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Thermal Biology of the Common Garter Snake *Thamnophis sirtalis* (L.)

I. Temporal Variation, Environmental Effects and Sex Differences

A. Ralph Gibson[1] and J. Bruce Falls
Department of Zoology University of Toronto, Toronto, Ontario M5S 1A1, Canada

Summary. This paper describes the thermal biology of the common garter snake, *Thamnophis sirtalis*, a diurnal, viviparous colubrid. The body temperatures of snakes caught in the field are cooler and more variable early and late in the day, and early and late in the active season. On sunny days in midsummer, females average about 1 C° warmer than males. The frequency distribution of body temperatures for females is skewed to the left, whereas that for males is nearly symmetrical. Under cloudy skies, body temperatures are lower and more variable than under sunny skies, and the difference between males and females disappears. This and related considerations suggest to us that males are less determined, or less precise, thermoregulators than are females. Air and ground-surface temperatures, and snout-vent length, are poor predictors of body temperature. In contrast with other studies, we found no indication that the body temperatures of gravid and nongravid females differ either in mean or variance. We discuss our conclusions in light of previous studies and identify in the latter, analytical shortcomings which we believe hinder interpretation and synthesis.

Introduction

Much of the research effort applied to the ecology and physiology of lizards and snakes has focussed on the temperature relations of these animals. Characteristically, even general or cursory studies have summarized an array of body temperatures. However, in this as in all areas of squamate biology, lizards are far better known than are snakes. The reviews of Cloudsley-Thompson (1971) and Heatwole (1976) underline this imbalance: in each, the treatment of temperature relations is organised largely around the biology of the Lacertilia, and is illustrated with examples from this group. As others have noted, the

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[1] Present address: Department of Ornithology Royal Ontario Museum 100 Queen's Park Toronto, Ontario M5S 2C6, Canada

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Ophidia are cryptic, both in appearance and in behaviour, and thus are difficult animals to study. The use of temperature-sensitive radio transmitters can be expected to alleviate this problem somewhat, but application of the technique has only begun (e.g. Brown, 1973; Naulleau and Marques, 1973; Parker, 1974).

Although it likely will prove challenging to substantially advance our understanding of the thermal relations of snakes, we believe the effort can be justified. The Ophidia, a group of highly derived reptiles, are distinctive morphologically and ecologically. It would be surprising, we feel, if snakes were indistinguishable from lizards in their temperature relations. Indeed, one possible basic difference has been suggested: on average, snakes appear to maintain lower body temperatures than do lizards (Brattstrom, 1965; St. Girons and St. Girons, 1956). In this context, our goal is quite elemental: viz., to describe general aspects of the thermal biology of the common garter snake, *Thamnophis sirtalis*. Specifically, we explore diurnal and seasonal variation in body temperature, as well as the effects of size, sex, reproductive status and environmental variables on body temperature. Major emphasis is placed on the integration of our findings with those of previous published studies of the thermal relations of snakes. The present paper forms part of a larger study (Gibson, 1978) of the ecological significance of a striped-melanic colour polymorphism in *T. sirtalis*. A companion paper (Gibson and Falls, 1979) will concern itself with the thermoregulatory consequences of this polymorphism.

Materials and Methods

The data presented herein were obtained in the course of a mark-recapture study carried out at the eastern end of Long Point, Norfolk County, Ontario (lighthouse at the eastern tip of the point: 42°33′N, 80°03′W). This point is a sand spit extending about 40 km east into Lake Erie from the north shore. The easternmost 3 km of the point, which included our main study area, are lightly wooded, with small cottonwoods (*Populus deltoides*). Most of this area is quite open and supports a light growth of short (<50 cm) grass. Where it is drier, there is bunched grass and unvegetated sand. Numerous shallow ponds are interspersed among vegetated sand ridges, most of which vary from 1 to 3 m in height. The study area tapers evenly from a maximum width of about 400 m at its western edge, and of course is bounded on all remaining sides by Lake Erie.

We found snakes by searching on foot, and captured them by hand. Body temperature was estimated with a flexible small-animal probe mounted on a Yellow Springs Instruments Telethermometer (model 43TD). When a snake was located, the observer retreated a few meters and prepared the telethermometer. He then attempted to capture the snake with gloved hands and to quickly take its rectal, not cloacal, temperature (hereafter body temperature). If there was any delay in relocating or capturing the snake, or if it fled into water, any temperature data collected were excluded from the quantitative analyses which follow.

We also measured ground surface temperature (unshaded), and air temperature (in our shade, about 1.3 m above ground) with the telethermometer. Cloud cover at the time of capture was described.

Field work took place primarily during May through August from 1971 to 1974; some additional search occurred in September and October mainly in 1971 and 1973. Search effort was distributed so as to cover the entire study area but was concentrated on regions that proved most productive. Most searches were in the morning and early afternoon. In the hot part of the summer, we searched in the early morning before snakes became inactive.

Statistical methods used are those of Snedecor and Cochran (1967) and Sokal and Rohlf

