动物学报　51（1）：38－45，2005
Acta Zoologica Sinica

Variation in body temperature as a consequence of the response to heating lights under a light-dark cycle in the Chinese cobra *Naja atra* *

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Abstract We used 7 Chinese cobras *Naja atra* to investigate variation in body temperature as a consequence of the response to heating lights under a light-dark cycle. Two trials of which each lasted 9 successive days were conducted，with one trial having lights on during the day（DPNS，day/photophase-night/scotophase）and the other having lights on during night（NPDS，night/photophase-day/scotophase）. Cobras could regulate their body temperatures when the lights were on；however，at no time during the photophase did all cobras simultaneously maintain higher body temperatures. Temporal variation in the percentage of thermally active cobras was evident in both trials，with the oscillations of activity being relatively more obvious in the NPDS trial. During the photophase，the percentage of thermally active cobras generally was higher in the DPNS trial than in the NPDS trial. Temporal variation in body temperature was not evident for thermally active cobras in either trial. Thermally active cobras maintained on average higher body temperatures in the DPNS trial than in the NPDS trial，whereas thermally inactive cobras did not differ in mean body temperature between both trials. The upper level of body temperatures selected by thermally active cobras was higher in the DPNS trial（31.1 ± 0.8 ℃）than in the NPDS trial（26.0 ± 0.9 ℃）. At no time during the course of each trial did cobras maintain body temperatures lower than ambient temperatures［*Acta Zoologica Sinica* 51（1）：38－45，2005］.

Key words Reptilia，Elapidae，*Naja atra*，Thermal activity，Body temperature，Thermoregulation，Radio-telemetry

舟山眼镜蛇对光暗周期加热光源反应所导致的体温变化 *

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摘　要　用7条舟山眼镜蛇（*Naja atra*）研究动物对光暗周期加热光源反应所导致的体温变化。设计两项实验，每项实验历时9 d。实验一光照期覆盖整个白天，实验二光照期覆盖整个晚上。眼镜蛇仅在加热光源开启期间进行体温调节，但光照期内任何阶段都未发现所有个体同时处于热活动状态。两项实验中热活动个体百分比的时间变化显著，实验二热活动个体百分比波动相对大于实验一。在加热光源开启期间，实验一热活动眼镜蛇的百分比总体上大于实验二。在两项实验中，热活动眼镜蛇体温的时间变化都不显著。实验一热活动眼镜蛇的体温高于实验二，而两项实验中不处于热活动状态的眼镜蛇的平均体温无显著差异。实验一热活动眼镜蛇（31.1 ± 0.8 ℃）选择的体温上限高于实验二眼镜蛇（26.0 ± 0.9 ℃）。在两项实验的任何时间段内，眼镜蛇的体温都不低于环境温度［动物学报 51（1）：38－45，2005］。

关键词　爬行纲　眼镜蛇科　舟山眼镜蛇　热活动　体温　体温调节　无线电遥测

Reptiles are subject to daily and seasonal fluctuations in body temperature due to thermal interactions

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Received June 18，2004；accepted Sep. 24，2004

* This research was funded by the grants from the National Natural Science Foundation of China（No.30070121）and the Ministry of Education of China

** Corresponding author. E-mail：xji@mail.hz.zj.cn between the animal and its environment. Because moderate to relatively high body temperatures usually maximize physiological and behavioral performances, reptiles should regulate body temperature during the active phase of the daily activity cycle, thereby maintaining body temperatures at some high and constant level (Huey, 1982; Huey and Kingsolver, 1989; Bennett, 1990). Reptiles regulate body temperature mainly by behavioral mechanisms such as habitat selection, restriction of periods of activity and selective exploitation of short-term environmental variations of thermal flux, although physiological thermoregulation through cardiovascular adjustments, endogenous heat production and evaporative cooling may be also important (Bartholomew, 1977, 1982; Huey, 1982; Wang and Xu, 1987; Sun et al., 2002; Pan et al., 2003; Zhang et al., 2003). In the environment where thermal conditions are uniform, behavioral thermoregulation can be rather constrained and, for species whose physiological thermoregulation is very limited or even negligible, variation in body temperature often mirrors variation in ambient temperature (Bartholomew, 1977; Wang and Xu, 1987; Ji et al., 2002; Sun et al., 2002; Pan et al., 2003; Zhang et al., 2003). Because physiological thermoregulation is weak in most reptiles, the existence of temporally and spatially variable heat sources in their general environment is thus a precondition for them to regulate body temperature behaviorally.

