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Thermal Ecology of Arboreal Green Snakes (*Opheodrys aestivus*)

Author(s): Michael V. Plummer

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1106, San Nicolás. ESTADO BARINAS: 53, 65, 87, 505, 510, 543, 544, 877.

APPENDIX 2

Character Values

The following are MCNG specimen numbers and observed values of character states of PO Stripe, SL Band, SL Spots, and Blotch Shape, respectively. Specimens are listed in the same order as in Appendix 1. 80: 2,1,0,1; 83: 2,3,0,2; 84: 0,1,0,3; 85: 1.5,3,0,3; 121: 2,2,0,2; 503: 2,2,0,1; 504: 2,2,0,2; 507: 2.5,1,0,1; 509: 0,2,0,1; 519: 1.5,2,0,2; 875: 2,2,1,1; 876: 2,3,3,2; 879: 2.5,2,2,1; 880: 2,2,2,2; 882: 3,2,0,3; 883: 2.5,3,1,1; 885: 2.5,2,0,1; 889: 1,1,0,3; 893: 1,2,0,3; 932: 2,3,1,1; 933: 2,2,3,1; 934: 0,2,0,1; 953: 1,3,1,3; 978: 2,2,0,3; 1321: 2,3,1,1; 1326: 1.5,1,1,2; 517: 2,1,0,1; 518: 2,2,0,3; 881: 2.5,3,3,1; 1327: 1,2,0,3; 82: 0,5,2,0,1; 93: 2.5,2,0,2; 516: 2,3,2,2; 878: 2,3,3,1; 1340: 1.5,3,0,3; 1341: 2,2,2,1; 366: 2,2,2,1; 508: 1,3,0,3; 511: 0.5,2,0,3; 513: 2,2,0,3; 514: 1.5,2,0,3; 515: 2.5,3,3,1; 886: 2,2,0,3; 887: 1.5,2,0,1; 884: 2,2,0,1; 888: 2,3,0,3; 890: 2,2,0,3; 1106: 1,3,0,3; 53: 2,1,0,3; 65: 2,2,0,3; 87: 1.5,2,0,3; 505: 2,2,0,2; 510: 2,2,0,3; 543: 2,2,0,3; 544: 1.5,1,0,3; 877: 3,2,2,1.

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APPENDIX 1

Specimens Examined

All specimens examined in the present study were from Venezuela and are in the collections of Museo de Ciencias Naturales (MCNG), Guanare, Estado Portuguesa. *Piedmont population*. ESTADO PORTUGUESA: 80, 83-85, 121, 503, 504, 507, 509, 519, 875, 876, 879, 880, 882, 883, 885, 889, 893, 932-934, 953, 978, 1321, 1326, Mesa de Cavacas; 517, 518, 881, 1327, Urbe San Francisco (north Guanare); 82, 93, 516, 878, 1340, 1341, La Colonia; 366, Represa del Rio Bocono. *Llanos population*. ESTADO PORTUGUESA: 508, 511, 513-515, 886, 887, Palmar de Marrones, Guanarito; 884, 888, 890,

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Thermal Ecology of Arboreal Green Snakes (*Ophedryx aestivus*)

MICHAEL V. PLUMMER

Department of Biology, Harding University, Searcy, Arkansas 72143, USA

ABSTRACT.—Body temperatures were measured on diurnally-active arboreal green snakes (*Ophedryx aestivus*) throughout their activity season and compared to operative temperatures measured with copper models. Green snakes were active over a broad range of body temperatures (17.9-36.8 C) and their mean activity temperature (29.3 C) was similar to that reported for a variety of snake species. Body temperatures of females tended to be higher than those of males, especially in June. Variation in perch heights selected by green snakes did not appear to have significant thermal consequences. Green snakes avoided basking and their body temperatures usually tracked cooler shaded air temperatures. Hypotheses for the lack of basking include biophysical constraint and antipredator strategy. Further study in a cooler climate is needed to confirm whether the lack of heliothermic thermoregulation of green snakes is typical of the species or whether it occurred in this study simply as a function of living in a thermally favorable environment.

