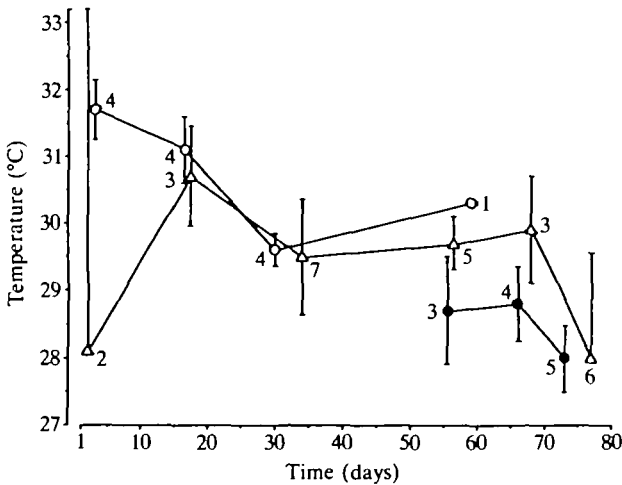


Fig. 2. Grand means for pregnant (○)/post-partum (●) and nonpregnant (Δ) *C. v. oreganus*. Each point (mean \pm s.e.) represents the pooled daily means of all individuals in a category during the sample period. The numbers on the figure are the numbers of daily means pooled per point. Sample periods were no longer than a week and each point is positioned over the time line on the median day of the sample period. Day 1 is 22 July, 1987.

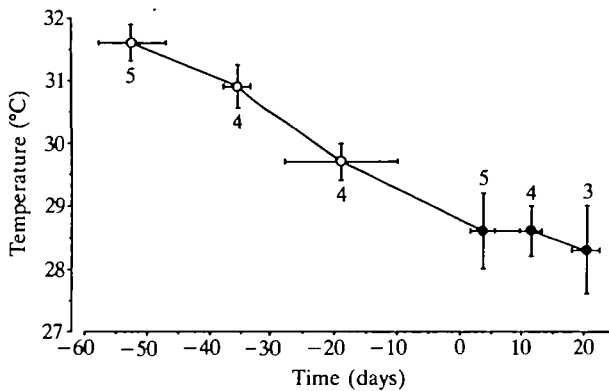


Fig. 3. Grand means of body temperature for pregnant (○) and *post-partum* (●) female snakes plotted relative to time of birth. Vertical bars represent the mean body temperature \pm s.e. and horizontal bars represent the mean date \pm s.d. Time periods were arbitrarily divided such that each snake was represented at least once, except for the last time period. Numbers on the figure are *N* values for temperature and days.

recently postulated that the pregnant lizard, *Sceloporus jarrovi*, thermoregulates lower than the nonpregnant female to minimize the exposure of the embryo to detrimentally high temperatures. This could explain the decrease in body temperature of the pregnant rattlesnake with the progression of pregnancy, and suggests that the developing embryo may become increasingly sensitive to high temperatures.

One proposed advantage of viviparity is the implied mechanism of a controlled thermal environment for the developing embryo (Shine & Bull, 1979). Preference for a higher body temperature by the pregnant reptile may be a reaction to an environment generally too cool, whereas preference for a lower body temperature in some may be a reaction to an environment too warm for optimum embryonic development. This could explain the apparent lack of a consistent pattern in the thermoregulatory behavior among the viviparous reptiles. Comparing thermal behavior of pregnant and *post-partum* reptiles from southern and northern populations should shed light on this possible explanation.

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