Body Temperatures of Snakes in the Fields 3. Concluding Remarks

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Abstract: Comparisons of body temperatures among five species of Japanese snakes revealed that they are divided into three groups based on mean body temperatures, namely high, intermediate, and low ones. On the other hand, from range of body temperatures, they are divided into two groups, i.e., wide and narrow ones. *Elaphe quadrivirgata* has body temperatures with a high mean and a wide range, while *Rhabdophis tigrinus* has intermediate mean body temperatures with a wide range. These two species with wide temperature ranges are active from late March to early December. *Elaphe climacophora* has intermediate mean body temperatures with a narrow range, and is active in rather mild weather from late March to late November. *Amphiesma vibakari* and *Elaphe conspicillata* have low mean body temperatures with narrow ranges, and are active mostly in spring and in autumn, and never appear in the daytime during the summer months.

Key words: Body temperature; *Elaphe*; *Rhabdophis*; *Amphiesma*

In the previous two papers (Fukada, 1985, 1989), I reported body temperatures in five species of snakes measured in the fields. In the present report, further comparisons for these snake species are made and a general discussion on snake body temperatures, including literature review, will be given.

MATERIALS AND METHODS

As noted in Fukada (1985, 1989), body temperatures and surrounding temperatures of the following 5 snake species were measured in Tambabashi study area, Fushimiku, Kyoto, in the period between May 1958 and October 1969: *Elaphe quadrivirgata*, *E. climacophora*, *E. conspicillata*, *Rhabdophis tigrinus*, and *Amphiesma vibakari*.

Throughout the text, figures, and tables, standard symbols (in parentheses) are used for *Elaphe quadrivirgata* (Eq), *E. climacophora* (Ec), *E. conspicillata* (Econ), *Rhabdophis tigrinus* (Rt), *Amphiesma vibakari* (Av), body temperature (BT), air temperature (AT), substrate temperature (ST), sample size (N), and standard error of the mean (SE).

RESULTS

Comparisons of mean BTs among the 5 species.—There are linear relationships between BT and AT or ST, in 5 species. In all species except Econ, BTs more closely correlate to STs than ATs, and STs are used for calculation of adjusted means of BT.

Table 1 shows mean BT, AT, ST, and ad-

justed BT to a constant ST in each species. Results of interspecific comparisons of mean BTs before and after adjustment are shown in Table 2.

Eq has the highest BT among the 5 species both in intact and in adjusted values. Rt is not significantly different from Ec, and Av is not significantly different from Econ in both values. In other combinations, each species differs significantly from the other.

Comparisons of monthly mean BTs.—Values of monthly mean BTs of 5 species before and after adjustment are shown in Table 3. Results of interspecific comparisons of monthly mean BTs before and after adjustment are shown in Tables 4 and 5, respectively.

As clearly seen in these tables, mean BTs are not different between any two different species in most cases. This fact may be partly explained by the small sample sizes of monthly catches.

Both in intact and adjusted values, the monthly mean BT of Eq is significantly higher than that of Rt in April, May, June and October. Between Rt and Ec, there are no differences in values of monthly mean BTs for all months except August, but in adjusted values, BTs did not differ significantly between any pairs of months compared.

DISCUSSION

The mean BT of Eq is significantly higher than that of Rt as shown in Tables 1 and 2. Monthly mean BTs of Eq are not significantly different from those of Rt in 6 out of 10 months in intact values, but are not different from those of Rt during only 3 summer months in adjusted values

TABLE 1. Mean BT, AT, ST, and mean BT when ST is held constant in 5 Japanese snakes (mean $\pm$ SE).

	N	Mean BT	Mean AT	Mean ST	Mean BT when ST held constant
Eq	1434	28.72 $\pm$ 0.098	24.01 $\pm$ 0.119	24.86 $\pm$ 0.123	28.30 $\pm$ 0.070
Rt	1099	26.75 $\pm$ 0.127	22.18 $\pm$ 0.146	23.23 $\pm$ 0.149	27.34 $\pm$ 0.080
Ec	83	27.67 $\pm$ 0.345	23.97 $\pm$ 0.502	24.85 $\pm$ 0.290	27.30 $\pm$ 0.290
Av	44	24.85 $\pm$ 0.558	22.67 $\pm$ 0.565	22.65 $\pm$ 0.561	25.98 $\pm$ 0.423
Econ	24	24.44 $\pm$ 0.778	21.24 $\pm$ 0.757	21.72 $\pm$ 1.007	25.86 $\pm$ 0.594