The existing knowledge concerning the thermal ecology of green snakes (*Ophedryx*) consists of a few body temperatures reported for *O. vernalis* (Brattstrom, 1965). The thermal ecology of the arboreal *O. aestivus* and of arboreal snakes in general is unknown. Rough green snakes (*O. aestivus*) are slender, arboreal snakes which commonly inhabit the thick shoreline vegetation surrounding bodies of water (Plummer, 1981; Goldsmith, 1984) in southeastern North America (Conant and Collins, 1991). Based on certain behavioral, physiological, and mor-

phological characteristics of *O. aestivus*, I predicted that it would be a precise heliothermic thermoregulator which maintained a relatively high body temperature. These characteristics are as follows: (1) Green snakes are active foragers which are strictly diurnally active throughout each day throughout a unimodal activity season from May-September (Plummer, 1981; Dalrymple et al., 1991). (2) Green snakes, as a species, do not reduce activity when either daily or seasonal temperatures are high (Gibbons and Semlitsch, 1987; Plummer, unpubl.). (3) Green snakes

inhabit edge habitats where solar radiation is readily available (Plummer, 1981; Goldsmith, 1984) and where physical costs of thermoregulation are probably low (Huey and Slatkin, 1976; Huey, 1982). (4) Green snakes have a high critical thermal maximum (Pough and Gans, 1982) (44.5 ± 0.21 C, $N = 10$; Plummer, unpubl.), a correlate of optimal body temperature during activity for squamate reptiles (Huey, 1982). Finally, (5) green snakes have a full body length dense black peritoneum (pers. obs.) believed to be an ultraviolet radiation shield and often found in diurnal reptiles which expose themselves to large amounts of solar radiation (Porter, 1967). In this paper, I test whether green snakes are, in fact, precise heliothermic thermoregulators by describing the behavior and body temperatures of green snakes in the field and comparing the body temperatures to various operative temperatures measured concurrently.

MATERIALS AND METHODS

Body temperatures were measured from *O. aestivus* found in the shoreline vegetation surrounding a small lake near Denmark, White County, Arkansas. The vegetation was searched from a boat throughout daylight hours, 2–4 times each week from April through September 1987. When a snake was discovered, I observed it briefly to determine its behavior, its position in the vegetation, and to estimate the proportion of its total body length that was exposed to direct solar radiation. Green snakes are insensitive to the presence of an immobile human seated in a boat at a distance of a few meters (pers. obs.). After observation, each snake was captured and its cloacal temperature (T_b) quickly measured to the nearest 0.1 C with a Schultheis quick-recording thermometer. Each snake was sexed, measured (snout-vent length, SVL), and released. Snakes with SVL <280 mm (males) or <360 mm (females) were classified as juveniles; snakes at and above these minima were classified as adults (Plummer, 1984; Aldridge et al., 1990).

I measured operative temperatures with "T_e thermometers" (Bakken and Gates, 1975; Bakken et al., 1985), constructed of 10 × 470 mm hollow copper models containing thermister probes and painted (Tru-Test X-O Rust, T-3 gray, no. 2252) to match the reflectivity of an *O. aestivus* (Peterson, 1987). Model verification was obtained by comparing equilibration temperatures of models against those obtained from anesthetized *O. aestivus* placed in various thermal environments (Peterson, 1987). Time constants, the time required for a model's temperature to change 63% of the way to a new temperature, averaged 2.6 min. Immediately af-

ter recording the body temperature for each snake, three models were placed in proximity of the capture site. To obtain T_{esn} , one model was placed in the specific microenvironment in which the snake was first observed. Placement included duplicating the estimated proportion of body length exposed to solar radiation. To obtain T_{esu} , a second model was placed in the nearest arboreal microenvironment with full solar exposure. To obtain T_{esh} , a third model was placed in the nearest arboreal microenvironment with full shade. Equilibration temperatures were recorded for each model. In practice, temperatures of models placed in full shade microenvironments did not differ from ambient shaded air temperatures. Thus, use of models in full shade microenvironments was discontinued in favor of the more quickly obtained ambient shaded air temperature (T_a). To determine the possibility of vertical temperature gradients within the vegetation, I measured exposed T_{esu} and shaded T_a in still air at successive 0.5 m levels above ground on a cloudy day and on a sunny day.

