MONITORING BODY TEMPERATURE AND NOCTURNAL ACTIVITY OF SNAKES WITH IMPLANTED TRANSMITTERS

James H. Withgott and Charles J. Amlaner, Jr.
Department of Life Sciences, Indiana State University, Terre Haute, IN 47809

ABSTRACT

We used two types of transmitters to gather data on free-ranging black rat snakes (*Elaphe o. obsoleta*). Temperature-sensitive transmitters provided information on body temperature with which we could draw inferences about the role of thermal factors in activity patterns and selection of retreat sites. Movement-sensitive transmitters enabled us to monitor snake activity at night when approach and visual observation was impractical. Data obtained with these transmitters show that snakes maintained body temperatures at moderate levels relative to fluctuating environmental temperatures, and that snakes are more active during the day in spring and during the night in summer.

INTRODUCTION

Radiotracking has greatly advanced the study of elusive vertebrates such as snakes, by allowing the investigator to repeatedly locate individual animals in the wild and monitor their behavior. However, researchers conducting standard radiotracking studies do not always take full advantage of opportunities for doing biotelemetry. Biotelemetry transmitters enable the investigator to collect data remotely, and to simultaneously gather physiological and behavioral information. In our study we used temperature-sensitive and motion-sensitive transmitters to address questions of thermal ecology and nocturnal activity in black rat snakes (*Elaphe o. obsoleta*).

For ectothermic animals like snakes, thermal factors strongly influence behavior, physiology, and ecology. Many researchers have investigated aspects of thermal biology in snakes (reviewed in Lillywhite 1987, Peterson et al. 1993). Transmitters that measure body temperature are now commonly used in these endeavors. Activity patterns in snakes are often influenced by temperature. A number of telemetry studies have focused on activity patterns (reviewed in Gibbons and Semlitsch 1987). Many temperate-zone snakes are thought to be mainly diurnal during cool times of year and to become nocturnally active during hotter months. However, this is often assumed rather than demonstrated. Motion-sensitive transmitters that allow remote monitoring of snake movement provide a way to document and quantify nocturnal activity of snakes.

Black rat snakes, common across eastern North America, are thought to undergo a diurnal-nocturnal seasonal activity shift, but strong evidence is lacking. Despite several excellent studies of rat snake ecology (Fitch 1963, Stickel et al. 1980, Weatherhead and Hoysak 1988, Durner and Gates 1993) – two of these using radiotracking – the best published evidence for summer nocturnality in rat snakes is an anecdotal account (Hensley and Smith 1986) of nocturnal predation on nests of bluebirds (Sialia sialis).

MATERIALS AND METHODS

We implanted radio transmitters into 25 rat snakes captured in the Ouachita National Forest, AR, USA, and radiotracked them in 1992 and 1993. Transmitters were surgically implanted as described in this volume (Amlaner and Withgott 1995), under

animal care protocol #A1482, University of Arkansas, Fayetteville. Tracking was conducted in mature stands of pine-oak forest and in young-aged clearcuts.

Temperature-sensitive transmitters

Fourteen snakes were fitted with temperature-sensitive transmitters (Holohil Systems Ltd. model # SI-2T) that emitted a pulse rate that increased with temperature. By consulting calibration curves, we determined temperature of the transmitter, and thus indirectly, body temperature. Following their release, snakes were located at varying intervals, generally 1-4 days, throughout their active season (April-October). At each location, we recorded body temperature, along with ambient air temperature measured by a thermometer in shade 1 m above the ground. We recorded whether the snake was actively moving ("active") or was resting in the open or in a retreat site ("inactive"). A total of 660 such locations was made from June 1992 to August 1993.

Motion-sensitive transmitters

Eleven rat snakes were fitted with motion-sensitive transmitters (Wildlife Materials Inc. model # LPB 2300 LDA). Each transmitter contained a mercury tilt switch oriented parallel to the snake's long axis that registered one of two pulse rates (fast or slow). Field tests confirmed that the undulating motion of a snake's body, as it crawled through leaf litter and over branches and rocks, would elicit frequent changes in the transmitter's pulse rate. The alternating pulse rate allowed us to monitor snake activity remotely at night, without approaching and disturbing snakes. Snakes were located once per week from 15 May to 31 August 1993 (N=89 locations). We located each snake's signal from a road and listened for 10 min. If the signal alternated between fast and slow rates we called the snake active; if it remained steady we called the snake inactive. During each 10-min. period we measured several variables, including ambient air temperature (at 1 m height), ambient "ground" temperature (air temperature 1 cm above ground), relative humidity, percent cloud cover, moon phase, and percent of the moon visible. These variables, along with Julian date, time (min. after sunset), and snake size (snout-vent length), were analyzed (SAS version 6.0) for correlation with snake activity.

