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Thresholds of Infrared Sensitive Tectal Neurons in *Python reticulatus*, *Boa constrictor* and *Agkistrodon rhodostoma* *

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Summary. Boas, pythons and pit vipers are known to use the heat radiated by warmblooded animals in order to hunt them. However, until now no comparative study to determine at what range these remarkable sense organs operate has been attempted.

The results from a comparative electrophysiological study on central infrared sensitive neurons in the tecta mesencephali of *Boa constrictor, Python reticulatus* and *Agkistrodon rhodostoma* are used to calculate thresholds and the associated maximal detection ranges. A discussion of the rationale behind radiation physics and its implications for the calculation of thresholds and the translation into a behavioural context is given.

The thresholds determined for *Boa*, *Python* and *Agkistrodon* are respectively: 42.28, 14.28 and 2.57 10^{-6} cal/cm^2·s which, in biological terms, is equivalent to that which is required to detect a mouse (10 °C warmer than the surrounding, radiating area 25 cm^2) at a distance of 16.4 cm, 28.3 cm and 66.6 cm.

Introduction

Several snake species possess a trigeminal nerve system specialized to detect infrared heat radiation (Bullock and Barrett 1968; Hartline 1974). Although the structure of the organs differs considerably between pit vipers, pythons and boas (Düring and Miller 1979), centrally the related path of the trigeminal system appears to follow a similar course. In Crotalidae three subsequent centers which deal exclusively with heat perception can be distinguished beyond the trigeminal ganglion: a) the nucleus descendens lateralis nervi trigemini (LTTD) (Molenaar 1974; Schroeder and Loop 1976), b) the nucleus reticularis caloris (Gruberg et al. 1979) (or the New Nucleus (Kishida et al. 1980)) and c) the stratum griseum centrale of the contralateral mesencephalic tectum (Molenaar and Fizaan-Oostveen 1980; Newmann et al. 1980). In *Python* the first two centers seem to be fused in the rostrally extended LTTD (Newman et al. 1980).

An integration of visual and heat information exists in the tectal region (Newman and Hartline 1981) which appears therefore to be the highest level at which infrared neural activity can be traced. At this level most research has been focussed on the spatiotopic organisation of the visual and heat sensitive neurons (Hartline et al. 1978; Haseltine 1978; Terashima and Goris 1975). Until now, little attention has been paid to the question of the distance at which this system is operational; a question of particular interest for the interpretation of ethological data on hunting behaviour (de Cock Buning 1983; de Cock Buning et al. 1978, 1981a).

The aim of the present study is to obtain a reliable indication, based on centrally obtained electrophysiological data, of the maximal range at which infrared sensitive snakes are able to perceive heat radiating objects (hereafter called the maximal detection range).

Materials and Methods

Single specimens of *Python reticulatus* (950 g, 175 cm), *Boa constrictor* (1,750 g, 150 cm) and *Agkistrodon rhodostoma* (400 g, 85 cm) were used for tectal penetration into the right lobe with

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* Recently, it became commonly accepted under taxonomists to rename *Agkistrodon rhodostoma* on systematical grounds to *Calloselasma rhodostoma* (Chernov 1957). However, the author prefers to use, in this physiologically and behaviourally oriented paper, the better known old name

Abbreviation: LTTD nucleus descendens lateralis nervi trigemini

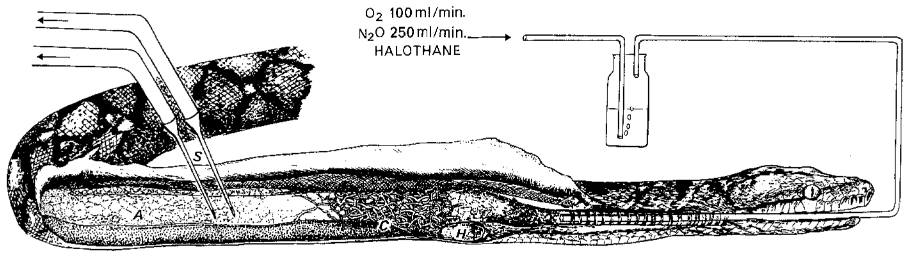

Fig. 1. Anesthesia of snakes. A mixture of O_2 (100 ml/min), N_2O (250 ml/min) and Halothane (0.5% vapour) is introduced into the trachea (T) by means of a cannula. An outlet is provided by two syringe needles (S) in the right pulmonary airsac (A) behind the heart (H) and the capillary network (C) around the lung