Under natural conditions reptiles are able to elevate their body temperatures over the ambient temperature when heat from the sun is available. When heat availability is not constrained for behavioral thermoregulation, they may maintain not only high but also constant body temperatures, at which various functions can be expressed at high levels (Van Damme et al., 1987; Huey and Kingsolver, 1989; Ji et al., 1995, 1996, 1997; Du et al., 2000; Xu et al., 2001; Chen et al., 2003; Le Galliard et al., 2003; Zhang and Ji, 2004). The thermal environments reptiles encounter in the field can be mimicked to some extent in the laboratory by using heating lights under a light-dark cycle, which allows animals to regulate body temperature behaviorally during the light phase and forces them to reduce body temperature during the dark phase (Ji et al., 1995, 1996; Du et al., 2000; Sun et al., 2002; Pan et al., 2003; Zhang et al., 2003; Zhang and Ji, 2004). Because the thermal condition in the light phase is different from that in the dark phase, reptiles can be expected to show different behaviors in the two phases. During the light phase, an animal's response to heating lights results primarily from the demand of thermoregulation and probably also from the evolved rhythm controlled by an endogenous circadian clock. Such a response is absent during the dark phase and may somehow modify the thermal interactions between the animal and its environment, which exert a pronounced effect on variation in body temperature (Sun et al., 2002; Pan et al., 2003; Zhang et al., 2003; Zhang and Ji, 2004).

We used the Chinese cobra *Naja atra* as a model animal to investigate the cobra's response to heating lights under a light-dark cycle and its influence on body temperature. The snake is particularly suitable for such a study, because it is basically a diurnal species but can actively regulate body temperature within the range of air temperatures from 15 – 35 ℃ without a clear-cut daily rhythm of activity (Hu et al., 1966; Liang, 1991; Huang, 1998; Ji et al., 2002). We address three questions: (1) how does a cobra's response to heating lights under a light-dark cycle affect its body temperature? (2) do the selected body temperature, the mean body temperature and variation in body temperature differ between cobras that are active during the day and during the night? (3) is thermoregulation regulated by an endogenous rhythm in this species?

1 Materials and methods

1.1 Animals

Naja atra is a large, highly venomous snake, which is widely distributed in southeastern China, including Taiwan, Hong Kong and Hainan, southward to Vietnam (Wüster, 1996). The cobra is found in a variety of habitats in the hilly countryside and, in Zhejiang (eastern China), the northern limit of the species' distributional range, the cobra can be very abundant in the southern region but absent in the northern parts of the province (Ji and Du, 2001). Cobras are occasionally active in winter when air temperatures are higher than 15 ℃ (Ji et al., 2002) and, during the active season, they are usually out of the nest for hunting prey and/or thermoregulating from 09:00 – 11:00 h (Beijing time) and 19:00 – 23:00 h in summer and from 09:00 – 15:00 h in spring and autumn (Hu et al., 1966; Liang, 1991; Huang, 1998).

Cobras (1 male and 6 non-reproductive females) used in this study were collected in mid-May 2003 from an island population in Dinghai (30° 02′ N, 122°10′E), Zhoushan, eastern Zhejiang. The captured cobras were transported to our laboratory at Hangzhou Normal College, where they were individually sexed, weighed and measured for length. All cobras were adults (Sheng et al., 1988), with snout-vent lengths ranging from 940 – 1 110 mm, and body masses from 320 – 590 g.

