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Body Temperature of Subtropical Snakes at Night: How Cold is Their Blood?

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Abstract: Thermal biology of snakes has been extensively studied, but vast majority of them deals with diurnal species distributed in temperate regions. During a long-term field study of a pitviper on subtropical Okinawa Island, the Ryukyu Archipelago, Japan, we had an opportunity to obtain body temperature data from six syntopic species of snakes belonging to the families Colubridae, Xenodermidae, Viperidae, and Elapidae that are active at night there. Mean body temperature of those nocturnally active snakes over a year was relatively low, ranging from 17.7 to 22.3°C, although research effort was largely biased to the cooler period of the year. Lowest body temperature of the six species ranged from 10.9 to 20.0°C. Irrespective of species, body temperature was highly correlated with both ambient air and substrate temperatures. Importance of future research on the activity of subtropical, nocturnal snakes under low temperature is briefly discussed.

Key words: Body temperature; Nocturnal activity; Snakes; Subtropics; Thermoregulation

Introduction

Historically, reptiles were called "cold-blooded" animals because they were believed to have little physiological ability to produce heat by their metabolic activity, and thus they were considered to be unable to maintain high body temperature unlike "warm-blooded" animals such as mammals and birds. Extensive studies on the thermal biology of reptiles, however, have revealed that many species of reptiles behaviorally, and even physiologically, regulate their body temperature. Indeed, some reptiles are reportedly able to maintain body temperature around values comparable to those of mammals and birds (Heatwole and Taylor, 1987; Vitt and Caldwell, 2014; Pough et al., 2016). Vast majority of these studies is based on those species that are mainly active in the day and are distributed in the temperate zone, where reptiles cease their activity and hibernate during the cool season. Thermal biology of nocturnal reptiles, which are not uncommon especially in subtropical and tropical zones (Greene, 1997; Vitt and Caldwell, 2014), have not been studied well: Even information regarding the simple active body temperature in the wild is much more

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limited for nocturnal reptiles than for the diurnal species (Ota, 2004; Rock and Cree, 2008). Because solar radiation, the primary external heat source for diurnal reptiles, is not available at night, thermal strategy of nocturnal reptiles could be different from that of the former. Therefore, basic information on thermal characteristics of nocturnal species is important to fully understand the thermal strategy of reptiles.

During a long-term field study on an Asian pitviper *Ovophis okinavensis* (Viperidae) in the northern area of Okinawa Island, Japan under the subtropical climate, we had a number of opportunities to collect data for active body temperature of six syntopic species of snakes at night. A previous study on the field body temperature of *O. okinavensis* in this study area (Mori et al., 2002) demonstrated that this species is active at night with relatively low body temperature (mean=16.1°C), and suggested a possible occurrence of adaptation to cool temperatures in subtropics. Here, we present body temperature data for six additional species of snakes from Mori et al.'s (2002) study area, which include representatives of three families besides Viperidae, to provide additional knowledges on the thermal biology of nocturnal reptiles. Based on body temperature data of these species, we briefly discuss the possible occurrence of the cool temperature adaptation as a common trait of subtropical snakes.

Materials and Methods

The field survey was conducted in a limited area of the northern part of Okinawa Island, the Ryukyu Archipelago, Japan between December 1996 and December 2017, when a long-term field study of *O. okinavensis* was concurrently conducted in the same area (see Mori et al., 2002; Mori and Toda, 2011). The main study area (ca. 0.25 km^2) encompasses the upper streams of Zatsun River and surrounding hilly environments of Yambaru (26°48'N, 128°16'E). Vegetation was dominated by primary and well-recovered secondary forests consisting of humid-subtropical broad-leaved evergreen trees such as *Castanopsis sieboldii*. Meteorological data of the study area is shown in Mori et al. (2002). Field study was made throughout the year but with particularly high intensities from December to March for the purpose of investigating the relationship of winter activity of *O. okinavensis* with the breeding activity of two species of frogs. Basically, we haphazardly walked at night along streams and trails, which run though the study area irregularly, searching for snakes on the surface. We also used a road cruising technique to find snakes on the road. The road is an approximately 7 km segment of the routes Benoki, I-e, and Chinufuku, which partially surrounds the main study area and crosses the Yambaru forests. These routes run through various habitats, such as forests along hill ridges, slopes and streams, and a forest park with more open habitats. The straight distance from the main study area to the farthest point of the segment is approximately 3 km.

