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Temperature Differences Between Head and Body in Garter Snakes (*Thamnophis*) at a Den in Central British Columbia

PATRICK T. GREGORY

Department of Biology, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2

ABSTRACT.—This study describes diel variation in differences between head and body temperatures of garter snakes (*Thamnophis sirtalis, T. elegans*) at a communal den in spring. Snakes emerged with low oral and cloacal temperatures but rapidly reached normal activity temperatures and maintained those temperatures with only a slight decline during the day. Oral temperatures were frequently much higher than cloacal temperatures during the heating phase, but were only moderately higher thereafter. The occurrence of "head basking" behavior suggests that differences between head and body temperatures are in part the result of activities of the snakes and not just the passive result of differential warming rates due to differences between size of head and body.

In the temperate zone, diurnal snakes usually begin their daily activity with a heating phase (Charland, 1987; Peterson, 1987). However, heating may occur at different rates in different parts of the body. Several species of snakes have been observed to exhibit positive differences between temperatures of head and body, especially during warming, with less variability in head than body temperatures (Johnson, 1973, 1975*a*, *b*; Hammerson, 1977). Such differences might be passive, resulting merely from size differences of head and body (Pough and McFarland, 1976). On the other hand, snakes might actively maintain differences in head and body temperatures by behavioral means. This is suggested by the observation that some species apparently do not emerge fully from night-time retreats until they have rested for a short period with only the head or anterior part of the body exposed to the sun (Hammerson, 1977, 1979, 1987). If differences between head and body temperatures are actively maintained by snakes, then this is potentially an important aspect of their thermal biology that merits further study.

Most studies of temperature differences between head and body in snakes have been conducted with captive snakes in the laboratory or in outdoor enclosures. Field data on this phenomenon are scarce and not very detailed (e.g., Vincent, 1975; Peterson, 1987). While collecting data for a long-term population study of garter snakes (*Thamnophis sirtalis* and *T. elegans*) during spring activity at a communal den in central British Columbia, I often saw snakes in rock crevices early in the day with only their heads exposed to the sun. Although activities of garter snakes at dens in spring are different from activities at other times of year (Gregory, 1984), dens offer an opportunity to observe many snakes simultaneously under fairly homogeneous conditions, thus reducing background variation and possibly yielding insight into more general patterns of behavior. My main objective here is to document the presence, magnitude, and diel variation of temperature differences between body and head in snakes in the field, using measurements taken at the den. A secondary objective is to determine if such differences are associated with behaviors that might distinguish "passive" from "active" mechanisms for maintaining them.

METHODS

Data were collected throughout the day on 19-20 April and 7-8 May 1984, but occasional measurements were also made on several other days in the spring of 1984 and 1985. The den where snakes were found is near Riske Creek, British Columbia, Canada (51°58'N, 121°32'W; 940 m). It consists of a large, conical volcanic plug (approximately 44 × 64 × 45 m) rising from the surrounding grassland. Although snakes emerge in spring from various parts of this structure, I concentrated on the area around the main den entrance, an area of rock rubble about 3 × 3.5 m facing approximately west at an angle of about 45° above horizontal.

For reference, I monitored two environmental temperatures: (1) underground temperature via a thermistor probe (YSI 420) inserted about 60 cm down an opening between the rocks (probably not straight down); (2) the temperature of a maximum-minimum (MaxMin) thermometer left in the open, unshaded, on top of the rocks. Temperatures were recorded to the nearest 0.1 C at intervals ranging from about 0.5-2 h over the course of the day, but no night-time temperatures were recorded other than the overnight minimum from the MaxMin thermometer.

At frequent intervals during the day, I approached the rocks and, using a Schultheis quick-reading thermometer, recorded the oral (T_o) and cloacal (T_c) temperatures to the nearest 0.1 C of as many snakes as possible. I only measured the temperatures of snakes whose behavior appeared to be normal and did not obviously change upon my approach. Temperatures were recorded only when the first was obtained within 10–15 sec of capturing the snake. Oral temperatures were taken by holding the snake a short distance behind the head between two fingertips (ungloved) and inserting the thermometer bulb via the side of the snake's mouth into its throat (thermometer bulb completely in snake's mouth). Cloacal temperatures were taken by holding the snake by the end of its tail and inserting the bulb completely through the cloacal opening. Snakes emerging from rocks always had T_o recorded first and then, if possible, were pulled out of the rocks for T_c measurements. Otherwise, the order in which T_o and T_c were taken varied (in no fixed way) from snake to snake, but temperatures always were taken within 10–15 sec of each other. For each snake, I noted whether it was under a rock, in a crevice in the rocks, in the open, or partly in the open. The rocks under which I looked for snakes were almost always small rocks (10 kg or less; see Huey et al., 1989).