1.2 Experimental design

We conducted two trials from 22 May – 10 June 2003, both with a light-dark cycle created by heating lights. One trial had the lights on during the day [hereafter DPNS (day/photophase-night/scotophase) trial], and the other trial had the lights during the night [hereafter NPDS (night/photophase-day/scotophase) trial]. Such a design allowed us to investigate not only the cobra's response to heating lights under a light-dark cycle and its influence on body temperature, but also the possible endogenous rhythmicity of temperature selection (and, thus, of body temperature). We firstly conducted the DPNS trial and then the NPDS trial, both in the same 4.5 m × 3.5 m × 3.0 m (length × width × height) room, with air temperatures never higher than 20 ℃ (Fig.2). We divided the room floor equally into 25 plots, and then randomly selected 4 plots. In the center of each selected plot, we suspended an incandescent bulb (300 W), which was approximately 200 mm above the floor. During the photophase, it created a thermal gradient ranging approximately from 18 – 60 ℃, which allowed cobras to regulate body temperature within their voluntary range. The light cycle of both trials was the same (14L∶10D), but differed in the onset of the lights. Lights were switched on at 06∶00 h in the DPNS trial, and at 1 400 h in the NPDS trial. We reduced costs of thermoregulation by providing food (common toads *Bufo gargarizans*) and water *ad libitum*, and by arranging bricks, debris and blocks of wood used for basking and hiding under the heat lamps. Each trial lasted 9 days and, during the 9-day trial, lamps were re-arranged every 3 days following the procedures described above, thereby simulating the temporal and spatial shifts in heat sources that occur in nature.

1.3 Methods

Data on body temperatures were obtained from temperature-sensitive transmitters (SB-2T, Holohil, Canada) that were force-fed to single cobras. Transmitters, each of which weighed 5 g, operated at frequencies of 160.200 and 160.800 MHz. All transmitters were calibrated by the manufacturer; we verified readings on nine separate occasions in a digital readout waterbath, using a standard thermometer (WBG Ltd., Shanghai, China). The Holohil calibrations and our waterbath recalibrations were always within 0.3℃. Immediately upon ingestion of a transmitter, cobras were released into the room. We allowed cobras to explore the new environment for 12 h, and then received signals at intervals of 1 h using a radio receiver (LA12-Q, AVM Instrument, USA) with a 3-element Yagi antenna, following the procedures described by Ji et al. (2002). Air temperatures in the room were recorded every 10 min using two Tinytalk dataloggers (Gemini Pty, Australia) placed near the two ends of the room, approximately 1.2 m above the floor. No transmitter was regurgitated or defecated during the course of the experiment. At the end of the experiment, we downloaded data stored in the dataloggers into a PC computer for later analysis, and removed transmitters without harming the cobras in accordance with the internationally accepted principles concerning the care and use of laboratory animals (National Research Council, 1985).

We arbitrarily considered a cobra to be thermally active when its body temperature was 4℃ higher than the mean of the lowest five consecutive body temperatures recorded for the cobra during the photophase. We calculated the mean of the highest five body temperatures for each thermally active cobra, and used it as an estimate of the upper level of body temperature selected by the cobra. We analyzed variances in body temperature using the coefficient of variation (= standard deviation divided by the mean).

1.4 Statistical analyses

All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Bartlett's test), and arc-sine transformations were performed on percentage data to achieve the conditions for using parametric analyses. We used repeated-measures ANOVA or one-way ANOVA to analyze the corresponding data when the assumptions for parametric analyses were met, and non-parametric analyses (Mann-Whitney *U* test) when these assumptions were violated. Descriptive statistics are presented as mean ± 1 standard error, and the significance level is set at $\alpha = 0.05$.

2 Results

One cobra in the DPNS trial remained thermally inactive, whereas all others were thermally active in both trials during the time when heat from the incandescent bulbs was available. However, at no time during the photophase did all cobras simultaneously maintain higher body temperatures (Fig.1). Temporal variation in the number (and, thus, in the percentage) of thermally active individuals during the photophase was evident in both the DPNS trial (Repeated-measures ANOVA; $F_{14,56} = 3.96$, $P < 0.0001$) and the NPDS trial (Repeated-measures ANOVA; $F_{13,52} = 4.77$, $P < 0.0001$), with the oscillations of thermal activity being relatively more obvious in the NPDS trial (Fig.1). When data on the percentage of thermally active cobras collected at different times were pooled on a daily basis, the mean percentage (for the 9-day trial) of thermally active cobras was higher overall in the DPNS trial than in the NPNS trial (Mann-Whitney *U* test, $P < 0.0001$).