RESULTS

Monthly mean body temperature (T_b) tracked operative snake temperature (T_{esn}) and was intermediate between minimum ambient air temperature (T_a) and maximum operative temperature (T_{esu}) (Table 1). Snakes most frequently (>75%) avoided direct solar radiation. Some exposure occurred in April and May, but little or none occurred in later months (Table 1). Variation in both T_{esn} and in T_a explained over 90% of the variation in T_b (Table 1; Fig. 1). Stepwise multiple regression revealed that the addition of T_{esu} (indicating exposure) explained an additional small (1%), but significant ($P < 0.05$), amount of variation in T_b compared to T_a alone ($R^2 = 0.92$).

Green snakes were active, exhibiting characteristic slow foraging movements throughout all daylight hours (Plummer, 1981), within a broad range of body temperatures ($\bar{x} = 29.3$, $SD = 3.9$; range = 17.9–36.8 C; $N = 220$). Snakes with body temperatures as low as 21.6 C were observed attempting capture of prey. On warm days ($T_{esu} \geq 30$ C), body temperatures averaged 31.3 C ($SD = 2.28$, range 26.1–36.8) and on cooler days ($T_{esu} < 30$ C), body temperatures averaged 24.4 C ($SD = 2.57$, range 17.9–30.6). Analysis of variance indicated that body temperatures varied according to sex and to month (Table 2). Significant variation among months resulted from low T_b s during May (Table 3). Mean T_b for juveniles was also lowest in May, but, probably because of the low sample size, the difference was not statistically significant (ANOVA, $F_{1,27} = 1.17$, $P > 0.35$). Overall mean T_b s for adults (29.2

TABLE 1. Body temperature, operative temperatures, air temperature, percent exposure, and the relationship of T_b to air and operative temperatures (simple r^2) according to month. Exposure is the percent of total body length exposed to direct solar radiation.

| Month | n | Mean | | | | % exposure | | | Prop. of variance in T_b explained by | | |
|-------|-----|-------|-----------|-------|-----------|------------|-----------|------|---|-------|-----------|
| | | T_b | T_{esn} | T_a | T_{esu} | \bar{x} | % of obs. | | T_{esn} | T_a | T_{esu} |
| | | | | | | | 0 | >50 | | | |
| April | 32 | 30.3 | 29.8 | 29.4 | 32.1 | 15.2 | 62.5 | 15.6 | 0.91 | 0.83 | 0.59 |
| May | 58 | 26.6 | 27.2 | 24.9 | 28.3 | 20.5 | 56.9 | 18.9 | 0.92 | 0.84 | 0.87 |
| June | 41 | 29.4 | 29.7 | 28.7 | 33.5 | 4.5 | 80.5 | 2.4 | 0.94 | 0.95 | 0.85 |
| July | 56 | 29.7 | 29.6 | 29.1 | 34.4 | 0.3 | 96.4 | 0.0 | 0.97 | 0.98 | 0.88 |
| Aug. | 18 | 33.2 | 32.9 | 32.3 | 36.4 | 6.1 | 77.8 | 5.6 | 0.85 | 0.72 | 0.40 |
| Sept. | 15 | 30.2 | 30.3 | 30.1 | 34.8 | 1.0 | 86.7 | 0.0 | 0.95 | 0.94 | 0.12 |
| All | 220 | 29.3 | 29.3 | 28.3 | 32.5 | 9.1 | 75.9 | 8.2 | 0.93 | 0.91 | 0.80 |