Because I moved quickly from one snake to another, I did not always note the individuals whose temperatures I measured (most snakes in this population are individually marked). Although I was careful not to measure the same individual snakes twice in a bout of sampling, it was not possible to avoid or identify repeated measurements on the same individuals in different bouts. Other factors (e.g., ambient temperatures and solar radiation) likely were the dominant influences on snake temperature. Therefore I believe that my observations can be considered to be effectively independent for the purposes of the statistical analyses performed herein.

For purposes of analysis, I considered snakes under cover or in crevices in rocks separately from snakes partly or fully in the open. For each group, I tested the correlation between T_o and T_c using Spearman's rank correlation. I compared the relationship between T_o and T_c with that expected if $T_o = T_c$ (the 1:1 line). However, I could not use linear regression techniques because the data were not linear. I therefore divided the data into upper and lower halves based on T_c and compared the number of points that fell above and below the 1:1 line using χ^2 (or by calculating exact binomial probabilities if N was small). I compared the difference between T_o and T_c (i.e., $T_o - T_c$) between the two halves of each data set using a Mann-Whitney U-test. Finally, I compared $T_o - T_c$ of snakes under cover and in the open using a Mann-Whitney test, but I restricted this analysis to lower temperatures (determined by the median T_c of snakes in the open to make the two groups comparable).

Because of small sample sizes, I pooled data from all sample days for analysis. I also did not distinguish between *T. sirtalis* and *T. elegans* since there were no discernible differences between them. All tests followed descriptions in Zar (1984) and a rejection level of $\alpha = 0.05$ was used throughout.

Results

Most snakes seen at the den were adult male *T. sirtalis* (snout–vent length, SVL, $\geq$ 400 mm); adult male *T. elegans* were the second most abundant group. Females and juveniles of either species were seldom seen. Both T_o and T_c were recorded for adult male *T. sirtalis* a total of 72 times. Both temperatures also were taken from four female *T. sirtalis* (including three small snakes ranging from 215–395 mm SVL) and 16 adult male *T. elegans*. In an additional six cases (5 male and 1 female *T. sirtalis*), it was not possible to obtain both T_c and T_o; these cases are therefore left out of the analyses involving comparisons of T_o and T_c, but are retained as behavioral observations. Most snakes sampled were >500 mm SVL.

Similar patterns of temperature variation were seen on all sample days. The MaxMin temperature showed a symmetrical pattern of increase and decrease, reaching a peak at about 1400 h (Pacific Standard Time). Daily maxima ranged from 25–33.9 C and overnight minima were 3.9 and 6.7 C. Underground temperatures were less variable, ranging from a low of 4 C early one morning to a high of 9.9 C late one afternoon. Temperatures of snakes were lowest early in the morning, approximating underground temperatures, but rose rapidly until around 1100–1200 h (Fig. 1A). Thereafter, they declined slowly during the course of the afternoon. The few low temperatures recorded in the afternoon were mainly from snakes found under rocks or emerging from openings in the rocks. Generally, T_o was much higher than T_c early in the morning, but this differential declined through the day and was small by late afternoon (Fig. 1B). The few large differences between T_o and T_c seen in early to mid-afternoon were recorded from emerging snakes.

Most snakes (60 of 98) whose temperatures were measured were found in the open. Several were found partly emerged from holes, with just the head or anterior part of the body exposed, or with just the tail still in the hole. Some

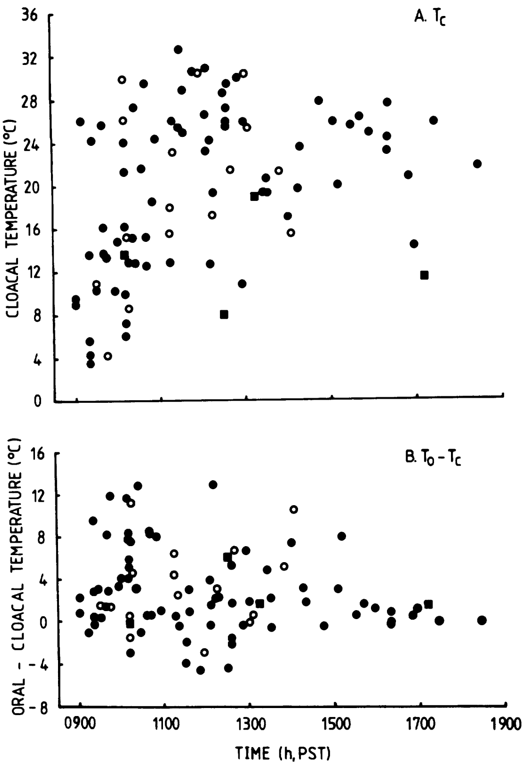

FIG. 1. A. Diel variation in cloacal (T_c) temperatures of snakes at den (all sample days combined). Closed circles = male *T. sirtalis;* closed squares = female *T. sirtalis;* open circles = male *T. elegans.* N = 92. B. Diel variation in difference between oral and cloacal ($T_o - T_c$) temperatures (all sample days combined). Symbols as in 1A. N = 92.