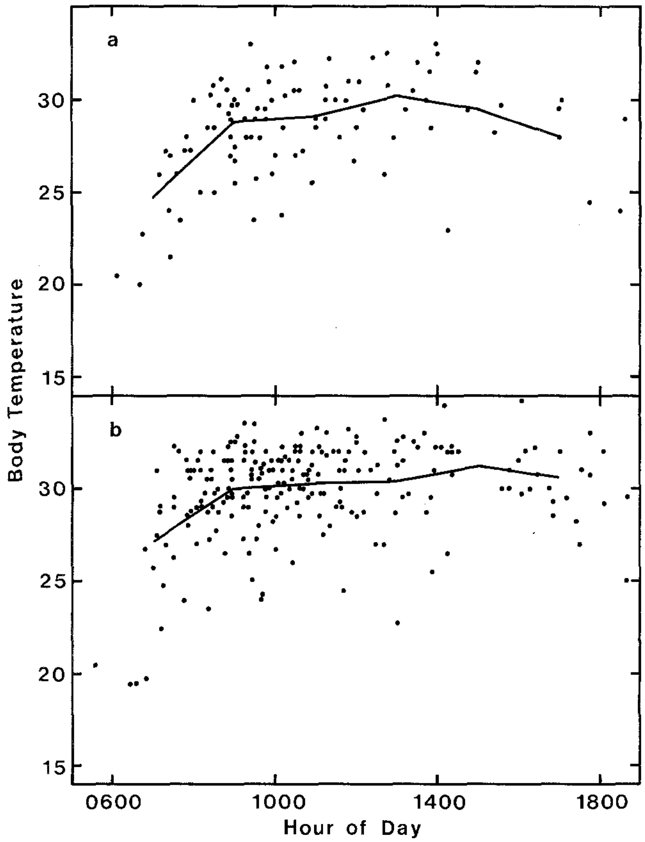

Fig. 1a and b. Body temperature of *T. sirtalis* plotted as a function of hour of day. Temperature readings (°C) are taken from snakes (**a** = males, **b** = females) captured under sunny skies from June through August. Heavy lines connect two-hour means; see Table 1 for summary statistics

(1969). Use of the term "borderline significance" refers to the range $0.025 < P < 0.075$. To conserve space, we have not included some of the scatter diagrams mentioned beyond. The interested reader may consult Gibson (1978) for such figures, or may request copies form the authors.

Results

Diurnal Variation

Body temperatures of snakes captured in the field on sunny days during the summer months of June, July and August were classified into consectutive two hour periods from 0600 until 2000 h (Eastern Standard Time throughout); males and females were considered separately (Fig. 1, Table 1). Results of tests of diurnal variation in body temperature (Table 1), indicate that, in both sexes, the period from 0800–1600 h is homogeneous. Before 0800 h and after 1600 h (especially after 1800 h in females) snakes are cooler. The variability of body temperatures increases during these early and late periods; this perhaps is most

Table 1. Daily variation in body temperature of snakes captured on sunny days from June through August at Long Point, and results of across-hour tests of differences in median temperature (Kruskal-Wallis procedure). $\bar{x}$ = mean body temperature; s^2 = sample variance; n = sample size

	Male			Female		
Hour	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
0600–0800	24.7	7.90	13	27.1	15.44	27
0800–1000	28.8	4.12	39	30.0	4.33	82
1000–1200	29.1	4.37	24	30.3	3.09	65
1200–1400	30.2	3.76	15	30.4	5.90	32
1400–1600	29.5	9.00	8	31.2	4.04	11
1600–1800	28.0	6.15	4	30.6	3.65	17
1800–2000	26.5	12.53	2	28.9	8.41	4
Kruskal-Wallis test						
0600–1800						
H		28.12			24.52	
DF		5			5	
P		$P<0.005$			$P<0.005$	
0800–1600						
H		5.90			5.59	
DF		3			3	
P		$0.05<P<0.10$			$0.05<P<0.10$	

meaningful during the 0600–0800 interval. Especially in females, sample variances at this time are conspicuously increased.

Body temperatures of male and female snakes were compared during the period of minimal hour effect, i.e. 0800–1600 h. The body temperature of female snakes is significantly greater than that of males (Table 2); in this period, the average difference is 1.0 C°. The frequency distributions of these temperatures for the two sexes appear in Fig. 2. The distribution for males is slightly but significantly skewed to the left; there is no significant kurtosis. The distribution for females is strongly and significantly skewed to the left. The range of temperatures spanned by the two sexes is almost identical.

Seasonal Variation

Body temperatures of snakes obtained in the field on sunny days between the hours 0800 through 1600 were classified according to month of capture; males and females were considered separately (Fig. 3, Table 3). Results of tests of seasonal variation in body temperature (Table 3) indicate significant across-month variation both for the entire period May through October, as well as for the more restricted period May through August. This trend obtains in males and in females. It is interesting to note that the variance of the monthly samples changes in a manner analogous to that of the hourly samples. In both male and female, spring and fall are periods of low and variable body

Table 2. The effect of cloud cover and sex on the body temperature of snakes captured during June, July and August between 0800 and 1600 h. The Wilcoxon procedure here tests differences in median temperature. The F ratio is a two-tailed test of homogeneity of variances. See Table 1 for abbreviations

	Male			Female		
	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
Sun	29.2	4.67	86	30.2	4.16	191
Cloud	27.5	9.80	32	26.8	18.37	92
Sun-cloud comparison:						
Wilcoxon two-sample test						
t	2.65			7.15		
P	$0.001 < P < 0.01$			$P < 0.001$		
F-test						
F	2.09			4.41		
P	$0.01 < P < 0.02$			$P < 0.001$		
Sex comparison:						
sunny skies						
Wilcoxon two-sample test						
t			4.09			
P			$P < 0.001$			
F test						
F			1.12			
P			$0.50 < P < 0.75$			
cloudy skies						
Wilcoxon two-sample test						
t			0.70			
P			$0.40 < P < 0.50$			
F test						
F			1.87			
P			$0.05 < P < 0.10$			

temperatures. October provides a unique situation: in this month alone the average body temperature of males exceeds that of females. Although sample sizes are not large, the more deviant mean (female) is associated with the larger sample!