FIG. 1. The relationship between width of range of body temperatures (°C) and relative abundance of each species within its mixed population (%). Data from Table 7. The regression equation is $y=3.65x-42.87$. Legend: Av, *Amphiesma vibakari*; Ec, *Elaphe climacophora*; Econ, *E. conspicillata*; Eq, *E. quadrivirgata*; Nc, *Nerodia cyclopion*; Ne, *N. erythrogater*; Nf, *N. fasciata*; Nr, *N. rhombifera*; Rg, *Regina grahamii*; Rt, *Rhabdophis tigrinus*; Tb, *Thamnophis butleri*; To, *T. ordinoides*; Tsa, *T. sirtalis sauritus*; Tsc, *T.s. concinnus*; Tsi, *T.s. sirtalis*.

TABLE 2. Interspecific comparisons of mean BT before and after adjustment.

	Intact value				ST held constant			
	Eq	Rt	Ec	Av	Eq	Rt	Ec	Av
Rt	*				*			
Ec	*	ns			*	ns		
Av	*	*	*		*	*	*	
Econ	*	*	*	ns	*	*	*	ns

Legends: * = $P < 0.05$, ns = $P > 0.05$.TABLE 3. Monthly mean BTs of each species before and after adjustment (mean $\pm$ SE).

	Eq			Rt		
	N	Mean BT	Mean BT when ST held constant	N	Mean BT	Mean BT when ST held constant
March	30	25.39 $\pm$ 0.845	28.62 $\pm$ 0.630	30	24.32 $\pm$ 0.676	26.51 $\pm$ 0.619
April	404	27.67 $\pm$ 0.175	28.37 $\pm$ 0.130	254	26.97 $\pm$ 0.196	27.79 $\pm$ 0.170
May	194	29.43 $\pm$ 0.210	29.04 $\pm$ 0.182	125	28.72 $\pm$ 0.265	28.42 $\pm$ 0.223
June	101	30.72 $\pm$ 0.229	29.25 $\pm$ 0.378	85	28.86 $\pm$ 0.295	27.34 $\pm$ 0.353
July	116	31.19 $\pm$ 0.209	28.60 $\pm$ 0.456	74	30.86 $\pm$ 0.218	28.20 $\pm$ 0.660
August	99	31.66 $\pm$ 0.180	28.79 $\pm$ 0.634	38	31.10 $\pm$ 0.267	28.41 $\pm$ 1.102
September	184	30.74 $\pm$ 0.171	28.67 $\pm$ 0.295	72	30.49 $\pm$ 0.264	28.66 $\pm$ 0.466
October	212	27.66 $\pm$ 0.216	28.14 $\pm$ 0.172	205	25.78 $\pm$ 0.231	27.40 $\pm$ 0.210
November	90	23.01 $\pm$ 0.367	25.93 $\pm$ 0.407	206	22.64 $\pm$ 0.265	26.96 $\pm$ 0.331
December	4	21.35 $\pm$ 1.707	24.91 $\pm$ 2.460	10	16.62 $\pm$ 1.049	31.08 $\pm$ 3.743

TABLE 3. (continued)

	Ec			Av		
	N	Mean BT	Mean BT when ST held constant	N	Mean BT	Mean BT when ST held constant
March	2	29.75 $\pm$ 1.750	29.46 $\pm$ 1.746	—		
April	21	26.09 $\pm$ 0.562	26.66 $\pm$ 0.717	14	24.14 $\pm$ 1.079	25.76 $\pm$ 0.790
May	18	27.80 $\pm$ 0.551	27.52 $\pm$ 0.592	7	24.51 $\pm$ 0.863	25.85 $\pm$ 1.622
June	9	29.29 $\pm$ 0.585	27.56 $\pm$ 1.294	7	29.24 $\pm$ 0.712	28.00 $\pm$ 1.197
July	11	30.01 $\pm$ 0.737	26.13 $\pm$ 1.672	—		
August	7	29.57 $\pm$ 0.796	26.74 $\pm$ 1.857	—		
September	6	29.75 $\pm$ 0.680	26.10 $\pm$ 2.658	1	24.0	—
October	4	25.13 $\pm$ 1.547	19.52 $\pm$ 4.384	11	24.34 $\pm$ 0.953	25.12 $\pm$ 0.769
November	5	21.84 $\pm$ 1.302	25.41 $\pm$ 2.674	4	21.93 $\pm$ 1.909	33.83 $\pm$ 4.554
December	—			—		