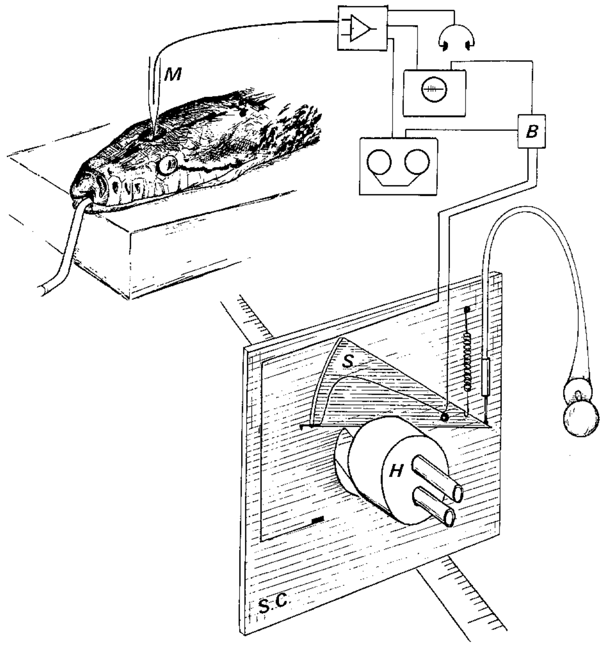

Fig. 2. Experimental apparatus. Behind a hole in the screen (SC) a copper heat exchanger (H) with a black painted surface is heated to any desired temperature by a continuous waterflow from a waterbath with controlled temperature. Radiation from the heat exchanger can be blocked by manually operating the shutter (S). Both shutter and screen are covered with heat reflective material. Neural responses are recorded from the right tectal lobe by means of the glass microelectrode (M) and transferred to the preamplifier, earphones, oscilloscope and tape-recorder. Signals from the shutter are transferred by means of a battery (B) to the recording equipment

3 mol/l NaCl glass micropipettes of 2–20 MΩ to record extracellular nerve spikes. Ten days later the specimens of *Python* and *Boa* were also operated upon to penetrate the left lobe. All animals survived the experiments and remained in good health.

Anestesia (Fig. 1). Anesthesia was applied in two steps; first the snake was put in a closed tank with two swabs soaked in Halothane (HOECHST). Second, after ±10 min when the snake was completely relaxed, a mixture of N_2O (250 ml/min), O_2 (100 ml/min) and Halothane (0.5% vapour) was administered via a cannula into the trachea. A constant airflow over the capillary tissue of the lungs was provided by cannulating the right caudal airsac by means of syringe needles. Careful regulation of the amount of Halothane and O_2 held the snake at a very light level of anesthesia for more than 10 h. After administration of chloramphenicol (SIGMA) the incisions were closed by suturing and glueing (CYANOLIT) and recovery was promoted by the application of pure O_2.

Procedure of Operation. With a dental drill a small hole was drilled rostro-medial to the attachment of the supratemporal bone, just behind the main lobe of the telencephalon. The tectum was exposed by carefully breaking away small slivers of bone with tweezers. The membranes covering the tectum were cut and the snake was fixed on a table in a cage of Faraday.

Stimulus Equipment (Fig. 2). Infrared stimulation was applied by a cylindrical copper heat exchanger (diameter: 2.6 cm) connected to a TAMSON temperature controlled waterbath. A continuous flow of warm water through the heat exchanger stabilized the temperature with an accuracy of 0.1 °C. The temperature of the heat exchanger was monitored by a FLUKE 2100A digital thermometer with a calibrated thermocouple, which was placed in the copper wall. The front of the heat exchanger was painted with blackboard paint to reduce light reflection and to increase the emissivity, and it was mounted behind a shutter in a screen. Both screen and shutter were made of PVC backed with a reflective material to reduce thermal conduction from the heat exchanger.