Among eight species of snakes distributed on Okinawa Island (Maenosono and Toda, 2007), six species were focused on in this study; three colubrids, *Hebius pryeri*, *Cyclophiopus semicarinatus*, and *Dinodon semicarinatum*; one xenodermid, *Achalinus werneri*; one viperid, *Protobothrops flavoviridis*; and one elapid, *Sinomicrurus japonicus boettgeri*. All of these species are endemic to the Central Ryukyus (Hikida and Ota, 1997). We excluded the other two species, *O. okinavensis* and *Indotyphlops braminus*, from this study because extensive thermal data have been already published (former species, Mori et al., 2002) or no individual was found during the survey (latter species). Quantitative field ecological studies of the six focal species are quite limited, but all of them, except for *C. semicarinatus*, are considered to be active mainly during the night (Takara, 1962; Sengoku et al., 1996). *Cyclophiops semicarinatus* is often found active during the day (Nakachi, 1995; Sengoku et al., 1996), but its nocturnal activity is not uncommon

(Nakaima, 1983; this study). All species mostly exhibit terrestrial activity, but *P. flavoviridis* also climbs trees occasionally, and *A. werneri* and *S. j. boettgeri* are considered partially semi-fossorial (Sengoku et al., 1996; Goris and Maeda, 2004).

During both the walking survey and road cruising, we attempted to collect snakes whenever we found them. Individual snakes found in exposed states after sunset and before sunrise (or before direct sun light became available) were considered active at night. We did not include data of snakes that were hiding themselves in shelters because we are interested in body temperature when snakes are engaging themselves in some activities. Most of the surveys were conducted at night, but we also occasionally made field surveys in the day as well. Because we focused on body temperature of active snakes at night, we limited use of data obtained in the daytime to comparative purposes.

Immediately after a snake was collected, we measured cloacal body temperature to the nearest 0.1°C with a thermistor (Takara, Digimulti D611 or Sato, Sk-1260). The ambient air temperature of 1 m above the ground (AT) (in shade in case of daytime) and substrate temperature (ST) of the site, at which the snake was first sighted, were also measured. If the snake was positioned in water, water temperature was measured as ST. After processing of the snake (measuring body size, examination of stomach contents, etc.), we marked it by ventral scale clipping for future identification and basically released it at the site of capture within 24 h after collection. If we captured marked individuals, we conducted the same measuring process, but we did not use data of recaptured individuals in this study to maintain the independency of the data.

Results

Body temperature was measured at night for 100, 15, 22, 6, 15, and 3 individuals of *H. pryeri*, *C. semicarinatus*, *D. semicarinatum*, *A. werneri*, *P. flavoviridis*, and *S. j. boettgeri*, respectively. Irrespective of species, body temperature in winter months (December to February) was relatively low, being under 20°C in most cases with monthly mean ranging from 13.3 to 20.0°C (Table 1). Lowest body temperature of the six species ranged from 10.9 to 18.8°C. On the other hand, body temperature in summer (June to August) was around 25°C although sample sizes in summer are quite small.

Body temperature at night highly depends on and nearly equals to both AT and ST in all species (Fig. 1). This tendency seems to be also true even when body temperature measured in the day was included for *H. pryeri* and *C. semicarinatus*, except for a few individuals of the latter. In *H. pryeri*, *C. semicarinatus*, *D. semicarinatum*, and *P. flavoviridis* body temperature at night was significantly correlated with both AT and ST (*H. pryeri*, AT, $r^2=0.971$, $P<0.0001$, ST, $r^2=0.981$, $P<0.0001$; *C. semicarinatus*, AT, $r^2=0.941$, $P<0.0001$, ST, $r^2=0.975$, $P<0.001$; *D. semicarinatum*, AT, $r^2=0.889$, $P<0.001$, ST, $r^2=0.958$, $P<0.001$; *P. flavoviridis*, AT, $r^2=0.966$, $P<0.001$, ST, $r^2=0.981$, $P<0.001$). No statistical analyses were made for *A. werneri* and *S. j. boettgeri* because of their small sample sizes.