Environmental Effects

The effect of cloud cover on the thermal biology of garter snakes was assessed for the summer months of June, July, and August, between the hours of 0800 and 1600. The body temperature of snakes caught when the sky was overcast, and insolation was much reduced in intensity, was compared with that of snakes caught under sunny, clear conditions. The sexes were treated separately. The results appear in Table 2. In both male and female, body temperatures are lower

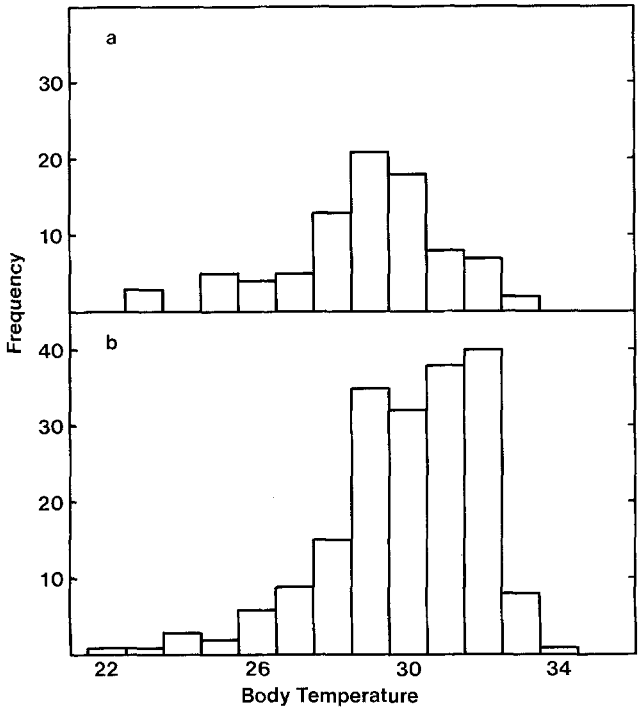

Fig. 2a and b. Frequency histograms of body temperature in *T. sirtalis*. Temperature readings (°C) are taken from snakes captured between 0800 h and 1600 h under sunny skies during June, July and August. **a** males: $g_1=-0.686$, $t=2.64$, $0.01<P<0.02$; $g_2=0.423$, $t=0.82$, $0.40<P<0.50$. **b** females: $g_1=-1.027$, $t=5.82$, $P<0.001$; $g_2=1.418$, $t=4.04$, $P<0.001$. Additional summary statistics appear in Table 2. For the histograms, the class interval is 1.0 C°; abscissa values are lower class boundaries

on cloudy days than on sunny, clear days. Similarly, in both sexes the variability is increased under cloudy skies, dramatically so in females.

The rather considerable variation in body temperatures observed in field captures, even during the restricted period of 0800–1600 h within the summer months, prompted us to examine the influence of substrate and air temperatures. Body temperature was regressed on the two environmental temperatures using stepwise multiple regression; the sexes were treated separately (Table 4). In males, both variables enter significantly and of course the overall test is significant. Nevertheless, R is not large; only about 26% of the variation in body temperatures can be accounted for by these two environmental temperatures. In females, the contribution made by air temperature achieves only borderline significance although the overall test is highly significant. Here the two environmental temperatures "explain" only about 17% of the body temperature variation. The degree of independence among these three temperature variables, inplied by these analyses, was evident in bivariate scatter plots (figures not included). The correlations genuinely are low, and are not merely "spoiled" by one or a few outliers.

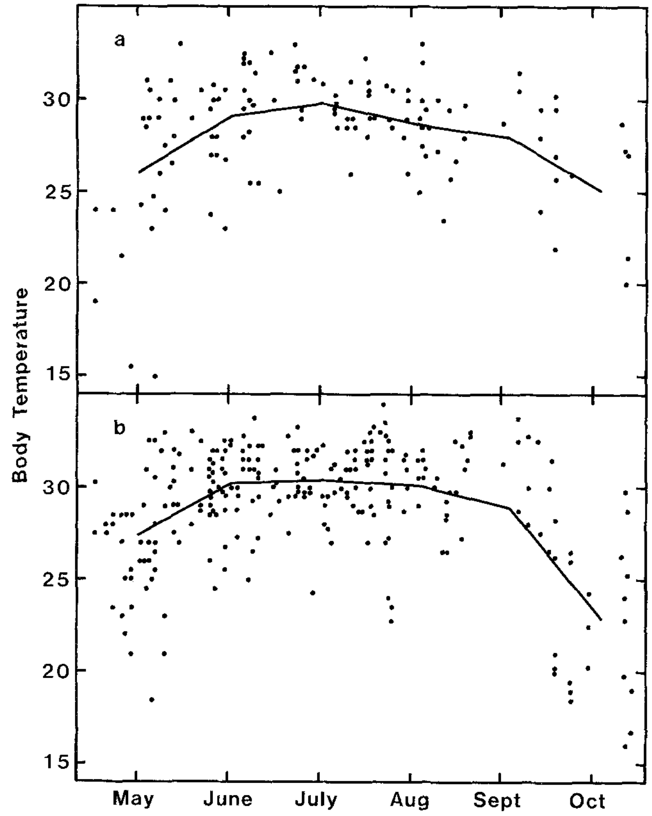

Fig. 3a and b. Body temperature of *T. sirtalis* plotted as a function of time of year. Temperature readings (°C) are taken from snakes (**a** = males, **b** = females) captured under sunny skies between 0800 h and 1600 h. Heavy lines connect monthly means; see Table 3 for summary statistics

Size Effects

The influence of "size" on body temperature in garter snakes was examined for captures made during the summer months of June, July and August between the hours of 0800 and 1600. Snout-vent length was used as the size variable. Non-parametric correlation assessed the relationship between these two variables; the sexes were treated separately.

In both male and female there is no evidence of a significant correlation between body temperature and snout-vent length (males: Spearman's rank order correlation coefficient, $r_s = 0.087$, DF = 67, $t = 0.72$, $0.40 < P < 0.50$; female: $r_s = 0.095$, DF = 132, $t = 1.10$, $0.20 < P < 0.40$). This independence is quite obvious in examination of scatter plots of the two variables (figures not included). There is perhaps a suggestion that the long snake – cool snake sector is underpopulated. Nevertheless, high temperatures are associated with snakes of all lengths in both sexes.