Temporal variation in body temperature was evident for thermally active cobras in the DPNS trial (Repeated-measures ANOVA; $F_{13,26} = 5.64$, $P < 0.0001$) but not in the NPDS trial (Repeated-mea-

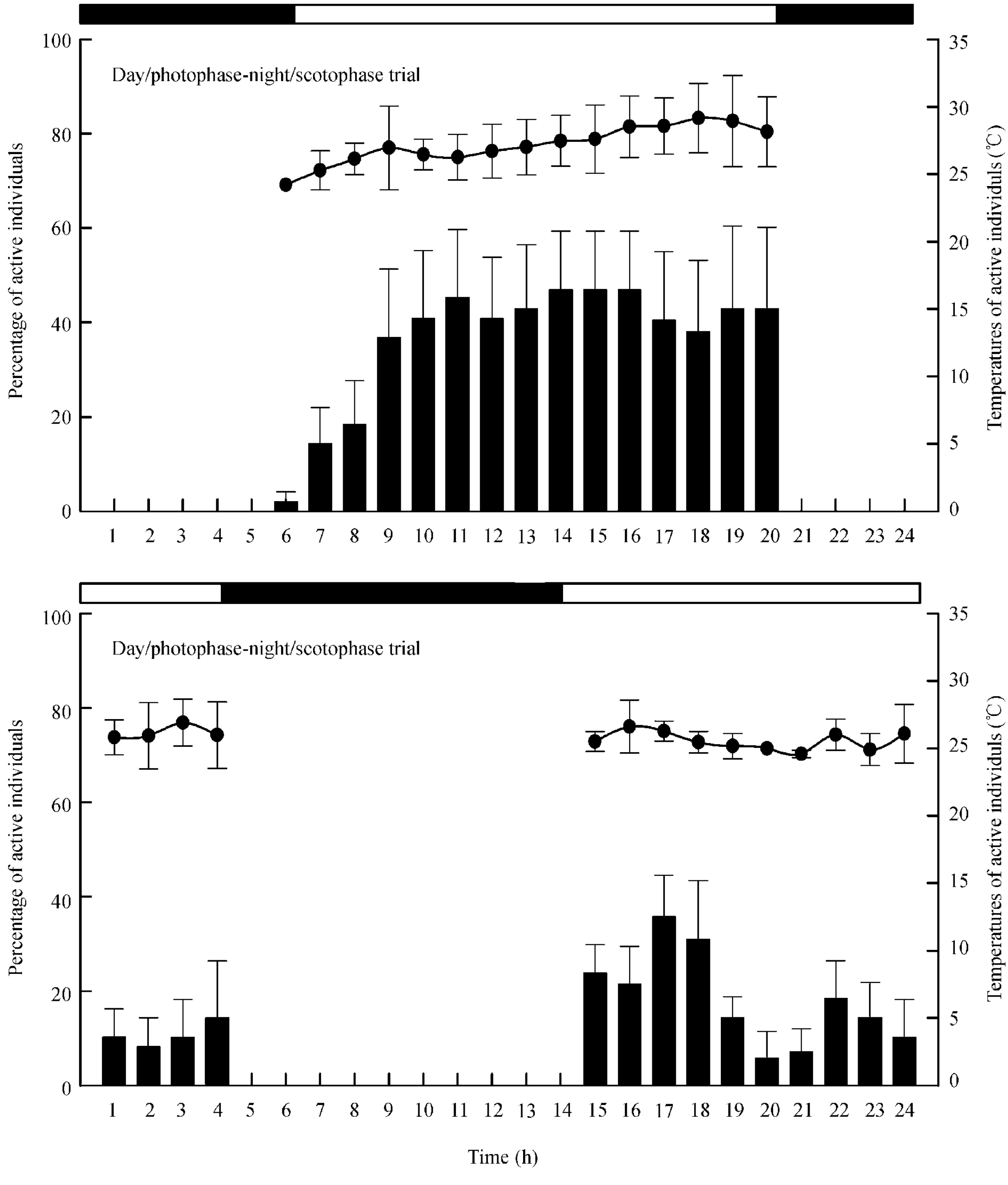

Fig. 1 Activities (indicated by the percentage of active individuals) of cobras under a light-dark cycle of which the photophase covered either the whole daytime or the whole nighttime