Discussion

To the present, a limited number of studies has been made on the thermal biology of nocturnally active snakes. These, nevertheless, have shown various thermal strategies: Snakes maintain activity at relatively low temperature, being as low as 10°C (Dorcas and Peterson, 1998), reduce activity when ambient temperature decreases (DeNardo et al., 2002), or maintain body temperature as high as that of typical diurnal snakes (Secor, 1995). On the other hand, nocturnal snakes in tropical regions may not need behavioral thermoregulation because of benign thermal conditions (Shine and Madsen, 1996) or may thermoregulate only under certain circumstances (Luiselli and Akani, 2002; Anderson

TABLE 1. Monthly mean body temperature of six species of snakes collected at night in the northern area of Okinawa Island. Snakes were collected between sunset and sunrise (or when direct sun light became available). Range and sample size are shown in parentheses.

Month	Species					
	Hebius pryeri	*Cyclophiops semicarinatus*	*Dinodon semicarinatum*	*Achalinus werneri*	*Protobothrops flavoviridis*	*Sinomicrurus japonicus boettgeri*
January	17.0 (12.7–20.2, 10)	15.6 (14.6–16.6, 2)	15.0 (14.0–16.0, 2)	18.0 (16.1–19.9, 2)	17.8 (14.4–21.5, 3)	—
February	16.5 (14.3–20.8, 16)	—	16.4 (13.4–19.4, 2)	16.3 (1)	13.3 (12.4–14.1, 2)	—
March	18.7 (16.9–20.6, 7)	18.6 (17.6–20.0, 3)	16.7 (15.6–17.8, 2)	22.4 (1)	22.2 (20.2–24.2, 2)	—
April	18.5 (1)	—	19.7 (1)	—	—	—
May	19.6 (19.1–20.1, 2)	—	—	—	—	—
June	24.7 (1)	—	22.4 (21.8–23.0, 2)	—	—	—
July	23.9 (22.9–24.6, 8)	—	25.2 (24.5–25.9, 2)	—	—	—
August	26.9 (26.3–27.4, 4)	30.1 (1)	25.2 (24.5–25.8, 3)	—	24.8 (24.7–25.0, 3)	28.6 (1)
September	25.1 (24.7–25.4, 4)	—	—	—	—	—
October	—	—	22.9 (21.0–24.9, 3)	—	22.8 (1)	—
November	18.9 (18.0–19.6, 7)	—	—	—	21.6 (1)	18.3 (1)
December	17.8 (10.9–22.9, 40)	16.5 (14.4–19.8, 9)	18.1 (16.4–19.3, 5)	18.6 (17.7–19.5, 2)	17.2 (13.4–20.5, 3)	20.0 (1)
Total	18.9 (10.9–27.4, 100)	17.7 (14.4–30.1, 15)	20.3 (13.4–25.9, 22)	18.7 (16.1–22.4, 6)	19.6 (12.4–25.0, 15)	22.3 (18.3–28.6, 3)