The infrared properties of this set-up were tested for time dependent phenomena with an AGA infrared camera (THERMOVISION 750) in the Thermal Control Laboraty of the European Space and Technology Centre (ESTEC), Noordwijk. The effective blackbody radiation of the shutter and the heat exchanger were measured in the Department of Biophysics, Leiden University (Thermopile DRC model 2M, KBR window; calibrated by a NPL calibrated EPPLEY thermopile). The shutter proved to be 99% effective and the actual emissivity appeared to depart negligibly from 1.

Signal Acquisition and Processing. The microelectrodes were connected to a BURLEIGH PZ-550 Inchworm Translator System by which penetrations were made with an accuracy in depth of 2 µm. The indifferent electrode was placed in the buccal cavity. Processing was carried out with a capacitance compensated pre-amplifier and monitored by an oscilloscope and headphone. When required the signal was transferred to an analog tape recorder.

Test Procedure. a) A heat sensitive neuron was located by moving a hand in front of the snake while slowly penetrating the tectum. b) A light test was performed to ensure that a particular unit was a true infrared unit and not (also) sensitive to visual input. When these criteria were fulfilled the penetration depth was registered. c) The receptive field was roughly delineated by moving the hand horizontally and vertically in front

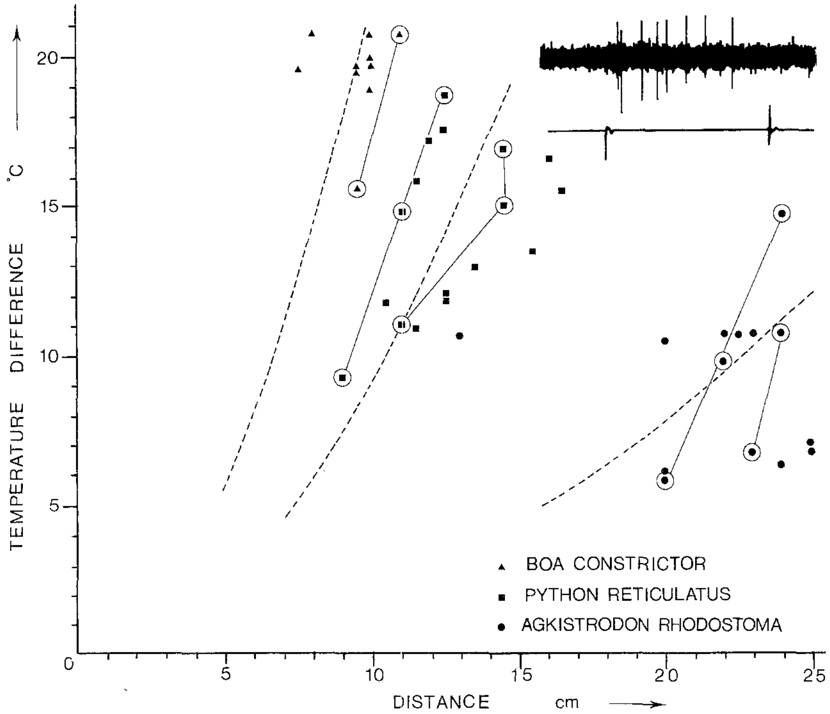

Fig. 3. Direct measurements. The critical distance at which a neural signal could be obtained in 50% of the trials plotted against temperature difference between heat exchanger and screen. In 5 units the critical distance was measured at different temperatures of the heat exchanger. Measurements within each unit are encircled and connected. Dashed lines indicates the Stefan-Bolzmann relation between temperature difference and distance according to the mean threshold values of the three snake species; see also Table 1. Inset: Extracellulary recorded response (suprathreshold) from an infrared sensitive tectal unit responding to a stimulus of 15 °C temperature difference at 8.5 cm distance, in *Python reticulatus*. Lower bar, stimulus duration of 3.6 s

of the head of the snake. d) The infrared stimulator was placed in the centre of this receptive field. e) While moving the infrared stimulator away from the head of the snake the neural response to the action of the shutter was monitored, both audibly and visually. When only 50% of the stimuli evoked a neural response the distance between the head of the snake and the heat exchanger was named the 'critical distance'. From every infrared unit the critical distance and the related temperatures of the heat exchanger and the shutter were registered. In five cases the unit could be kept long enough to obtain data with different temperatures of the heat exchanger.