A cobra was arbitrarily considered to be thermally active when its body temperature was 4 ℃ higher than the mean of the lowest five consecutive body temperatures recorded for the cobra during the photophase. Body temperatures of active individuals are showed in the figure. All data are expressed as mean ± 1 standard error. Vertical solid bars represent activities, and solid dots body temperatures of active cobras; horizontal solid bar represents the scotophase, and horizontal open bar the photophase.

sures ANOVA; $F_{12,12}=0.554$, $P=0.840$). Thermally active cobras maintained on average higher body temperatures in the DPNS trial than in the NPDS trial ($F_{1,11}=14.11$, $P<0.004$), whereas thermally inactive cobras did not differ in mean body temperature between both trials ($F_{1,12}=0.14$, $P=0.713$) (Table 1). The upper level of body temperatures selected by thermally active cobras (see definition in Methods) was 31.1 ± 0.8 ℃ ($n=6$, range = 28.6 − 33.2 ℃) in the DPNS trial and 26.0 ± 0.9 ℃ ($n=7$, range = 22.5 − 29.4 ℃) in the NPDS trial, and the difference was evident ($F_{1,11}=16.35$, $P<0.002$). The coefficient of variation in body temperature was greater in thermally active cobras than in thermally inactive cobras in the DPNS trial ($F_{1,11}=29.21$, $P<0.0002$), but it did not differ between thermally active and inactive cobras in the NPDS trial ($F_{1,12}=0.37$, $P=0.556$). Neither thermally active ($F_{1,11}=3.33$, $P=0.095$) nor thermally inactive ($F_{1,12}=0.01$, $P=0.913$) cobras differed in the coefficient of variation in body temperature between the two trials（Table 1）．At no time did cobras（either thermally active or thermally inactive）maintain body temperatures lower than ambient temperatures（Fig.2；repeated-measures ANOVA，$P<0.0001$ in either the DPNS trial or the NPDS trial）．

Table 1 Body temperatures of Chinese cobras *Naja atra* maintained under a light-dark cycle created by heating lights

	Day/photophase-night/scotophase trial		Night/photophase-day/scotophase trial	
	Active individuals	Inactive individual	Active individuals	Inactive individual
Sample size	6	7	7	7
Body temperature（℃）	27.3±0.5 26.4－29.1	20.6±0.3 19.3－21.9	24.7±0.5 22.5－26.2	20.4±0.3 18.9－21.4
Coefficient of variation（%）	8.9±0.7 6.3－11.2	4.8±0.4 3.2－6.4	5.8±1.5 1.4－11.6	4.9±0.2 3.9－5.7

Note：Data in the table are expressed as mean±1 standard error and range.