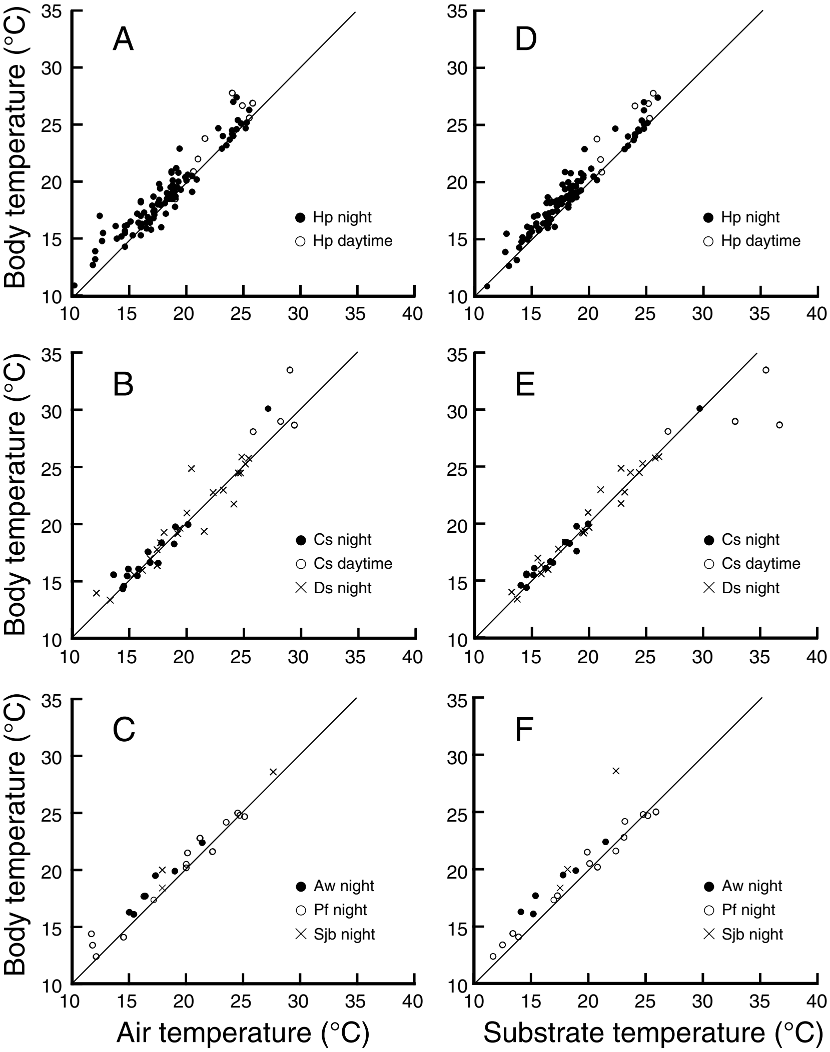

FIG. 1. Thermal relations of six species of snakes observed at night. Relationships between air temperature and body temperature in (A) *Hebius pryeri* (Hp), (B) *Cyclophiopus semicarinatus* (Cs) and *Dinodon semicarinatum* (Ds), and (C) *Achalinus werneri* (Aw), *Protobothrops flavoviridis* (Pf), and *Sinomicrurus japonicus boettgeri* (Sjb). Relationships between substrate temperature and body temperature in (D) *H. pryeri*, (E) *C. semicarinatus* and *D. semicarinatum*, and (F) *A. werneri*, *P. flavoviridis*, and *S. j. boettgeri*. For *H. pryeri* and *C. semicarinatus*, data measured in the day are also shown. The line where body temperature is equal to ambient temperature is also shown in each figure.

et al., 2005). Considering that preferred or active body temperature of snakes hitherto studied usually ranges from 25 to 35°C (Avery, 1982; Lillywhite, 1987, 2014; Mori et al., 2002), mean body temperatures of the six species in our study are relatively low, but this is apparently underestimated due to the biased research effort to the cool season. Nonetheless, activity in cool months with low body temperature (less than 20°C and as low as 11 to 14°C) indicate that they are capable of voluntary activity under the low temperature condition. In addition, strong correlations of body temperature with ambient temperatures, which is a typical pattern of thermoconformers (Huey, 1982), indicate that these snakes do not actively thermoregulate, at least during the night.

Nocturnal snakes living in subtropics would offer an interesting opportunity to investigate the evolution of thermoregulatory strategy in this group of organisms. In subtropical regions, ambient temperature at night in the cool season may not still become a critically lethal level for snakes. However, it may not be high enough to maintain their body temperature at the level of those in the typical diurnal snakes in the temperate zone or nocturnal snakes in the tropical zone, unless special heat sources, such as geothermal ones, are available. Mori et al. (2002) suggested that *O. okinavensis* on Okinawa Island, which exhibits an extensive foraging activity in the cool season, have behaviorally and/or physiologically adapted to low temperatures of the season in its habitats. Ota (2004) also documented relatively low body temperature (lower than 20°C; 16.4°C at lowest) in the cool season for individuals in active state at night of a semi-aquatic colubrid species *Opisthotropis kikuzatoi* on Kumejima, an island ca. 70 km west of Okinawa Island. All six species in our study as well as *O. okinavensis* and *Op. kikuzatoi* are endemic to the Amami and Okinawa Groups of the Central Ryukyus, which are located in the subtropical zone (Hikida and Ota, 1997). The activity of the six species with relatively low body temperature in the cool season, as well as Ota's (2004) observations, implies that snakes of this region with at least partial nocturnal activities have evolved physiological adaptation to low temperature conditions, although it may not be as prominent as *O. okinavensis*. Comparative studies of thermal characteristics, including preferred body temperature, of these snakes, as well as some nocturnal lizards of the Central Ryukyus, such as *Goniurosaurus kuroiwae*, for which occasional activities during the cooler season in the field and even preference for relatively low ambient temperature in experiments are reported (Tanaka and Nishihira, 1987; Werner et al., 2005), are necessary to clarify the unique aspects of thermal adaptations in snakes and other squamate reptiles occurring in subtropical regions.

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