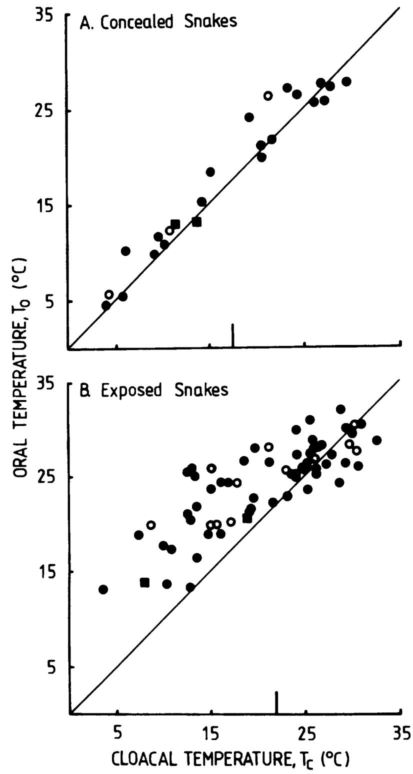

FIG. 2. Relationship between oral (T_o) and cloacal (T_c) temperatures for snakes under cover or in rocks (A. Concealed, N = 24) or in open (B. Exposed, N = 68) for all sample days combined. Symbols as in Fig. 1. Diagonal line represents equality of oral and cloacal temperatures. Vertical line on abscissa divides data set into halves.

of the snakes recorded as lying in the open had their tails near holes, as if they had just emerged from underground. By combining the 14 snakes classed as partly in the open with the seven in the open with their tails near openings, I derived a sample of 21 snakes whose temperatures apparently were taken during emergence or just after emergence from the rocks. These snakes were found at times of day ranging from 0920–1555 h; however, the median time of capture of these snakes was 1025 h, and 14 of them were caught before 1200 h. At midday and in early afternoon there was considerable snake activity, consisting mainly of constant movement in and out of the rocks. Courtship and mating usually occurred during this period. Snakes were found rarely under rocks and then mainly early in the day (8 of 10 before 1100 h). Snakes were often seen sheltering in spaces between the rocks near the surface, especially in afternoon and early evening (12 of 14 after 1200 h). Because of the difficulty of recording the total numbers of individuals in each activity category, these data should not be construed as representing a random sample. Snakes emerging in the morning and tucked into crevices in late afternoon are almost certainly underrepresented because several were seen, but not caught.

Snakes found under cover or in rocks exhibited a range of temperatures similar to that seen in snakes in the open, but the pattern of T_o-T_c differed in the two cases (Fig. 2). There was a significant correlation between T_o and T_c for both snakes under cover ($r_s = 0.97$, N = 24, $P < 0.001$) and in the open ($r_s = 0.80$, N = 68, $P < 0.001$). For snakes under cover, there was no significant difference in the number of points above and below the 1:1 line at higher temperatures (6 above, 5 below, one on the line; $P = 1.0$), but there was a significant excess of points above the line (i.e., higher T_o than T_c; 10 above line, 2 below; $P = 0.038$) at lower temperatures. Despite this, there was no significant difference in T_o-T_c between higher and lower temperatures for snakes under cover ($U_{12,12} = 83.5$, $P = 0.48$). For snakes in the open, there were similar numbers of points above and below the line at higher temperatures (19 above, 14 below, one on the line; $\chi^2_{1\ \text{corrected}} = 0.485$, $0.25 < P < 0.50$), but all 34 points were above the line at lower temperatures ($\chi^2_{1\ \text{corrected}} = 32.029$, $P < 0.001$). The difference between T_o-T_c at higher and lower temperatures was significant (higher at lower temperatures) for snakes in the open ($U_{34,34} = 1077.5$, $P < 0.001$). Finally, snakes at lower temperatures had significantly larger T_o-T_c values when in the open than when under cover ($U_{17,34} = 518.5$, $P < 0.001$).