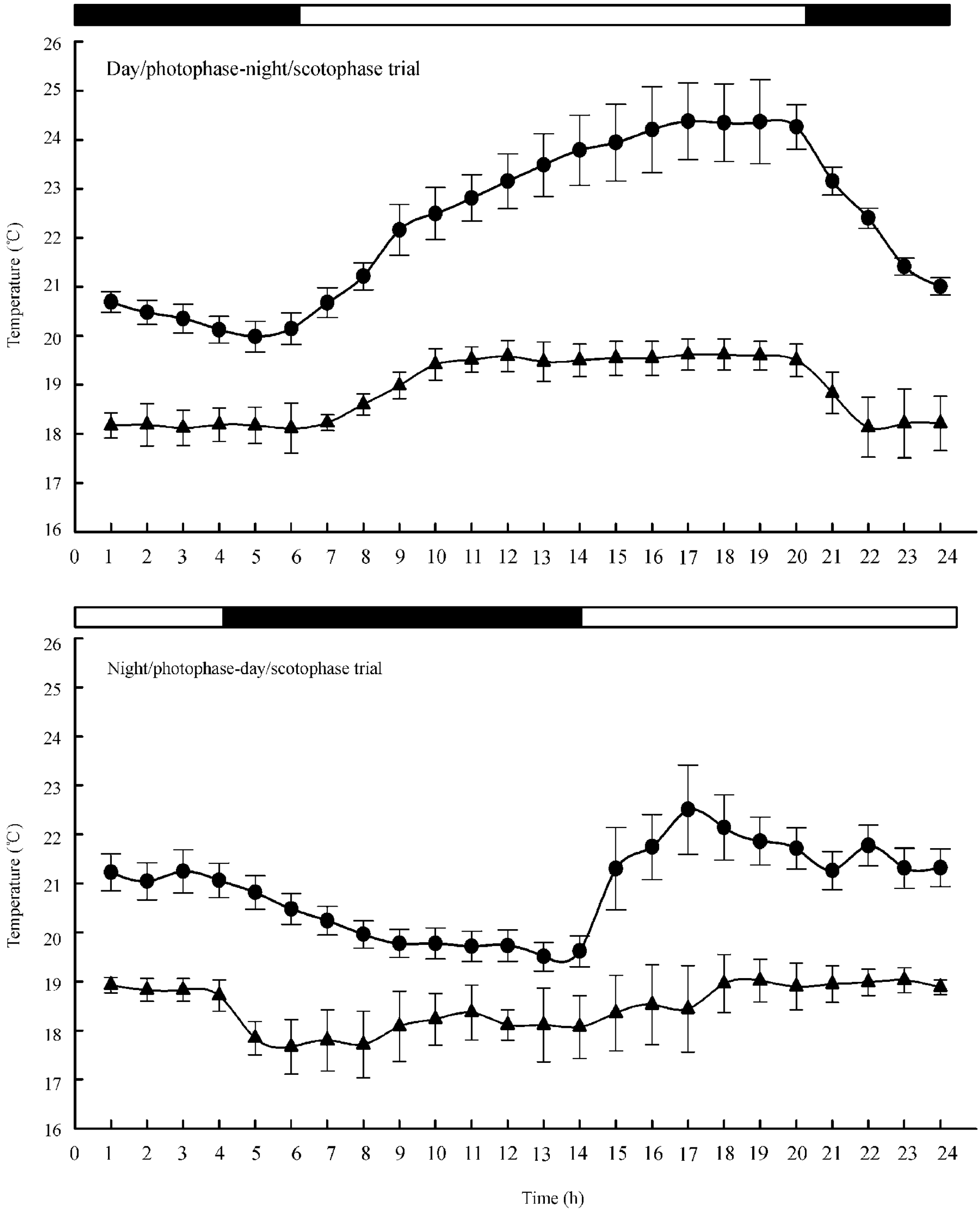

Fig.2 Diel variation in body temperatures of cobras and ambient temperatures they encountered during the course of each trial

All data are expressed as mean±1 standard error. Solid dots represent body temperature，and solid triangles ambient temperature；horizontal solid bar represents the scotophase，and horizontal open bar the photophase.

3 Discussion

Naja atra is considered to be a diurnal snake (Huang et al., 1985; Liang, 1991; Huang, 1998). This consideration is often true for cobras in spring and autumn when nighttime activities are rare due to relatively low ambient temperatures during the night. However, in hot summer months (from June to August), cobras are often active not only during the day but also during the night (Hu et al., 1966; Liang, 1991; Huang, 1998). As in other terrestrial ectotherms (Bartholomew, 1977; Sun et al., 2002; Pan et al., 2003; Zhang et al., 2003), *Naja atra* has a species-specific and restricted range of body temperatures during the period of activity, that it maintains mainly by habitat selection and by selective exploitation of the temporal and spatial variety in the conditions of temperature and radiation in its general environment (Ji et al., 2002). Our field work on *N. atra* has revealed that the disparity between the mean body temperature of active cobras and the mean ambient temperature is apt to be greatest in early spring and late autumn when air and substratum temperatures are low. Earlier work on cobras living through the winter in a laboratory enclosure also provides evidence that they are able to maintain an average body temperature up to 29.4℃ through thermoregulation in winter months during the time when ambient temperatures are elevated by direct solar radiation over 15 ℃ (Ji et al., 2002). Taken together, the previous observations suggest that the activity of *N. atra* might be more thermally than physiologically dependent.