Results and Discussion

Measurements

In contrast to the surface of the tectum, where abundant activity of visual units was recorded, the deeper layers showed only sparce activity of infrared sensitive units. Neural activity of exclusively heat sensitive neurons was detected in *Agkistrodon* at a depth of 156–600 µm (11 units); in *Python* between 400–1,412 µm (13 units) and in *Boa* between 750–1,864 µm (9 units). These penetration depths do not differ from those reported in the literature: *Python reticulatus* 600–1,500 µm (Haseltine 1978) and *Agkistrodon blomhoffi brevicaudus* about 200 µm (Terashima and Goris 1975).

Most units showed a clearly distinguishable burst at the action of the shutter without background discharge (Fig. 3). However, in some units a low frequency background discharge was present (5–11 spikes/min) but this did not obscure the response to the infrared stimulus.

In Fig. 3 the difference between background temperature and stimulus temperature are plotted against the critical distance measured. It is obvious that the three snake species produce three different groups of data (one way analysis of variance: $F=109.526$; $df=2\ 39$; $P \ll 0.01$).

The two parameters of temperature and distance can be substituted in a simplified formula of Stefan-Bolzmann, which describes in more comparable terms the amount of energy flux per square centimeter per second:

$$\text{radiation density } (\mathrm{cal/cm^2 \cdot s}) = \frac{\sigma \times A \times (T2^4 - T1^4)}{\pi \times D^2},$$

where: σ = constant of Stefan-Bolzmann: $1.35\ 10^{-12}\ \mathrm{cal/cm^2 \cdot s \cdot K^4}$; A = the radiating area: $5.31\ \mathrm{cm^2}$; $T2$ = temperature (°K) of the heat exchanger; $T1$ = temperature (°K) of the shutter; D = critical distance in cm.

The critical radiation densities at the level of the sense organs can be thus computed for the three snake species (see Table 1). The most sensitive units measured in the three species appear to respond to change in heat flux of $42.28\ 10^{-6}\ \mathrm{cal/cm^2 \cdot s}$ in *Boa constrictor*; $14.28 \cdot 10^{-6}\ \mathrm{cal/cm^2 \cdot s}$ in *Python reticulatus* and $2.57 \cdot 10^{-6}\ \mathrm{cal/cm^2 \cdot s}$ in *Agkistrodon rhodostoma*.

Table 1. Critical radiation density

Species	Mean ($\mathrm{cal/cm^2 \cdot s}$)	SD ($\mathrm{cal/cm^2 \cdot s}$)	Lowest value ($\mathrm{cal/cm^2 \cdot s}$)
Boa constrictor ($n=10$)	$48.96 \cdot 10^{-6}$	$13.53 \cdot 10^{-6}$	$42.28 \cdot 10^{-6}$
Python reticulatus ($n=17$)	$19.52 \cdot 10^{-6}$	$4.9 \cdot 10^{-6}$	$14.28 \cdot 10^{-6}$
Agkistrodon rh. ($n=14$)	$4.38 \cdot 10^{-6}$	$2.74 \cdot 10^{-6}$	$2.57 \cdot 10^{-6}$

The Relation between Temperature and Distance

The five units which could be tested at different stimulation temperatures show a similar slope in their relation between critical distance and stimulus temperature (Fig. 3). The units from *Boa* and *Python* resemble the expected function of the simplified Stefan-Bolzmann formula, but the two units of *Agkistrodon* have a considerably larger slope. In other words, the infrared sensitive system in boids behaves, qua temperature-distance relation, as a thermopile, whereas in crotalids larger temperature differences are necessary to evoke the same minimal threshold response at larger distances than expected, a phenomenon which can not be explained yet.