Table 3. Seasonal variation in body temperature of male and female snakes captured on sunny days during the hours 0800 through 1600, and results of across-season tests of differences in median temperature. See Table 1 for abbreviations

	Male			Female		
	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
May	26.0	22.47	24	27.4	10.82	55
June	29.1	6.40	29	30.2	3.88	77
July	29.8	3.10	28	30.4	2.76	67
August	28.7	4.16	29	30.1	6.76	47
September	28.0	8.07	12	28.9	18.40	20
October	25.1	12.25	6	22.9	16.40	20
Kruskal-Wallis test						
May–October						
H		20.72			71.33	
DF		5			5	
P		$P<0.005$			$P<0.005$	
May–August						
H		13.50			35.28	
DF		3			3	
P		$P<0.005$			$P<0.005$	

Gravidity Effects

The influence of reproductive state on the body temperature of female snakes was examined for captures made on sunny days during the months of June and July, between the hours of 0800 and 1600. Females were classified as gravid or nongravid; body temperatures of females in the two reproductive categories do not differ significantly, either in median or in variability (Table 5).

Discussion

Diurnal Variation

Under sunny skies in the summer, the body temperatures of garter snakes are high and homogeneous over much of the day. Early in the morning and in the late afternoon and beyond, body temperatures are lower. This pattern of change is most naturally interpreted as an initial period of emergence and basking, during which body temperatures are raised from over-night low values to within a desired range, succeeded by a long interval during which behavioural adjustment maintains body temperatures within this range, and completed by a period of declining insolation during which body temperatures necessarily drop. The period of relative constancy of mean body temperature is most well defined in females.

The increased variance associated with lower mean body temperature in

Table 4. Results from the multiple regression of snake body temperature on two environmental temperatures. Ts = substrate temperature; Ta = air temperature; Tb = body temperature

Males	
Simple correlation coefficients:	
Ts with Ta = 0.18	
Ts with Tb = 0.42	
Ta with Tb = 0.37	
Multiple regression coefficient	R = 0.51
Goodness of fit (R^2)	$F(2, 82) = 14.57$
	$P < 0.001$
Partial correlation coefficients:	
Ts with Ta = 0.03	
Ts with Tb = 0.38	
Ta with Tb = 0.33	
Females	
Simple correlation coefficients:	
Ts with Ta = 0.14	
Ts with Tb = 0.39	
Ta with Tb = 0.18	
Multiple correlation coefficient	R = 0.41
Goodness of fit (R^2)	$F(2, 186) = 18.67$
	$P < 0.001$
Partial correlation coefficients:	
Ts with Ta = 0.07	
Ts with Tb = 0.37	
Ta with Tb = 0.14	

Table 5. The effect of reproductive state on the body temperature of female snakes captured on sunny days during June and July, between the hours of 0800 and 1600. See Table 1 for abbreviations, and Table 2 for an explanation of the tests

Non gravid			Gravid		
$\bar{x}$	s^2	n	$\bar{x}$	s^2	n
30.1	3.93	56	30.5	2.94	88
Wilcoxon two-sample test					
t		1.18			
P		$0.20 < P < 0.40$			
F test					
F		1.34			
P		$0.20 < P < 0.50$			

the early morning has one obvious explanation. The body temperatures reached before morning emergence are substantially below both the mean value maintained during the plateau period and the minimum values usually observed during that time. The first two-hour interval spans both emergence and attainment of plateau values (i.e. the time required to warm is short with respect to two hours) and thus is expected to display greater variance. By this argument, a more nearly instanteous assessment of body temperatures would be expected to reveal no dramatic change in variance.

The scatter diagram of temperatures for males (Fig. 1) does not militate against this view. Maximum observed temperatures rise over the first two-hour period and moreover, do not appear to plateau until almost 1000 h, near the end of the second two-hour period. Females present a very different picture. Temperatures near the maximum observed for the sex occur at about 0700 h, about midway through the first two-hour period. The lower mean and increased variance associated with this period owe much to a few very early, very low temperatures. Thus, after about 0700 h in the summer, females can attain a desired range of body temperatures.

Snakes did not seem to choose particular basking sites in early morning. Some snakes were located in sites protected from the wind where the ground was inclined more nearly normal to the sun, and early one morning, with the sun near the horizon, we observed a snake that had climbed 15–20 cm into a small cedar, presumably to better intercept the weak insolation. However, with disconcerting frequency, we encountered snakes "basking" in thermally much less desirable locations, and not infrequently where a move of just a metre or two apparently would result in a considerable improvement. On midsummer mornings there is only a short period after sunrise before the sun is high enough to rapidly warm a snake to desired levels. Thus there may be only a transient thermal advantage to superior basking sites, an advantage insufficient to outweight the effort and risk involved in locating them. Moreover, if a snake is basking in order to attain a desired temperature range prior to foraging, then there seems little reason in reaching that level much before the environment through which it must forage generally is warm enough to permit such a temperature to be maintained.

The variance in body temperatures during the plateau period has no precise explanation. Certainly the general weather would exert some effect, but, as discussed more fully below, two potentially influential variables here (air and substrate temperature) accounted for very little variation in body temperature. The leopard frog, *Rana pipiens*, is the principal prey species of adult *T. sirtalis* at Long Point (personal observation) and, presumably as a consequence, garter snakes frequently were captured both about the periphery of, and occasionally actually in, small ponds. Evaporative cooling resulting from foraging in wet or damp habitats would tend to lower a snake's body temperature. It may be, then, that the particular temperature profile observed for snakes between the hours of 0800 and 1600 on sunny days in the summer results from a combination of basking and foraging activities. Most snakes were detected as they flushed underfoot and it was not possible to assign an activity to each capture. Thus, with the data at hand, we cannot test the supposition. It was obvious to us, however, that the body temperature of wet snakes characteristically was low.

Diurnal temperature changes and associated behaviour in lizards have been studied rather intensively (for example, see Cloudsley-Thompson, 1971 and Heatwole, 1976, and references therein), aided in no small part by the relative ease with which lizards are observed. The tripartite pattern of diurnal temperature changes we observed in *T. sirtalis* appears to be the norm in lizards. Snakes are far less well known than are the Lacertilia however, and for no other species of ophidian does there appear to be information similar to that presented here. Body temperatures frequently are obtained in the course of field ecological studies of snakes, but none of these describes diurnal variation.

