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Thermoregulation in pythons. IV Thermoregulation in the Papuan-New Guinean pythons within the genera *Python, Liasis* and *Chondropython*

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The thermal preference, voluntary maxima, and thermal control were studied in the Papuan-New Guinean pythons *Python spilotus, P. boeleni, Liasis albertisii, L. papuanus, L. boa,* and *Chondropython viridis.* Preferred temperature data were similar for all species and mean preferred head temperatures were lower than those for the body. In general preferred and voluntary means were higher for the Papuan-New Guinean pythons than those found for Australian species and likely reflect adaptation to hotter tropical environments.

CONTENTS

INTRODUCTION

Recent studies of thermoregulation in pythons (Webb & Heatwole, 1971; Johnson, 1972, 1973; Johnson *et al.*, 1975, in press) have dealt mainly with these boid snakes in Australia from temperate and subtropical environments. This study reports on a comparative investigation of thermal preference, voluntary maxima, and behavioural thermal control in *Python spilotus, P. boeleni, Liasis albertisii, L. papuanus, L. boa,* and *Chondropython viridis* and relates the findings to Australian studies on pythons.

METHODS AND MATERIALS

Pythons for this study were collected from the following locations: one *Python spilotus,* snout-vent length 82 cm, body wt 205 g (Six Mile area, near

Port Moresby); one *P. boeleni,* SVL 257 cm, body wt 5.5 kg (Waitapo); two *Liasis albertisii,* SVL 138.5 and 141 cm, body wt 1.2 and 1.4 kg, respectively (near Lae); one *L. papuanus,* SVL 351 cm, body wt 10.0 kg (Brown River); one *L. boa,* SVL 112.5 cm, body wt 488 g (Rabaul, New Britain); and two *Chondropython viridis,* SVL 111 and 119 cm, body wt 291 and 498 g, respectively (near Madang). The snakes were experimented on immediately after capture.

One thermocouple (38-gauge constantan-copper) was implanted on the left side of the neck immediately behind the head so that the thermocouple bead penetrated the posterior part of the head; a second thermocouple was implanted deep in the epaxial musculature of the body, midway between the head and the cloaca. After the thermocouples were sutured to the skin, they were attached to a Comark electronic thermometer (model 1625, accuracy ± 0.05° C) through a Comark selector unit (model 1698). After implantation of the thermocouples, the pythons were placed in enclosures (74 x 31 x 31 cm) on a sand substrate and either heated radiantly with a 275 W infrared heat lamp 46 cm above the unrestrained snake, or solar heated outdoors in enclosures (of the same size) simulating natural heating conditions. The pythons were allowed to move freely either away from or towards the lamp or between sun and shade during solar heating sequences. The cessation of basking behaviour and the initiation of shuttling was assumed to herald the achievement of the preferred temperature and the data collected during these periods were used in the calculation of thermal preferenda for each species. The pythons were used several times, but with 24 hours elapsing between experiments. Environmental temperatures (substrate and ambient in the sun) were recorded during the solar heating sequences with the Comark electronic thermometer. For further details of methods and experimental procedures see Johnson (1973, 1974). All experimentation was conducted at the Department of Biology, The University of Papua New Guinea during October to December 1972.

RESULTS AND DISCUSSION

Considerable similarity was found among the different pythons. Preferred head temperature ranged from 33.6° to 36.7° C and preferred body temperature from 34.4° to 36.7° C (Table 1). Within all species, preferred head temperature was lower than preferred body temperature (Fig. 1), and with the exception of *P. boeleni,* the values found were significantly different (5%, non-overlap of 2 S_x). Little intraspecific variability was found in preferred temperatures where more than one individual was available for experimentation (*L. albertisii, C. viridis*); less variability occurred in head temperature than in body temperature. Greater precision of head temperature regulation has been shown in a variety of reptiles and Heatwole (1970) suggested that it is of greater biological significance than body temperature and that it should be used in the calculation of preferred temperature. The standard errors for preferred body temperature were less than those for head temperature in *P. spilotus, L. albertisii, L. papuanus,* and *L. boa* suggesting that temperature regulation of the head is not always more precise than that of the body. However, differences were small (Fig. 1). *P. boeleni* and *C. viridis* had less variation in head