Threshold

In the literature two different equations to calculate the threshold (=minimum radiation density necessary to evoke a neural response) on the basis of distance and temperature are used. Terashima et al. (1968) used the Stefan-Bolzmann formula simplified by the assumption that all objects emit radiation with an emissivity of 1.0. Bullock and Diecke (1956) used an approximation of the Stefan-Bolzmann formula in which the temperature appeared as a linear function instead of a function to the power four:

$$\text{radiation density } (\mathrm{cal/cm^2 \cdot s}) = 1.3 \times 10^{-4} \times (T2 - T1) \times (\text{radius/distance})^2.$$

However, this approximation departs 5% from the Stefan-Bolzmann values for temperature differences of 3 °C, while larger temperature differences, as in the experiments with *Boa constrictor* ($\Delta T = 20$ °C), show a departure of more than 15%. For this reason and for the reason that the experimental verification by means of a thermopile showed no significant difference from the theoretical values of the simplified Stefan-Bolzmann formula, it is justifiable to adopt the simplified Stefan-Bolzmann formula as used by Terashima et al. (1968).

Regarding the Stefan-Bolzmann formula which is central to this discussion, I would like to make the following comment.

Originally this formula was designed to describe the net flux of radiation between two heat radiating objects with temperatures $T1$ and $T2$. Therefore, one tends to substitute for $T1$ the temperature of the pit organ (or the snake) and for $T2$ the temperature of the warm test object (or mouse/rat). However, in terms of physics the test situation described in this paper implies a change of radiant flux between before and after opening the shutter. Consequently, in the final formula the temperature of the snake is cancelled.

$$\text{radiation density } (\mathrm{cal/cm^2 \cdot s}) =$$

$$\frac{\sigma \times A}{\pi \times D^2}\left((\mathrm{T}^4 \text{ stimulus} - \mathrm{T}^4 \text{ snake}) - (\mathrm{T}^4 \text{ shutter} - \mathrm{T}^4 \text{ snake})\right) =$$

$$\frac{\sigma \times A}{\pi \times D^2}(\mathrm{T}^4 \text{ stimulus} - \mathrm{T}^4 \text{ shutter}).$$

In other words, the change of radiant heat influx on the pit organs can be regarded as the result of a change in the infrared environment, i.e., that small area which only changes in temperature (in this case the shutter and heat exchanger or the presence or absence of a mouse).

This implicates that the temperature of the sensor is not relevant for the ability of the system to discriminate temperature differences in the environment. Although, the intensity of the receptor response towards a specific stimulus is, of course, a function of a biologically related optimum temperature of the body (de Cock Buning 1981b, c; Hensel 1975), on the other hand, there is no argument from the physics to expect a relation between the threshold value and the temperature of the body. The same conclusion was reached by Bullock and Diecke (1956) and illustrated by one of their experiments. 'Experimentally, in a certain whole nerve preparation the response to a hand at 20 cm in a room equilibrated to 21 °C was about threshold. Wheeling the preparation and equipment into a cold room at 15 °C nearly doubled this distance, to 37 cm. There was no noticeable difference in threshold between the first moments when the snake's body temperature was still warm and spon-