The only data available for comparison have been obtained using temperature-sensitive radio transmitters (Brown, 1970; Brown, 1973; Dill, 1972; Goodman, 1971; Johnson, 1972, 1973; Johnson et al., 1975; McGinnis and Moore, 1969; Moore, 1978; Naulleau and Marques, 1973; Osgood, 1970; Parker, 1974). Telemetry promises to yield considerable insight into many aspects of snake biology, but application of the technique is yet in its infancy. Many of the studies have been on snakes confined to small artifical or "semi-natural" enclosures. Much of the monitoring of free-ranging snakes has been of short duration, and of species (water snakes, large boids) not easily compared the temperate zone *T. sirtalis*. The work of Brown (1973) and Parker (1974) is exceptional in these regards. The authors placed transmitters in three species of colubrid snakes dispersing from a communal den in northern Utah and were able to record activities and temperatures for periods of up to 40 days. A tripartite pattern of behaviour and temperature, such as described in the present study, characterizes at least active individuals. The ability of Brown and Parker to locate inactive individuals underground or otherwise concealed under shelter revealed more complex patterns that can have no parallel in the data presented here for *T. sirtalis*. As well there was no indication that snakes active in the hot and dry habitat of nothern Utah necessarily would encounter cooler conditions while foraging; indeed the opposite probably prevails. Nevertheless, their observations do suggest that snakes can maintain high and fairly constant body temperatures over much of the day.

The body temperature information obtained from telemetric monitoring of snakes must be interpreted with some caution. The transmitters used in these pioneering studies have been rigid structures and frequently of an appreciable size relative to the snake. If placed in the stomach, the transmitter usually is force fed to the animal. In some cases a string then has been tied around the snake's body and sutured to a ventral scale to prevent regurgitation. Alternatively, transmitters have been inserted "surgically" into the coelom. None of the studies has presented evidence, or even argument, that would allow assessment of the extent to which the technique is influencing the results. Our general ignorance of the normal behavioural and thermoregulatory activities of snakes will make it difficult to detect even moderate disruptions therefrom.

Seasonal Variation

The seasonal trend in body temperatures of snakes caught under sunny skies between 0800 and 1600 h is quite analogous to the diurnal trend. Early and late in the active season, body temperatures are low and variable; the higher means in June, July and August are associated with reduced sample variances. Again, the midregion of the "tripartite" pattern more nearly describes a "plateau" in females than in males.

Heatwole (1976) notes that seasonal variation in mean body temperatures has been reported for several species of lizards. The possible explanations he provides fall into two categories: either the thermal environment in spring and fall does not permit the animal to attain the desired range, or the temperature preferences themselves change. The predictable decrease in insolation intensity and increase in air temperature variability associated with spring and fall, at least at higher latitudes, parsimoniously and more nearly ultimately accounts for the observed pattern in *T. sirtalis.* Seasonal changes in temperature preferences, themselves consequences of seasonality, do not easily account for variation in sample variances.

Several field studies have described seasonal variation in the body temperatures of snakes (Carpenter, 1956; Clark, 1970; Hirth and King, 1969; Stewart, 1965). None of these has explicitly excluded the influence of diurnal patterns or weather, and some have not distinguished between male and female. Carpenter (1956) reports lower temperatures for *T. sirtalis* captured in April through June than in July through September. Sample variances are not provided but the range is must greater in the early period. The sex ratio in this population favours males early in the year and females in midsummer (Carpenter, 1952). If the sexual differences in body temperatures described in the present study prove general, part of Carpenter's "seasonal" differences may reflect the different proportions of males and females in the two samples. Carpenter also studied *T. sauritus* and *T. butleri* at the same locality. Butler's garter snake shows a pattern similar to that reported for the common garter snake, but body temperatures of the ribbon snake do not appear to differ between the two seasons, either in mean or variance. Stewart (1965) studied the temperature relation of *T. sirtalis* and *T. ordinoides* in northwestern Oregon. The climate at this site is sufficiently mild that *T. sirtalis* can be captured during all months of the year, and for this reason, presumably, the author classified body temperature readings into winter (October through April) and summer (May through September) periods only. For both species, and within sex categories, winter temperatures are consistently, and generally significantly, lower than summer values. Sample variances are not provided. Readings obtained under different weather conditions were combined and thus part of the "seasonal" differences may be due to more frequent occurrence of cloudy weather during the winter period. In his study of worm snakes, *Carphophis vermis*, Clark (1970) found low body temperatures in spring and fall and higher temperatures in summer. The magnitude of the seasonal differences suggests significance but sample sizes are small. As in Carpenter's (1956) study, a greater range is associated with a lower mean. Weather and diurnal effects are considered by Clark. Hirth and King (1969) report spring, summer and fall temperatures for three species of snakes in northwestern Utah. Diurnal, weather and sex effects are combined in the "Dice-grams" presented. In all three species, mean body temperatures are lower, and the ranges greater, in spring and fall than in summer, but these comparisons are not tested. Only in one species is a clear difference evident: the mean body temperature of the spring sample of *Crotalus viridis* is substantially lower than either the summer or fall samples. Brown (1973) and Parker (1974) later studied two of these species (*Coluber constrictor, Masticophis taeniatus*), as well as a third (*Pituophis melanoleucus*), using telemetry. Both authors distinguished carefully between different activity categories and weather conditions but of necessity the number of snakes monitored was small. Their data indicate that the body temperatures of snakes thermoregulating on the surface on clear sunny days show very limited seasonal variation; in some cases, autumn temperatures were lower.

The data available for comparison with those presented here for *T. sirtalis* are of mixed quality, and in consequence summary is difficult. Of the relatively few species for which data of any sort are available, and these are temperate zone species, most appear to show lower, more variable "spring" and "fall" temperatures. The greater variance associated with the lower means suggests to us that opportunity and not preference, has changed. At Long Point, some body temperatures observed in spring (May) were near the maximum recorded throughout the active season, again suggesting that preferences do not change.