TABLE 3. (continued)

	Econ		
	N	Mean BT	Mean BT when ST held constant
March	—		
April	10	23.15 $\pm$ 1.081	25.01 $\pm$ 1.120
May	3	26.57 $\pm$ 1.260	26.45 $\pm$ 1.414
June	2	29.35 $\pm$ 3.650	25.26 $\pm$ 2.586
July	—		
August	—		
September	—		
October	4	26.68 $\pm$ 0.907	27.07 $\pm$ 1.467
November	5	22.00 $\pm$ 1.658	26.54 $\pm$ 2.162
December	—		

TABLE 4. Monthly interspecific comparisons of mean BT.

	Eq-Rt	Eq-Ec	Eq-Av	Eq-Econ	Rt-Ec	Rt-Av	Rt-Econ	Ec-Av	Ec-Econ	Av-Econ
March	ns	ns			ns					
April	*	*	*	*	ns	*	*	ns	*	ns
May	*	*	*	ns	ns	*	ns	*	ns	ns
June	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns			ns					
August	ns	*			*					
September	ns	ns			ns					
October	*	ns	*	ns	ns	ns	ns	ns	ns	ns
November	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
December	ns									

Legends: * = $P < 0.05$, ns = $P > 0.05$.

TABLE 5. Monthly interspecific comparisons of mean BT when ST is held constant.

	Eq-Rt	Eq-Ec	Eq-Av	Eq-Econ	Rt-Ec	Rt-Av	Rt-Econ	Ec-Av	Ec-Econ	Av-Econ
March	*	ns			ns					
April	*	*	*	*	ns	*	*	ns	ns	ns
May	*	*	ns	ns	ns	ns	ns	ns	ns	ns
June	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
July	ns	ns			ns					
August	ns	ns			ns					
September	ns	ns			ns					
October	*	*	*	ns	ns	*	ns	ns	ns	ns
November	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
December	*									

Legends: * = $P < 0.05$, ns = $P > 0.05$.

(Tables 4 and 5). Furthermore, monthly mean BTs of Eq are significantly higher than Rt in April to June, and October and November.

Table 6 shows mean width of monthly ranges of BT, AT, and ST for the respective species. This table indicates the resemblance between Eq and Rt, since they have wider ranges than the other 3 species. The mean BT of Ec is not significantly different from that of Rt, but Ec has a narrower range of temperature than Rt. Av and Econ have lower mean BTs and have narrower ranges.

From these results, the present five Japanese species of snakes are divided into 3 groups based on their mean BTs, namely high, intermediate, and low ones. On the other hand, based on the width of temperature ranges, they are divided into two groups, i.e., wide and narrow ones. Eq has a high mean BT with a wide range, while Rt has an intermediate mean BT with a wide range. Both Eq and Rt have wide ranges and are active from late March to early December at a wide range of temperatures. However, Eq with high BT prefers more sunny places while Rt with intermediate BTs prefers more humid

places like a paddy field. Ec has an intermediate mean BT with a narrow range of BTs and is active in rather mild weather from late March to the end of November. Av and Econ have low mean BTs with narrow ranges and are active mostly in spring and autumn; they never appear in the daytime of summer months.

Although a number of papers have been published concerning thermoregulation of snakes, only a few include field studies of BT throughout an extensive period of one or more years. Carpenter (1956) recorded BTs of three species of garter snakes, *Thamnophis sirtalis sirtalis*, *T. s. sauritus*, and *T. butleri*, throughout

TABLE 6. Mean width of monthly ranges of BT, AT, and ST in 5 Japanese snakes.

Species	BT	AT	ST
Eq	14.35	12.89	16.34
Rt	13.52	13.00	15.34
Ec	6.53	5.87	7.83
Av	8.36	7.24	7.84
Econ	6.46	5.88	9.74

TABLE 7. Summary of published data of mean BTs in the field.