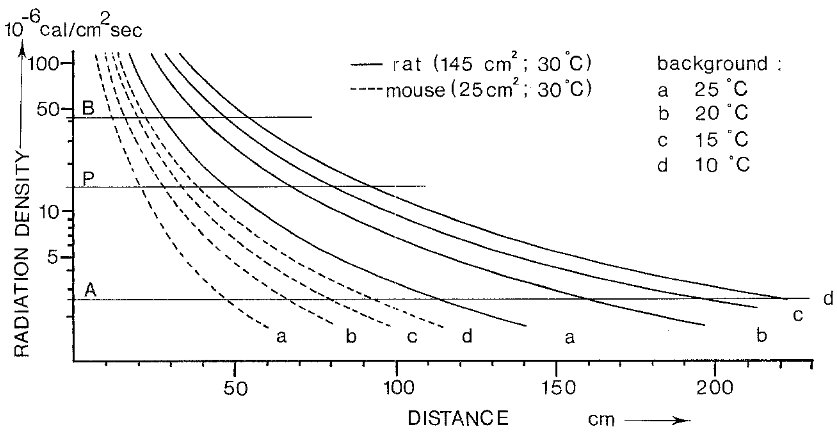

Fig. 4. Relation between radiation density and distance from the radiating object according to the simplified Stefan-Bolzmann formula (see text). Dashed curves are plotted for a radiating area of 25 cm^2 (estimation for a mouse, see text), and solid curves for a radiating area of 145 cm^2 (estimation for a rat, see text). Also the impact of the temperature difference between radiating object (= 30 °C) and the background plotted for four background temperatures (a, b, c, d). Lowest threshold values of the three snake species examined (see Table 1) indicated by lines B (*Boa constrictor*), P (*Python reticulatus*) and A (*Agkistrodon rhodostoma*). Crosspoints with curves are calculated in Table 2 and indicate the maximal detection range at which the snakes can perceive a mouse or rat under the given background temperature

Table 2. Maximum distance of detection according lowest threshold value (mouse = 25 cm^2, 30 °C; rat = 145 cm^2, 30 °C)

		Background temperature			
		25 °C	20 °C	15 °C	10 °C
Boa constrictor	Mouse	11.8	16.4	19.9	22.7
	Rat	28.3	39.6	47.9	54.6
Python reticulatus	Mouse	20.2	28.3	34.2	39.0
	Rat	48.8	68.1	82.4	93.9
Agkistrodon rh.	Mouse	47.7	66.6	80.6	91.9
	Rat	114.9	160.5	194.2	221.4

taneous activity still high (following adaptation from the initial cold background inhibition) and later when lowered body temperature and lowered spontaneous activity came about.' (Bullock and Diecke 1956, p. 61).

When the temperature difference, the radiating area of a mouse or a rat and the threshold are known, the maximal range at which the prey can be perceived can be computed with the simplified Stefan-Bolzmann formula:

maximal detection range (cm) =

$$\sqrt{\frac{\sigma\times A\times(T2^4-T1^4)}{(\text{threshold})\times\pi}}.$$

Recent research in our laboratory with an AGA infrared camera indicates that most radiation comes from the trunk plus the fur (H.A.J. in den Bosch, personal communication). Therefore, the area included by the profile of the animal is taken as an approximation of the radiating area: mouse (30 g) = 25 cm^2; rat (400 g) = 145 cm^2. Figure 4 shows the computed relation between radiation density received at the pit organ and the distance between the pit organ and the prey, plotted for four different temperature differences (see also Table 2).

Comparison with Other Literature

As is shown in Table 1 the lowest value found for the radiation density which still activates in 50% of the trials the pit organ in *Agkistrodon* appears to be 50 times lower than reported by Bullock and Diecke (1956) in *Crotalus*: $3\cdot10^{-4}$ cal/cm$^2\cdot$s. This discrepancy can be explained as follows: Firstly, the oscilloscopic endpoint method used by Bullock and Diecke gives always a higher value than the 50% method used in this paper. Secondly, their value is based on neurophysiological recordings from the peripheral maxillary branch of the nervus trigeminus. These preparations show continuous background discharge in crotalids (Bullock and Diecke 1956; de Cock Buning et al. 1981b; Goris and Nomoto 1967), which means that the experimenter has to decide audibly or visually whether there is an increase of firing during stimulation. In other words, the very small changes near the threshold value tend to be obscured by the background activity. By way of contrast, at the tectal level very low activity of background activity (Goris and Terashima 1973) makes it easy to decide whether a response is present or not. This phenomenon appears to be independent of the anesthesia; applied procedures: Tubocurarine hydrochloride (Goris and Terashima 1973; Terashima and Goris 1975), methoxyflurane (Hartline 1974; Hartline et al. 1978; Haseltine 1978; Newman and Hartline 1981) or Halothane [present paper]. Thirdly, Terashima (1980) found that from the periphery via the medulla to the tectum, the neural response to a standard stimulus is internally amplified in crotalids. A minor increase of frequency at the periphery becomes an obvious burst in the tectal units. The tectum is therefore the most suitable place to detect electrophysiologically small increments of response.