The data set presented in this study is preliminary as the data are measurements of body temperature and thermal activity carried under the laboratory conditions over a short time period. Given that environmental conditions in nature are temporally (seasonally and daily) and spatially much more variable and, thus, more complex than the laboratory conditions, data from the laboratory may be less informative. Nonetheless, our data have some implications for the following issues.

First, a cobra's response to heating lights may greatly affect its body temperature. Cobras in this study kept thermally inactive during the scotophase when ambient temperatures were relatively low (<20 ℃) and almost uniform, but actively regulated body temperature during the photophase when heat from the incandescent bulbs was available (Fig.1, Fig.2). When lights were switched on, a cobra was able to elevate body temperature in a short time, presumably as a consequence of the cobra's behavioral thermoregulatory response to heat from the lights. The mean body temperature of thermally active cobras, although greater in the DPNS trial than in the NPDS trial, varied within a very narrow range and did not show significant temporal variation in either trial (Fig.1). This result provides additional evidence supporting that *N. atra* has a restricted range of body temperatures during the period of activity. Moreover, the result also implies that the cobra's behavioral thermoregulatory responses to heating lights might be rather elaborate and precise.

Second, thermally active cobras select higher body temperatures during the daytime than during the nighttime. Given that the thermal conditions in this study, either during the photophase or during the scotophase, were very similar in both trials (Fig.2), selecting higher body temperatures in the DPNS trial (31.1 ± 0.8℃) than in the NPDS trail (26.0 ± 0.9℃) presumably reflects an endogenous circadian rhythm of body temperature selection. A similar rhythm has been reported for both diurnal and nocturnal reptiles (Myhre and Hammel, 1969; Jarling et al., 1989; Autumn et al., 1994; Sievert and Paulissen, 1996; Tosini and Menaker, 1996; Refinetti and Susalka, 1997), and is generally consistent with the extensive literature on the circadian rhythm of body temperature in endotherms (Refinetti and Menaker, 1992). In diurnal lizards the circadian rhythm of body temperature selection has been proved to be exhibited even in the absence of environmental time cues (Cowgell and Underwood, 1979; Innocenti et al., 1993) and, therefore, is at least partially controlled by an endogenous circadian clock. Our results, together with those reported for other species, support the prediction that selection of higher body temperature during the day results from a common evolutionary constraint imposed by the natural association between sunlight and high ambient temperature (Refinetti and Susalka, 1997).

Third, the cooling rate of body temperature in cobras can be retarded to some extent when *N. atra* encounter cold environments where thermoregulation is impossible. Our result showed that body temperatures were lower and less variable in inactive cobras (during the scotophase) than in active cobras (Table 1), but were never lower than ambient temperatures (Fig.2). Since body temperature should be indistinguishable from that of their surroundings in a short time when reptiles are put under thermally constant conditions, the mismatch between body temperature and ambient temperature during the dark phase is thus particularly interesting, presumably suggesting that there are some mechanisms by which cobras use to retard the cooling rate of body temperature. We are presently unaware to what extent the cooling rate of body temperature is retarded by physiological mechanisms, but aggregation of cobras observed during the scotophase, cannot be precluded from one of the most efficient mechanisms. Cobras living through the winter prevent their body temperatures from falling below the lethal level by aggregating (Ji et al., 2002).

Acknowledgements We thank CHEN Hui-Li, GAO Jian-Fang, HAN Jun, LI Li-Hua, WANG Guo-Qiao and ZHU Bing-Quan for their tireless laboratory efforts.

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