Environmental Temperature Effects

On sunny days during the summer months, between 0800 and 1600 h, air and substrate temperatures, as measured in this study, can account for little of the variation observed in snake body temperatures (26% in males, 17% in females). "Perfect" thermoregulation presumably would imply complete independence of body temperature from environmental effects (Huey and Slatkin, 1976). In this sense, males are less precise, or less determined, thermoregulators than are females.

Snakes the size of *T. sirtalis* have very limited capacity for thermogenesis (Bennet and Dawson, 1976; but see Aleksiuk, 1977). As a consequence, it is easy to increase the apparent explanatory power of air and substrate temperature. Immediately after emergence in the early morning, the snake and its environment are cool. Increasing the relative frequency of captures from this time of day would improve the correlation among body and environmental temperature variables. The same argument applies to captures from early and late in the active season, and from cloudy days. However, we consider the variation in body temperature that occurs under more restricted conditions (e.g. 0800–1600 h on sunny days in the summer) to be of greater interest, precisely because it cannot have the "global" explanations offered above. This "residual" body temperature variation requires careful explanation for it characterizes snakes involved in gestation, parturition, and reconstitution of fat body reserves (Gibson and Falls, MS in preparation).

Other workers have examined the relationships among body and environmental temperatures in the course of their ecological studies of snakes (Carpenter, 1956; Clark, 1970; Fitch, 1975). The data presented by Carpenter (1956) suggest a positive association between body and substrate temperatures for each of the three *Thamnophis spp.,* but no correlations are provided. In two of the three species, body temperature increases with substrate temperature in the low range, but reaches a plateau at higher substrate temperatures. This pattern characterizes many diurnal lizards (Heatwole, 1976). The two species studied by Clark (1970) and Fitch (1975) are fossorial or nearly so, and their body temperatures then might be expected to closely follow environmental temperatures. No plateau is particularly evident in the scatter diagrams relating body to air temperature in *Diadophis punctatatus* (Fitch, 1975). Clark (1970) reported a very high correlation (0.97) between body and substrate temperature in *Carphophis vermis.* These snakes were found beneath rocks and a close relationship is expected. In all three studies, temperatures are combined from all seasons, and all hours of the day.

In the present study, the mean body temperature of snakes captured under cloudy skies (during June, July and August, between 0800 and 1600 h) is lower than it is for those captured under sunny skies. This temperature drop, strongly expressed in both male and female, is quite understandable, but it is not so obvious why sample variances should increase. Two factors could be influential here. There certainly is greater variability in insolation among the capture conditions classified as cloudy than among those classified as sunny. Moreoever, snakes apparently can cool less rapidly than they warm (Brown, 1973; Dmi'el and Borut, 1972; Parker, 1974; Skoczylas, 1969) and the body temperature of an individual caught under overcast skies could be influenced by an earlier sunny period.

Most papers reporting body temperatures of snakes in the field have not explicitly treated cloud-cover effects; presumably data from both sunny and cloudy days have been combined. No clear generalizations emerge from the telemetric work of Brown (1973) and Parker (1974). If cloudy days exerted any influence on the body temperature of snakes on the surface, it was to lower them. Apparently environmental temperatures in this hot and dry desert habitat were sufficiently high to permit snakes to maintain normal body temperatures even under cloudy skies. Brown (1973) found moves to be more common on cloudy days. Reduced insolation intensity actually may be advantageous to snakes in midsummer.

Size, Sex and Gravidity Effects

During the plateau period on sunny days in the summer, there is no relationship in either sex between snout-vent length and body temperature. The variation in body temperature observed in this period, then, does not relate to the particular snout-vent length frequency distribution of the population studied. Of those workers who have treated temperature relations in snakes, only Carpenter (1956) explored the effect of body size. He calculated mean temperatures for snakes above and below 300 mm snout-vent length. Inspection of the figures he presents does not suggest significant differences, but the comparison is not very sensitive. In determining the means, Carpenter apparently combined data from both sexes, all seasons and weather conditions. Goodman (1971) concludes that there is no real evidence for a size-associated change in preferred body temperature in lizards, and neither Heatwole (1976) nor Cloudsley-Thompson (1971) treat the question empirically in their reviews. Male *T. sirtalis* are smaller than females, and they display lower body temperatures. It is worth noting that combining both sexes in one sample thus would tend to produce an artifactitious positive association between body temperature and body size. A similar effect could occur in species or populations showing sexual differences in size and seasonal activity.

On sunny days in the summer, the body temperatures of male garter snakes are significantly lower than those of females. Indeed, males were cooler than females on sunny days in all months but October; here males actually were warmer by about 2.0 C° but the sample sizes do not inspire confidence. Cloud cover lowers the mean body temperature of both male and female, more so in the latter than the former for it abolishes the difference between the sexes. A number of factor together suggest that males are less determined thermoregulators than are females. The "plateau" periods during the day and the active season are better defined and longer in females than in males. In males, the frequency distribution of body temperatures is nearly symmetric whereas that of females is strongly skewed to the left. We interpret this as an indication that females are crowding closer to upper thermal limits. Finally, as noted above, air and substrate temperature are somewhat better predictors of body temperature in males than in females. All these considerations argue that females thermoregulate more precisely than do males.

We can suggest one possible explanation that is congruent with this interpretation. *T. sirtalis* is viviparous and over much of the active season the female is involved in the production of young: the processes of vitellogenesis and embryogenesis. The female presumably is much "concerned" with the rates at which these processes occur, and this concern reasonably could be expressed in thermoregulatory precision. The male does not have comparable concerns, and the costs associated with more determined thermoregulation (time, and perhaps exposure to predation) thus may return less substantial benefits. Moreover, spermatogenesis takes place during the summer in this species and high temperatures actually might be detrimental (Cloudsley-Thompson, 1971). For such reasons it is interesting to note that only in October, when courtship and copulation are occurring (Blanchard and Blanchard, 1941; Blanchard, 1942; personal observations), were males observed to have a higher mean body temperature than females. The comparison of oviparous and viviparous species on the basis of sexual differences in body temperature of course suggests itself, but we suspect that a fair and feasible test would prove difficult.