Table 1. Thermal preferenda for Papuan-New Guinean pythons

Species	T_H(°C)				T_B(°C)			
	$\bar{x}$	Range	N	$2S_x$	$\bar{x}$	Range	N	$2S_{\bar{x}}$
P. spilotus								
82 cm, 205 g	34.0	30.6-36.0	124	0.23	34.9	32.5-36.6	123	0.16
P. boeleni								
257 cm, 5.5 kg	35.4	32.1-36.9	71	0.19	35.6	33.3-37.6	67	0.25
L. albertisii								
238.5 cm, 1.2 kg	34.0	30.1-36.4	216	0.20	35.0	32.2-37.1	195	0.17
141 cm, 1.4 kg	34.2	33.2-35.4	33	0.25	36.6	35.6-37.8	30	0.20
grouped	34.1	30.1-36.4	249	0.18	35.2	32.2-37.8	225	0.15
L. papuanus								
351 cm, 10.0 kg	35.6	32.4-37.6	83	0.37	36.7	33.0-38.3	95	0.26
L. boa								
112.5 cm, 488 g	33.6	31.3-36.3	112	0.24	34.4	31.6-36.0	102	0.23
C. viridis								
111 cm, 291 g	35.2	34.1-36.6	62	0.21	36.2	34.7-37.8	62	0.23
119 cm, 498 g	34.7	32.8-36.8	50	0.34	35.6	33.6-37.2	35	0.41
grouped	34.9	32.8-36.8	112	0.19	36.0	33.6-37.8	97	0.20

temperature than in body temperature. Clearly further study of such relationships is necessary.

The high degree of difference observed between preferred body temperature between two specimens of *L. albertisii* (138.5 cm, mean T_B = 35.0° C; 141 cm, mean T_B = 36.6° C) may be attributed to the 141 cm female being gravid at the time of experimentation. This female commenced egg-laying one week after experimentation, and the higher temperature selection might be attributed to

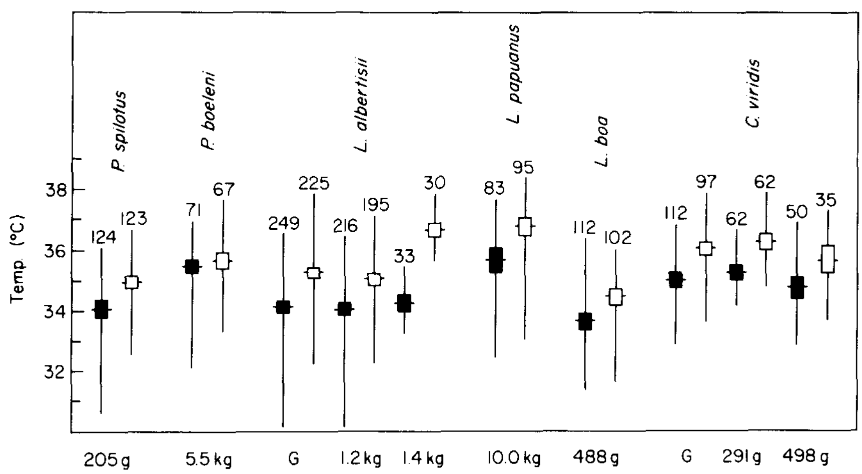

Figure 1. Head and body thermal preferenda for Papuan-New Guinea pythons. Dark rectangles, head temperature; open triangles, body temperature; horizontal lines, means; vertical lines, ranges; rectangles, twice standard error of the means; numbers above vertical lines refer to sample size.

some pre-egg-laying or pre-brooding metabolic change. Physiological thermoregulation during brooding has been well documented in some pythons (Vinegar *et al.*, 1970). The nocturnal python, *L. boa,* had the lowest preferred values whereas the highest preferred levels were recorded for *L. papuanus. L. papuanus* and *P. boeleni* had the highest tolerance to temperature for both the head and body; the least tolerance was experienced by *L. boa* and again correlated with preferred levels (Table 2).

Data on thermal preferenda and voluntary maxima are now available for *P. spilotus* from both Australia and Papua-New Guinea. Both mean preferred temperatures and voluntary maxima are several degrees higher for the Papuan individual than those inhabitating more temperate Australian climates. It must be remembered that the Papuan data are based upon only one specimen and the differences found may be those of individual variability. In general, however, overall preferred and voluntary means are higher for Papuan-New Guinea pythons than those found for various Australian species (Table 3) and likely reflect adaptation to the hotter and more constant tropical climate.

Head-body temperature gradients of considerable magnitude were found with radiant heating and to a lesser extent with solar heating. In most cases when the head was exposed to the heat source during basking, it heated faster than the body and gradients of up to 6.3° C were observed with radiant heating; gradients of up to 2.5° C were more often the case during solar heating sequences. Exceptions did occur when the head was hidden either beneath or among body coils as demonstrated in *L. papuanus* by Fig. 2. The body heated up faster while little heat gain occurred to the head until minute 18. The head was still hidden among the body coils with none of it or the neck visible at this time and the subsequent slow heat gain can probably be attributed to

Table 2. Voluntary maxima temperatures for the head and body of Papuan-New Guinean pythons