Species	N	BT $\pm$ SE (range)	Width of range	Authority
<i>Thamnophis s. sirtalis</i>	144	25.6 $\pm$ 0.40 (9.0–35.0)	26.0	Carpenter (1956)
<i>T. s. sauritus</i>	123	26.0 $\pm$ 0.41 (12.6–34.0)	21.4	"
<i>T. butleri</i>	54	26.1 $\pm$ 0.63 (12.4–34.0)	21.6	"
<i>T. s. concinnus</i>	481	27.2 (10.4–35.5)	25.1	Stewart (1965)
<i>T. ordinoides</i>	197	26.1 (16.6–33.6)	17.0	"
<i>Nerodia cyclopion</i>	124	27.2 (20–33)	13	Mushinsky (1980)*
<i>N. fasciata</i>	197	26.2 (15–33)	18	"
<i>N. erythrogaster</i>	51	26.3 (15–31)	16	"
<i>N. rhombifera</i>	343	27.5 (15–33)	18	"
<i>Regina grahamii</i>	27	25.9 (22–34)	12	"
<i>Notechis ater niger</i>	402	25.5 $\pm$ 0.18 (11.9–34.5)	22.6	Schanner (1989)
<i>Elaphe quadrivirgata</i>	1434	28.7 $\pm$ 0.10 (10.0 $\pm$ 36.2)	26.2	Fukada (1985)
<i>E. climacophora</i>	83	27.7 $\pm$ 0.35 (17.3 $\pm$ 33.5)	16.2	Fukada (1989)
<i>E. conspicillata</i>	24	24.4 $\pm$ 0.78 (18.8–33.0)	14.2	"
<i>Rhabdophis tigrinus</i>	1099	26.8 $\pm$ 0.13 (10.3–35.5)	25.2	"
<i>Amphiesma vibakari</i>	44	24.9 $\pm$ 0.56 (17.5–33.0)	15.5	"

* Values of ranges are originally given in round numbers and extremes are used here.

one year in Michigan. Stewart (1965) collected field data of BTs of two species of garter snakes, *T. sirtalis concinnus* and *T. ordinoides*, for three years in northern California. Mushinsky et al (1980) studied BTs of five sympatric species of water snakes, *Nerodia cyclopion*, *N. fasciata*, *N. erythrogaster*, *N. rhombifera*, and *Regina grahamii*, in the swamp-bayou systems of southern Louisiana for four years. Schwanner (1989) studied BT of the black tiger snake, *Notechis ater niger*, in the Franklin Islands, South Australia in four seasons of a year.

The results shown in above four papers are summarized in Table 7 together with my results. Most of these studies lack information about values of monthly ranges of BTs. Therefore, the mean width of monthly ranges is omitted from this table and the width of ranges is given as a substitute.

This table shows that mean BTs of 16 species and subspecies range continuously from 24.4 to 28.7°C, and are not divided into clear groups. On the other hand, based on the width of ranges, or the difference of maximum and minimum BTs, these snakes are divided into three groups, namely wide (25.1 to 26.2°C), intermediate (21.4 to 22.6°C), and narrow (12 to 18°C) ones.

When these 15 taxa are combined, the width of ranges in BTs (°C) is correlated to the relative abundance (%) of each species within its mixed population (*Notechis ater niger* is excluded because it is a single population), there is a strongly significant linear relationship (correlation coefficient $r=0.814$, $F=25.6$, $df=1, 13$, $P<0.001$, see Fig. 1). This relationship seems to show that a snake with a wider range of BTs is able to be active for a long period in the year, and is adapted to the surrounding environment

more than a sympatric snake with a narrower range does.

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要 旨 野外における蛇の体温 3. 総合考察

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5種の蛇の体温を比較したところ、平均体温からは高・中・低の3群に分けられ、一方最高最低体温の範囲からは広・狭の2群に分けられることが判った。シマヘビは高い平均体温と広い体温範囲を有し、ヤマカガシは中等の平均体温と広い体温範囲を有する。そしてこの両者は

共に3月下旬から12月上旬にかけて活動する。アオダイショウは中等の平均体温と狭い体温範囲を有し、3月下旬から11月下旬までの温和な日に活動する。ヒバカリとジムグリは低い平均体温と狭い体温範囲を有し、主に春と秋に活動し、夏期の日中には出現しない。

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