Carpenter (1956) found the mean body temperature of females to exceed that of males in *T. sirtalis* and *T. sauritus*; in *T. butleri*, however, males were warmer. The differences appeared to be nonsignificant in *T. butleri*, perhaps significant in *T. sauritus*, and quite probably significant in *T. sirtalis*. As noted elsewhere, Carpenter's samples combined captures from all seasons, all hours and all weather conditions. The difference he found between male and female *T. sirtalis* exceeded 3 C°, which much surpasses the 1.0 C° difference observed in this study. Carpenter's (1952) data seem to suggest that females prevailed in samples from June and July, whereas the opposite obtained early and late in the season. At Long Point, snakes caught near the beginning and end of the active season have lower body temperatures than do those caught in summer. If such seasonal variation in body temperatures also characterizes the population Carpenter studied, and it would be surprising if it did not, then it could be responsible for some part of the large sex difference he observed.

Stewart (1965) presents mean body temperatures for *T. sirtalis* captured during "summer" (May to September) and "winter" (October to April) periods. In both samples males are cooler than females, although not significantly so despite substantial sample sizes. Again, seasonal variation in body temperature within each period would reduce the sensitivity of these tests. In the same study, Stewart also found a similar "significant" difference between males and females when placed in a thermal gradient. The observations here are repeated measurements on relatively few snakes; thus, the degrees of freedom in his test are inflated improperly, and the significance levels as reported are not correct. Heatwole (1976) has summarized a number of factors which tend to compromise the results obtained from thermal gradients. We can note also that Stewart's experimental chamber was a light gradient as well as a thermal gradient. On the other hand, none of these qualifications address directly the observation that males displayed a lower mean than did females. Mention of a general feature of reptilian thermoregulation is germane here: the mean or modal body temperature is much closer to the upper temperature limits (lethal maximum, voluntary maximum) than it is to lower limits. The immediate and simple consequence of this is that any factor acting to increase the variance of observed temperatures will necessarily decrease their mean as well. Fitch (1965) reported males to have larger "home ranges" than females. Our observations on garter snakes both in captivity and in the field indicate males to be more "high-strung", "nervous" animals than are females. If either, or both, of these sexual differences are expressed in a thermal gradient chamber, males would move about more than females and thus would have lower mean body temperature. To the extent that the microhabitat of *T. sirtalis* shows strong thermal heterogeneity, the same mechanism could be operating in the field and can account parsimoniously for the significant sexual differences observed in this study. This interpretation is pleasantly congruent with the suggestion, presented above and based on independent information, that males are less determined thermoregulators than are females.

The data obtained in this study indicate that the body temperature of gravid and nongravid females captured between 0800 and 1600 h on sunny days in June and July do not differ either in mean or variance. This finding contrasts sharply with sentiments expressed, and with results reported, by other workers. Fitch (1960) opined that gravid females prefer higher temperatures, and observed that of 5 snakes confined in an outdoor enclosure, the highest average body temperature was shown by the single gravid female. Osgood (1970) found that gravid females maintained their body temperature over a shorter range within the limits of males and nongravid females. His sample sizes were very small and the results obtained were not tested. Hirth and King (1969) found the mean body temperature of female rattlesnakes, *Crotalus viridis*, to exceed that of males in spring and summer; in autumn, the sexes were "similar". The authors relate this pattern to viviparity but apparently did not test the differences observed. Stewart (1965) found that gravid females captured in the field displayed a higher mean body temperature than did nongravid females, but the difference was not significant. This pattern obtained in both species he studied, *T. sirtalis* and *T. ordinoides*. Results from Stewart's thermal gradient again showed gravid females to be warmer, and here the difference was "significant" in both species. As noted above, these tests are difficult to interpret. A number of factors might act to give the impression that gravid female snakes prefer or actively maintain higher body temperatures than do nongravid females. In most species gravid females are most likely to be caught, or most likely to be recognized as being gravid, during midsummer. Nongravid females will predominate in spring and fall. If the comparison is not restricted to the period when females can be gravid and easily recognized as being so, then gravid-nongravid tests are likely to reflect seasonal differences in body temperature. Stewart's (1965) "summer" period includes the months May through September. Shine's (1979) evidence from two Australian elapids indicates that gravid females are less errant than are nongravid females. There are two reasons why this probably is generally so. The physical encumbrance of the developing embryos reduces the mother's mobility (personal observation). As well, detection by predators presumably is greater when a snake is moving than when it is at rest. Even though capable of moving, gravid females may become more sedentary simply to protect an investment that is near "maturity". Both considerations are reasonable and if either renders gravid females less mobile, they can be expected to display higher mean body temperatures, by virtue of the mechanism applied above to male-female differences.

Thus, the evidence taken to indicate that gravid female snakes elevate their "preferred" temperature, or *thermoregulate* more precisely, not only is weak but also is open to other, more parsimonious interpretations. It is the strong statement of the data reported herein, with weather, season and hour effects removed, that body temperatures of the two reproductive classes of females differ neither in mean nor variance.