Discussion

Two main points emerge from this study. First, snakes at the den in spring begin the day with very low body temperatures, but rapidly warm to activity temperatures. These higher temperatures then are maintained with only a slow decline for the rest of the day. This diel pattern of variation in body temperature is consistent with the "plateau pattern" described by Peterson (1987) for *T. elegans*, in which body temperatures rise rapidly in the morning and are maintained at a more or less constant level until a late afternoon decline. Similar observations have been made for other species by de Bont et al. (1986), Hammerson (1977, 1979, 1987), Saint Girons and Bradshaw (1981), and Charland (1987), all of whom used radiotelemetry to follow individual animals. Not surprisingly, their patterns are generally much clearer than my observations derived from spot measurements of various individuals.

The second point is that snakes begin morning activity by warming the head more quickly than the body, then more or less equilibrate temperatures between head and body for the rest of the day. Although one might argue that early morning T_os were artificially inflated by heat transfer from my fingers holding the snake, I was careful to minimize contact with the snake. Furthermore, snakes in the open with low T_cs clearly had higher T_os than snakes under rocks with similar T_cs (Fig. 2); since I measured temperatures in the same manner in each case, I conclude that the difference between T_o and T_c is real, even if there was a small heating effect from my fingers. Data from other field studies reveal no consistent pattern. D. Hart (pers. comm.) found a small but significant elevation of T_o over T_c for both *Thamnophis sirtalis* and *T. radix* from measurements at various times of day in Manitoba. Vincent (1975) found no difference between T_o and T_c of *T. sirtalis* at a den on warm, sunny days, but did find a small significant difference on cool days (direction of difference not specified). Peterson (1987), on the other hand, found no difference between mean esophageal ($\simeq$oral) and cloacal temperatures of *T. elegans* (although the former temperature was significantly less variable), but time of day was not specified.

The significance of differences between head and body temperatures is equivocal (Heatwole, 1976; Hammerson, 1977). Pough and McFarland (1976) argue that differences in heating rates of head and body in lizards simply could be the result of physical differences in size of head and body. The temperature data in this paper are entirely consistent with this hypothesis. If differences between T_o and T_c are maintained passively, snakes under cover would not be expected to have significant T_o-T_c values at any temperature, assuming that temperatures under cover are homogeneous at any given time (an untested assumption, but one that often will be true for small rocks; see Huey et al., 1989). By contrast, for snakes in the open, the difference between T_o and T_c should be large at low temperatures, as the head warms up fastest, and should decrease with increasing temperature as equilibration occurs throughout the body. However, exactly the same results would be expected if snakes at low temperatures actively warmed their heads before their bodies. In fact, the snakes observed by me and by Hammerson (1977, 1979, 1987) clearly exhibited behavior that would expose only the anterior part of the body to the source of heat in the morning. Snakes might exhibit this behavior as a means of "testing" the environment to determine whether or not it is safe to emerge, especially if they are most vulnerable to predators during the morning heating phase (Stevenson et al., 1985). In this case, differential warming of head and body would simply be a by-product of vigilance. On the other hand, Hammerson (1977) argued strongly that snakes exhibit this behavior because they regulate head (brain) temperature more closely than body temperature. Although Hammerson (1989) found no significant difference in mean duration of head exposure of *Masticophis flagellum* between mild and hot days, his analysis was not definitive and further study is needed. If snakes do differentially regulate head temperatures, perhaps venous shunts associated with cephalic sinuses also play a role (Heath, 1966; Webb and Heatwole, 1971; Heatwole and Johnson, 1979). Georges (1979) showed that head-body temperature gradients were greater in restrained living specimens of the lizard *Tiliqua scincoides* than in dead ones, but did not identify the physiological mechanisms involved. Differential regulation of head and body temperatures also would suggest that the cloacal temperatures commonly recorded in field and laboratory are not always the most relevant temperatures to take (e.g., Webb and Witten, 1973). The problem of measuring ecologically meaningful temperatures, when temperatures in different parts of the body vary (Webb and Heatwole, 1971; Dill, 1972; Heatwole and Johnson, 1979), is a general one.

The data in this study indicate that differences between T_o and T_c of garter snakes are maintained in part by the activities of the snakes themselves and are not solely the result of passive differences in heating rates of head and body (Pough and McFarland, 1976). Whether or not it serves a thermo-regulatory purpose, I suggest that "head basking" is an important component of emergence behavior of snakes, especially at low temperatures during warming. Its function will remain unknown until we have more rigorous and innovative studies than those reported to date. At the very least, we need studies that document in detail simultaneous observations of behavior (perhaps via video recordings) and head and body temperatures (e.g., using telemetry) of known individual snakes under different circumstances (different temperature regimes, different risks of predation, etc.). Experimental studies in both field enclosures and laboratory seem appropriate at this stage.

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