Species	T_H(° C)			T_B(° C)		
	$\bar{x}$	Range	*N*	$\bar{x}$	Range	*N*
P. spilotus						
82 cm, 205 g	36.2	35.1-37.1	9	37.6	36.0-41.8	8
P. boeleni						
257 cm, 5.5 kg	37.2	35.9-38.1	8	38.2	37.5-39.5	3
L. albertisii						
238.5 cm, 1.2 kg	35.6	33.8-37.1	5	36.7	35.5-38.1	4
141 cm, 1.4 kg	36.2		1	37.7	37.4-38.3	3
grouped	35.8	33.8-37.1	6	37.1	35.5-38.3	7
L. papuanus						
351 cm, 10.0 kg	37.8	36.3-39.4	7	38.4	37.4-39.4	4
L. boa						
112.5 cm, 488 g	35.2	33.1-36.6	7	35.9	35.7-36.2	4
C. viridis						
111 cm, 291 g	36.8	35.3-37.7	7	38.6	38.0-39.1	3
119 cm, 498 g	35.7	34.8-37.0	4	37.3	37.2-37.4	2
grouped	36.4	34.8-37.7	11	38.1	37.2-39.1	5

Table 3. Thermal preferenda and voluntary maxima temperatures for the head and body of Australian pythons. Data from Johnson (1972, 1973)

Species	Thermal preferenda				Voluntary maxima			
	T_H(°C)		T_B(°C)		T_H(°C)		T_B(°C)	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Liasis childreni	29.1	21.0-34.8	28.8	21.3-34.3	32.9	30.1-36.8	37.3	36.2-38.4
L. mackloti	33.2	32.5-33.8	35.7	35.1-36.2	33.4	31.8-35.5	36.1	35.2-36.8
Python amethistinus			34.3	34.0-34.4				
P. spilotus			31.3	30.7-32.0	33.0	32.7-33.4	35.7	34.5-37.6
Aspidites melanocephalus					35.3	33.5-36.8	36.4	34.3-38.0

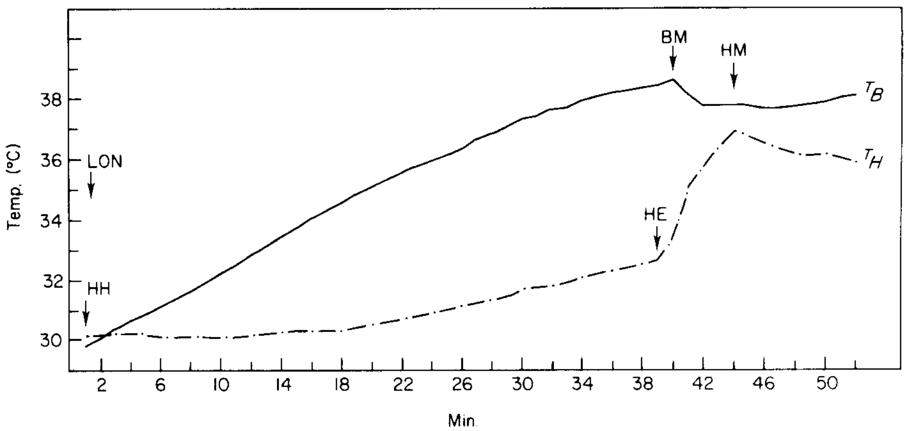

Figure 2. Heating curves for *L. papuanus*. HM, Head moved away from lamp; BM, body moved away from lamp; HH, head hidden among body coils; HE, head exposed; LON, lamp on.

conduction of heat to the head from the warm body (min 18-39). At minute 39, the head was exposed and its temperature rose rapidly until the head was moved into the shade at minute 44.

Moving into the shade was the most effective method employed for reducing head and body temperature. Table 4 shows the variety of behavioural methods employed by the different species for reducing head temperature. All species effectively reduced head temperature by moving into shade and by raising the head above the substrate toward the heat source, thus reducing the absorptive area and reducing conductance from the warm substrate. Shielding the head behind, or among the coils, or hiding the head beneath them, or burying it within the substrate were not nearly as effective as the previous methods. Conductance of heat from the body coils and substrate to the head when both are hot would tend to limit the effectiveness of these latter methods. Some of these behavioural methods were employed by the Australian pythons, *L. childreni, L. mackloti, Aspidites melanocephalus,* and *P. spilotus* in reducing head temperature (Johnson, 1973). Reduction of head temperature by gaping,

Table 4. Behavioural methods employed by Papuan-New Guinean pythons for the reduction of head temperature

Species	MS	HOS	HICP	SHBC	HUBC	BS
P. spilotus	X	X	X	X	X	
P. boeleni	X	X	X	X		
L. albertisii	X	X	X	X	X	X
L. papuanus	X	X	X	X	X	
L. boa	X	X			X	X
C. viridis	X	X	X		X	

MS, Moving head into shade; HOS, raising the head above the substrate; HICP, head placed inside coil posture; SHBC, shielding head behind the coil posture; HUBC, head hidden beneath the body coils; BS, burying the head in the substrate.

such as occurs in *L. childreni* (Johnson, 1973) was not observed in any of the Papuan-New Guinean pythons.

Tight circular coiling which prevented body heat loss was assumed by all the python species examined. These coils were either of the flat one layer type or were two to three layers deep. The advantages of each type of posture have been previously discussed (Johnson, 1972).

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