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References

Aleksiuk, M.: Cold-induced aggregative behavior in the red-sided garter snake (*Thamnophis sirtalis parietalis*). Herpetologica **33**, 98–101 (1977)

Bennett, A.F., Dawson, W.R.: Metabolism. In: Biology of the Reptilia, Vol. 5, Physiology A (C. Gans, W.R. Dawson, ed.), pp. 127–223. New York-London: Academic Press 1976

Blanchard, F.C.: A test of fecundity of the garter snake *Thamnophis sirtalis sirtalis* (Linneaus) in the year following the year of insemination. Pap. Mich. Acad. Sci. Arts Lett. **28**, 313–316 (1942)

Blanchard, F.N., Blanchard, F.C.: Mating of the garter snake *Thamnophis sirtalis sirtalis* (Linneaus). Pap. Mich. Acad. Sci. Arts Lett. **27**, 215–234 (1941)

Brattstrom, B.H.: Body temperatures of reptiles. Amer. Midl. Nat. **73**, 376–422 (1965)

Brown, T.W.: Autecology of the sidewinder (*Crotalus cerastes*) at Kelso Dunes, Mojave Desert, California. Ph.D. dissertation, Univ. California, Los Angeles (1970)

Brown, W.S.: Ecology of the racer, *Coluber constrictor mormon* (Serpentes, Colubridae), in a cold temperate desert in northern Utah. Ph.D. dissertation, Univ. Utah (1973)

Carpenter, C.C.: Comparative ecology of the common garter snake (*Thamnophis sirtalis sirtalis*), the ribbon snake (*Thamnophis s. sauritus*), and Butler's garter snake (*Thamnophis butleri*) in mixed populations. Ecol. Monogr. **22**, 235–258 (1952)

Carpenter, C.C.: Body temperatures of three species of *Thamnophis*. Ecology **37**, 732–735 (1956)

Clark, D.R., Jr.: Ecological study of the worm snake *Carphophis vermis* (Kennicott). Univ. Kans. Publ. Mus. Nat. Hist. **19**, 85–194 (1970)

Cloudsley-Thompson, J.L.: The temperature and water relations of reptiles. Watford, England: Merrow 1971

Dill, C.D.: Reptilian core temperatures: variation within individuals. Copeia **1972**, 577–579 (1972)

Dmi'el, R., Borut, A.: Thermal behavior, heat exchange and metabolism in the desert snake *Spalerosophis cliffordi*. Physiol. Zool. **45**, 78–94 (1972)

Fitch, H.S.: Autecology of the copperhead. Univ. Kans. Publ. Mus. Nat. Hist. **13**, 85–288 (1960)

Fitch, H.S.: An ecological study of the garter snake *Thamnophis sirtalis*. Univ. Kans. Publ. Mus. Nat. Hist. **15**, 493–564 (1965)

Fitch, H.S.: A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. Univ. Kans. Mus. Nat. Hist. Misc. Publ. **62**, 1–53 (1975)

Gibson, A.R.: The ecological significance of a colour polymorphism in the common garter snake, *Thamnophis sirtalis* (L.). Ph.D. dissertation, Univ. Toronto (1978)

Gibson, A.R., Falls, J.B.: Thermal biology of the common garter snake *Thamnophis sirtalis* (L.) II. The effects of melanism. Oecologia (Berl.) (in press, 1979)

Goodman, D.E.: Thermoregulation in the brown water snake *Natrix taxispilota*, with discussion of the ecological significance of thermal preferenda in the order Squamata. Ph.D. dissertation, Univ. Gainesville, Florida (1971)

Heatwole, H.: Reptile ecology. St. Lucia, Australia: University of Queensland Press 1976

Hirth, H.F., King, A.C.: Body temperatures of snakes in different seasons. J. Herpetol. **3**, 101–102 (1969)

Huey, R.B., Slatkin, M.: Cost and benefits of lizard thermoregulation. Quart. Rev. Biol. **51**, 363–384 (1976)

Johnson, C.R.: Thermoregulation in pythons – I. Effect of shelter, substrate type and posture on body temperature of the Australian carpet python, *Morelia spilotes variegata*. Comp. Biochem. Physiol. **43A**, 271–278 (1972)

Johnson, C.R.: Thermoregulation in pythons – II. Head-body temperature differences and thermal preferenda in Australian pythons. Comp. Biochem. Physiol. **45A**, 1065–1087 (1973)

Johnson, C.R., Webb, G.J.W., Johnson, C.: Thermoregulation in pythons – III. Thermal ecology and behaviour of the black-headed rock python, *Aspidites melanocephalus*. Herpetologica **31**, 326–332 (1975)

McGinnis, S.M., Moore, R.G.: Thermoregulation in the boa constrictor, *Boa constrictor*. Herpetologica **25**, 38–45 (1969)

Moore, R.G.: Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and the Colorado desert sidewinder (*Crotalus cerastes laterorepens*). Copeia **1978**, 439–442 (1978)

Naulleau, G., Marques, M.: Etude biotélémétrique préliminaire de la thermorégulation de la digestion chez *Vipera aspis*. C.R. Acad. Sciences, Paris, 276, Série D. 3433–3436 (1973)

Osgood, D.W.: Thermoregulation in watersnakes studied by telemetry. Copeia **1970**, 568–571 (1970)

Parker, W.S.: Comparative ecology of two colubrid snakes, *Masticophis T. taeniatus* (Hallowell) and *Pituophis melanoleucus deserticola* Stegneger in northern Utah. Ph.D. dissertation, Univ. Utah (1974)

Saint Girons, H., Saint Girons, M.-C.: Cycle d'activité et thermorégulation chez les reptiles (lézards et serpents). Vie Milieu 7, 133–226 (1956)

Shine, R.: Activity patterns in Austrialian elapid snakes (Serpentes: Elapidae). Herpetologia **35**, 1–11 (1979)

Skoczylas, R.: Preliminary observations on gastric temperature in the grass snake *Natrix natrix (L.)*. Zool. Pol. **19**, 525–544 (1969)

Snedecor, G.W., Cochran, W.G.: Statistical methods. Ames, Iowa: Iowa State University Press 1967

Sokal, R.R., Rohlf, F.J.: Biometry. San Francisco: W.H. Freeman 1969

Stewart, G.R.: Thermal ecology of the garter snake *Thamnophis sirtalis concinnus* (Hallowell) and *Thamnophis ordinoides* (Baird and Girard). Herpetologica **21**, 81–102 (1965)

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