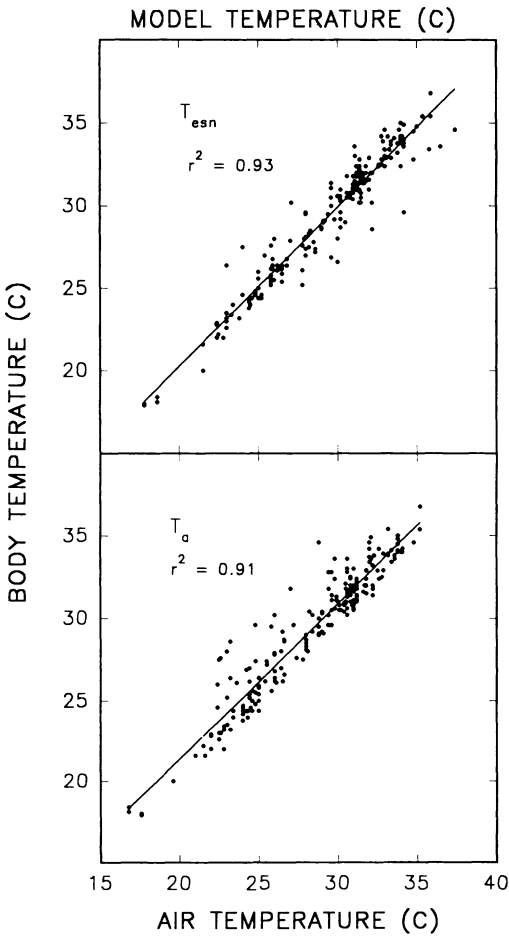


FIG. 1. The relationship between body temperature (T_b) and operative snake temperature (T_{esn}), and the relationship between body temperature (T_b) and ambient air temperature (T_a) in green snakes.

C, SE = 0.28) and for juveniles (29.8 C, SE = 0.75) were not statistically different (ANOVA, $F_{1,218} = 0.59, P > 0.40$). Adult females had higher mean T_b s than adult males in each month (Table 3) but the monthly difference was significant only in June when females maintained temperatures 2.4 C above that of males ($t = -2.11, P < 0.05, df = 36$). Adult males had greater variances in T_b s than adult females in most months (Table 3), but none of the differences was significant ($F_{max}, P > 0.05$). Mean T_b for juvenile males (28.6 C, SE = 1.63) was lower (1.6 C) than that for juvenile females (30.2 C, SE = 0.85) but the difference was not significant (ANOVA, $F_{1,26} = 0.78, P > 0.35$).

Figure 2 compares body temperatures to minimum temperatures available (T_a) and to maximum temperatures available (T_{esu}) in an early season cool month (May) and in a later season warm month (July). In May, the distribution of T_b s was shifted slightly to the right compared to that of T_a s. In July, the distribution of T_b s was similar to that of T_a s and was shifted to the left of those temperatures made possible by basking (T_{esu}). Within the range of T_b s exhibited by active snakes on cool, sunny days in May, T_b s were always less than available operative temperatures (T_{esu}) (Fig. 3A). The same pattern of $T_b < T_{esu}$ in active snakes was also true on the few cool, sunny mornings in June and July (Fig. 3B). Variation in mean operative temperatures vertically was ≤ 0.5 C on a cloudy day and ≤ 0.7 C on a sunny day except for exposed models at < 1 m (Fig. 4).

DISCUSSION

This study suggests that *O. aestivus* is not a strong heliothermic thermoregulator. The generally intermediate position of body temperature between T_a and T_{esu} suggests that some solar exposure occurs but the results of the regression analysis show that it contributes little (1%) to body temperature. Throughout most of the ac-

TABLE 2. ANOVA of body temperatures (T_b) of all *O. aestivus* and of adults according to sex and month.

| Source of variation | All snakes | | | | Adult snakes | | | |
|---------------------|------------|-------------|------|--------|--------------|-------------|------|--------|
| | df | Mean square | F | P | df | Mean square | F | P |
| Sex | 1 | 54.48 | 4.54 | 0.034 | 1 | 54.03 | 4.50 | 0.035 |
| Month | 5 | 92.01 | 7.68 | <0.001 | 5 | 85.62 | 7.13 | <0.001 |
| Sex × month | 5 | 3.70 | 0.31 | 0.907 | 5 | 1.69 | 0.14 | 0.983 |
| Residual | 208 | 11.98 | | | 180 | 12.01 | | |

tivity season, green snakes usually avoided higher body temperatures resulting from solar exposure and permitted their body temperatures to track cooler shaded air temperatures. The behavior of active snakes appeared similar throughout an approximate 19 C range in T_b , and snakes were observed attempting capture of prey at T_b s as low as 22 C. Mean body temperatures of active snakes were always below mean maximum operative temperatures, including occasions when T_b s were well below the probable preferred body temperature of approximately 30 C. In May, the coolest month of this study, snakes did not take full advantage of available higher operative temperatures resulting in a significantly lower mean T_b compared to other months. Although I commonly observed basking by other snakes on the study area (*Nerodia sipedon*, *N. erythrogaster*, *T. sirtalis*), I observed basking (exposed inactive snakes) in *O. aestivus* on only three occasions. The higher exposure values for green snakes obtained in April and May appeared to result not from basking per se, but from foraging in more exposed microhabitats.