Harris and Gamow (1971) are the second to mention a threshold value. They found, by means of evoked potentials in *Boa constrictor* with permanently implanted electrodes on the surface of the telencephalon, a threshold of $1.8 \cdot 10^{-3}$ cal/cm^2·s. However, there are few grounds for reasonable comparison with the data presented here because of the different placement of the electrodes, and the interpretational difficulties of evoked potentials.

Bullock and Diecke (1956) computed from ethological data mentioned in the article of Noble and Schmidt (1937) a threshold value similar to their own reported threshold ($= 1.3 \cdot 10^{-5}$ cal/cm^2·s for *Crotalus*). However, it is unclear upon which of the figures presented in Noble and Schmidt (1937) their calculation is based.

Indeed, Noble and Schmidt (1937) give sufficient relevant data to enable the application of the simplified Stefan-Bolzmann formula. *Boa hortulana* (= *Corallus enydris*) with pit organs similar to that of pythons is able to discriminate a 25 W lamp bulb wrapped in cloth at 48.5 cm distance. The temperature of the wrapped bulb was 69 °C, the surrounding 25.2 °C and the snakes were blindfolded. Unfortunately, the diameter of the bulb has to be estimated: probably at that time (1937) quite large, say $R = 3$ cm. With these figures the Stefan-Bolzmann formula gives a radiation density of $30.0 \cdot 10^{-6}$ cal/cm^2·s, which is of the same order as the data presented in this paper.

Recently, a similar infrared sensitive trigeminal system was described in another vertebrate, the common vampire bat *Desmodus rotundus* (Kürten and Schmidt 1982). The anatomical construction of the sense organ, as well as the behaviourally obtained threshold ($0.5 \cdot 10^{-4}$ W/cm $= 11.9 \cdot 10^{-6}$ cal/cm^2·s) resemble the situation reported here in *Python reticulatus*. This seems to confirm again the explanation of the Stefan-Bolzmann law proposed here: Whether the sensing animal is coldblooded or warmblooded, in other words whether the sensitive area with receptors is at room temperature or above room temperature (as in the case of the bat: resp. 24.2 °C and 29 °C) is not relevant for detecting changes in heat radiation from the environment.

Behavioural Implications

Regarding the strike distance, behavioural reports mention for *Python* 8 cm (de Cock Buning et al. 1978), *Agkistrodon* 2–3 cm (de Cock Buning et al. 1981a) and *Boa* 5–10 cm (R.G. Bout, personal communication) which are all well within the maximal detection range. Therefore, the advantage gained by the maximalization of the infrared detection range, as seen in crotalids, has to be sought in other behavioural phases, e.g., the arousal and/or the hunting phase (de Cock Buning 1981a).

The small and slender *Agkistrodon rhodostoma* is known to hunt small rodents such as mice. This means, according to Fig. 4 and Table 2, that the maximal detection range varies between 47 and 91 cm, depending on the background temperature. On the other hand large constricting boids like *Python reticulatus* and *Boa constrictor* can easily feed on larger rodents such as rats. This implies, according to Fig. 4 and Table 2, that the maximal detection ranges of these species are also in the same order as for *Agkistrodon rhodostoma*: between 28 and 93 cm (depending on the background temperature). This detection range is not beyond that expected for animals which show a 'sit-and-wait' hunting strategy in dense vegetation (de Cock Buning 1983).

Figure 4 also reveals that the influence of the temperature difference between the background and the prey is an important factor. In biological terms, as the sun goes down the role played by vision diminishes, the temperature of the surroundings decreases, but at the same time infrared discrimination and thus the ability to detect warmblooded animals increases. Generally speaking, the behavioural hunting strategies are expected to be adapted to environmental circumstances. This correlates well with the observation that *Agkistrodon blomhoffii brevicaudus* (the Japanese mamushi) hunts at sunset in low shrubs and open fields (de Cock Buning et al. 1981a) where the drop of temperature is already considerable during the early evening. *Trimeresurus flavoviridis* (the Japanese habu) is known to hunt birds just before sunrise (Tanaka et al. 1967) in the tropical woods where the moist atmosphere retains the heat in the trees until a sudden drop of 3–5 °C just before dawn. Similar activity patterns are also described by Klauber (1972) in rattlesnakes.

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