Why do green snakes bask rarely? There are at least two non-exclusive possibilities. One possibility is that a slender 10–25 g snake with a high surface-to-volume ratio and a high convective heat loss may be below the minimum size necessary for maintaining a body temperature significantly above air temperature without continuous exposure (Porter and Gates, 1969; Stevenson, 1985). Continuously exposed snake models were capable of maintaining temperatures averaging <4 C above air temperatures

and rapidly lost heat when removed from exposure. In addition, small perches such as those chosen by green snakes (Plummer, 1981; Goldsmith, 1984) may not be significant sources of conductive or boundary layer convective heat (Bakken, 1989). In addition to biophysical grounds, another possibility for the lack of basking involves antipredator strategy. Green snakes eat frequently as a result of foraging daily throughout most daylight hours (Plummer, 1984, 1991), and thus potentially expose themselves to various diurnal predators such as bluejays, *Cyanocitta cristata* (Sledge, 1969; Hammerson, 1988; Plummer, 1990). An observation consistent with an antipredation hypothesis is that green snakes normally do not ascend into their primary microhabitat of shoreline vegetation in the spring until the vegetation is nearly completely leafed out (pers. obs.).

Variation in perch heights selected by green snakes did not appear to have significant thermal consequences. Operative temperatures were noticeably higher (>1.0 C) only close to the water (<1 m) where use by green snakes was uncommon (Plummer, 1981; present study). Furthermore, temperatures were increased primarily in fully exposed models on sunny days, requiring body exposure not exhibited by green snakes. Because of the high specific heat of water, temperature extremes and vertical temperature gradients may be moderated compared to those in similarly structured vegetation in terrestrial habitats. Operative temperatures on the ground surface in close proximity were up to 20 C warmer on sunny days in August. Despite being moderated thermally compared to ter-

TABLE 3. Mean monthly T_b (C) for all *O. aestivus* and for adult males and females. Data are mean \pm 1 SD (N). T_b values in May are significantly lower than in other months ($P < 0.05$, Scheffé).

| Month | All snakes | Adult males | Adult females |
|------------|-----------------------|----------------------|-----------------------|
| April | 30.3 \pm 3.40 (32) | 30.0 \pm 2.95 (19) | 31.3 \pm 3.79 (10) |
| May | 26.6 \pm 3.64 (58) | 25.9 \pm 4.50 (19) | 27.1 \pm 2.83 (35) |
| June | 29.4 \pm 3.53 (41) | 27.9 \pm 3.52 (14) | 30.3 \pm 3.29 (24) |
| July | 29.7 \pm 4.09 (56) | 28.6 \pm 4.83 (19) | 30.2 \pm 3.77 (25) |
| Aug. | 33.2 \pm 1.58 (18) | 32.4 \pm 1.59 (3) | 33.4 \pm 1.68 (13) |
| Sept. | 30.2 \pm 1.97 (15) | 29.7 \pm 2.42 (4) | 30.4 \pm 1.41 (7) |
| All months | 29.3 \pm 3.90 (220) | 28.4 \pm 4.19 (78) | 29.7 \pm 3.65 (114) |

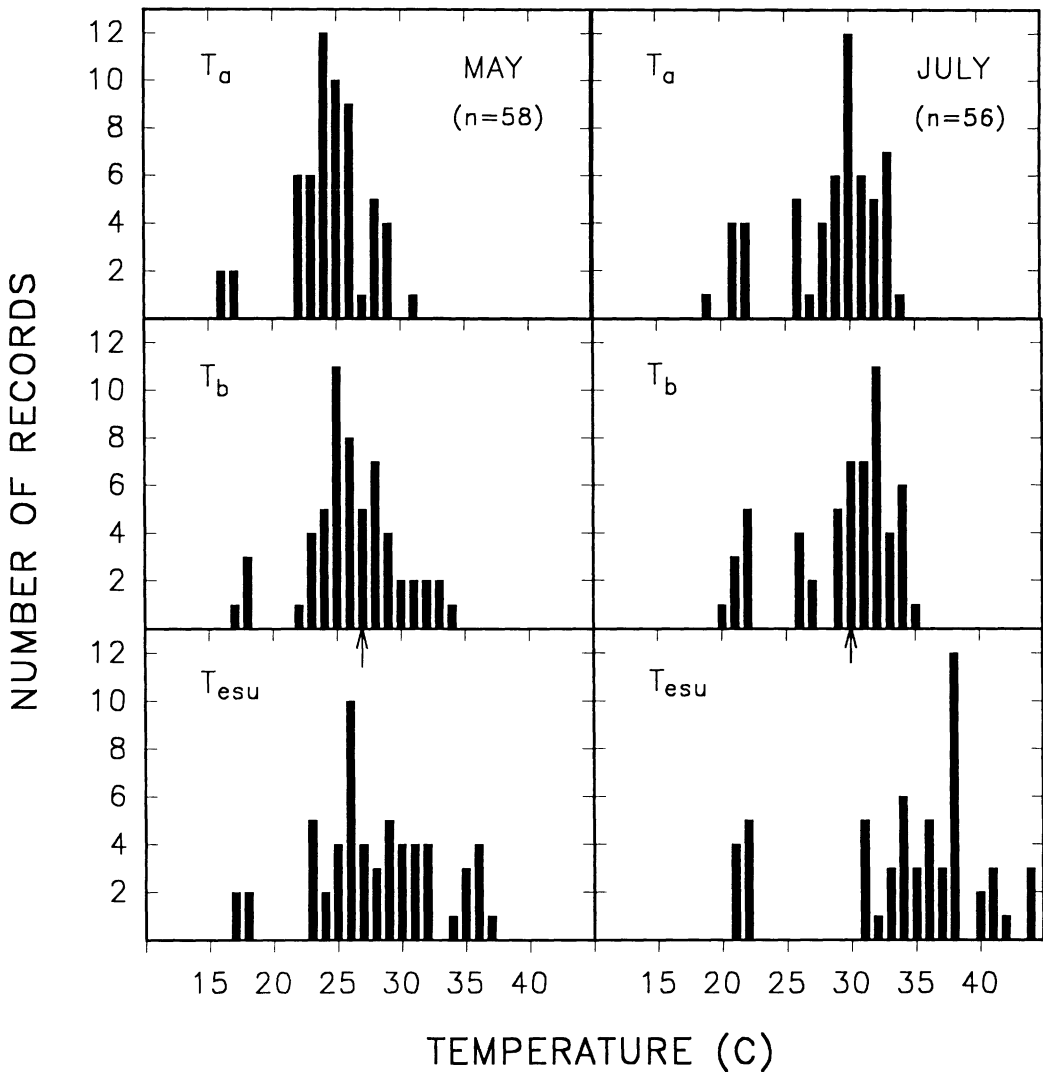


FIG. 2. Distribution of body temperatures (T_b) of green snakes compared to the distribution of ambient air temperatures (T_a) and maximum operative temperatures (T_{esu}) in May and in July. Arrows indicate mean body temperatures of snakes.

restrial environments, sunlit aboveground perches may be significant heat sources for small arboreal animals. Bakken (1989) found that operative temperatures of animal models placed on arboreal perches increased with increasing diameter of perch. It is known that *O. aestivus* prefers perches with small diameters (Plummer, 1981; Goldsmith, 1984), but the extent, if any, to which the thermal properties of physical perches influence perch selection by green snakes is unknown.

The mean activity temperature of *O. aestivus* (29.3 C) falls within the range of the majority of preferred body temperatures published for snakes (28–34 C) and is near the frequently re-

ported temperature of 30 C (Avery, 1982; Lillywhite, 1987; Peterson, 1987; Rosen, 1991). Adult females had higher T_b s than adult males in June when ovulation occurs and oviposition begins (Plummer, 1984). Finding a similar sexual difference in *Thamnophis*, Gibson and Falls (1979) argued that gravid females thermoregulate more intensively than males.

Some researchers have stressed the need for work on the thermal biology of daily and seasonally inactive periods of reptiles (Huey, 1982; Peterson, 1987; Huey et al., 1989). During the period of this study, it did not appear that the behavior of green snakes was constrained by low environmental temperatures. However,

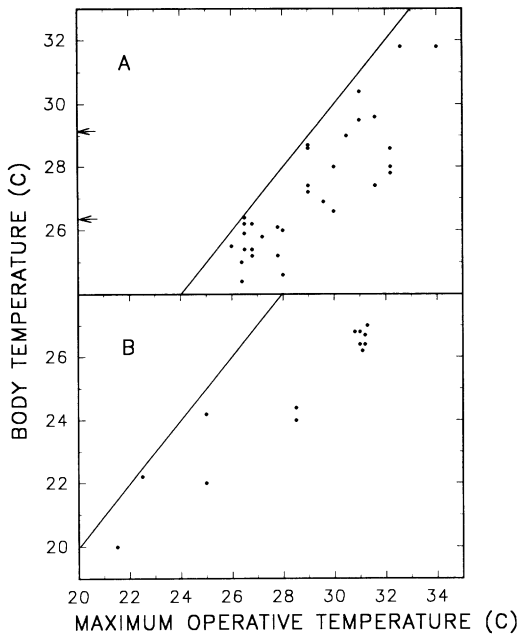


FIG. 3. (A) The relationship of body temperature (T_b) and maximum operative temperature (T_{esu}) available on sunny days in May (maximum operative temperatures ≤ 35.0 C). Lower arrow indicates the mean activity temperature in May; upper arrow indicates the annual mean activity temperature. (B) The relationship of body temperature (T_b) and maximum operative temperature (T_{esu}) available on cool ($T_a < 27$ C), sunny mornings in June-July. For A and B, the diagonal line denotes $T_b = T_{esu}$. "Sunny" means that sufficient sun was available to elevate maximum operative temperatures at least 1.0 C above ambient air temperatures (T_a).

further study earlier in the season immediately after emergence from winter dormancy may reveal thermal constraints on behavior. Such a study may be difficult because green snakes typically are not found in their characteristic activity season habitat (bushes and trees) until late April. Earlier in the season (late March-mid April), when low thermal constraints would be most likely, the few snakes that are found are generally located under ground debris (Plummer, unpubl.). Terrestriality early in the season may, in fact, confer a thermal advantage as T_s probably would be greater than in arboreal environments. In 1987, green snakes were found commonly in trees earlier (16 April) than in other years. Air temperatures from May-September 1987 were typical for the locality, but April 1987 was unusually warm, with a mean T_a higher than that of May. Furthermore, mean T_a exceeded a ten year mean maximum daily air temperature for April by 7.5 C, whereas mean T_a was within 3 C of the 10 year mean maximum

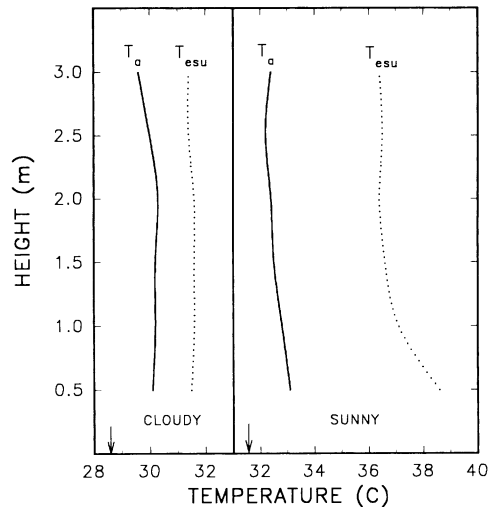


FIG. 4. Vertical profiles of mean shaded air temperature (T_a) and mean maximum operative temperature (T_{esu}) for an afternoon with still air on a cloudy day and on a sunny day. Arrows indicate water temperatures under each profile.

air temperatures for each month from May to September (Plummer, 1983). Operative temperatures for various microenvironments in April were also more similar to those of June and later months (Table 1). Thus, the body temperatures I obtained in April in expectation of representing early season post-dormancy thermal behavior of green snakes were probably atypical.

Opheodrys aestivus ranges north of my study area into higher latitudes (Conant and Collins, 1991) where, coincidentally, the most thorough studies of snake thermal ecology have been done, and where thermoregulation may be intensified compared to that in more southern latitudes (Rosen, 1991). In the present study, the lack of heliothermic thermoregulation and the lack of a daily pattern of emergence, basking, activity, and cooling reported for many snakes may be a function of the relatively warm humid climate where there is little daily variation in temperature for most of the activity season. In such a thermally-favorable environment, precise thermoregulation may be relaxed in lieu of other activities. A comparative study of the thermal ecology of green snakes in a cooler climate would be useful to confirm the role of basking and the extent of thermoregulation in this species.

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