To complement these data we also sought to quantify another aspect of nocturnal activity – movement from one site to another during the night. To do this we located snakes by direct visual means at dusk one day and at dawn the next day, noting whether the two sites were different. Forty-five such dusk-dawn locations were obtained with 13 snakes with both types of transmitter, from May to August, 1992 and 1993.

RESULTS

Temperature-sensitive transmitters

Snakes showed higher body temperatures when actively moving than when inactive. From April to October, mean body temperature (\pm SE) for active snakes (N=45 locations) was $28.3\pm0.6^{\circ}$ C, while that of inactive snakes (N=514 locations) was $24.9\pm0.2^{\circ}$ C; (t=4.37, df=557, P<0.0001). When inactive, snakes were usually hidden from view in retreat sites. These sites included logs (N=154 locations); tree cavities (N=119); underground caverns such as those created by tree roots (N=110); and piles of dirt, leaf litter, or rocks (N=98). Inactive snakes were found resting in the open only 46 times, and in most cases were completely concealed under vegetative cover.

When inactive, snakes generally maintained body temperatures at more moderate levels than ambient air temperatures. At ambient temperatures below 29.0°C, most

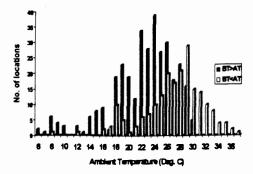


Figure 1. Number of locations for which snake body temperature was above ambient (dark) and below ambient (light), by ambient temperature.

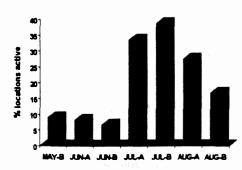


Figure 4. Nocturnal activity: Percent locations snakes were active, using remote monitoring at night, by half-month period.

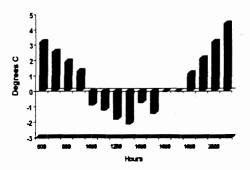


Figure 2. Circadian pattern: Mean differentials between snake body temperature and ambient temperature, by hour of the day.

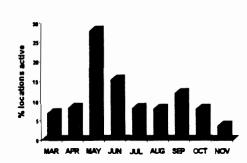


Figure 5. Diurnal activity: Percent locations snakes were active, using direct visual location during daytime, by month.

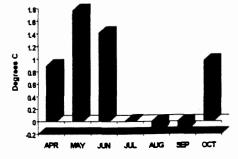


Figure 3. Seasonal pattern: Mean differentials between snake body temperature and ambient temperature, by month of the year.

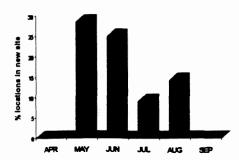


Figure 6. Nocturnal site-to-site movement: Percent times snakes moved between sites at night, using direct visual locations at dusk and dawn, by month.

snakes maintained body temperature above ambient, while at ambient temperatures exceeding 29.0°C, most snakes maintained body temperature below ambient (Fig. 1). The two distributions shown in Fig. 1 differ significantly (Kolmogorov-Smirnov test, D=0.44, $n_1=n_2=32$, P=0.004).

Throughout each day, snakes maintained moderate body temperatures relative to fluctuating ambient air temperatures. Average body temperature was above ambient in early morning, below ambient in late morning and afternoon, and again above ambient as air temperatures decreased toward dusk (Fig. 2). A similar seasonal pattern was observed (Fig. 3). After snakes emerged from hibernacula in March, body temperatures averaged higher than ambient temperatures through June, but then fell slightly below ambient during the hotter months of July, August, and September. As ambient temperatures decreased in October, snakes tended to maintain body temperatures above ambient. Data from winter months were not included in Fig. 3 due to small sample sizes, but snakes generally maintained body temperatures well above ambient temperatures during hibernation. July and August are the hottest months of the year in our study area; average daily temperatures for 1992 and 1993 at nearby Fort Smith, AR, were: April, 15.5°C; May, 19.8°; June, 24.8°; July, 28.8°; August, 27.0°; September, 22.2°; October, 16.2° (data from National Climatic Data Center, Asheville, NC).

Motion-sensitive transmitters

Snakes showed some degree of nocturnal activity in every month between May and August, but nocturnal activity peaked in July and August (Fig. 4). Sample sizes did not allow activity levels to be statistically compared among weeks, but activity was greater for July and August than for May and June (χ^2 =4.99, df=1, P=0.026). This seasonal pattern contrasts markedly with the seasonal pattern of diurnal activity gathered from daytime locations of snakes with both types of transmitters. During the day, snakes were most active in May, and showed less activity in July and August (Fig. 5; χ^2 =23.65, df=7, P=0.001). Taken together, these results indicate that rat snakes are more active during the day in the spring and more active during the night in the summer.

Measurements of variables during nocturnal periods suggested that temperature may be driving snake activity. Of all variables compared between active (N=18) and inactive (N=18) snakes, only ambient air temperature and ambient ground temperature differed. Average ambient air temperature was $24.1\pm0.6^{\circ}$ C when snakes were active and $22.4\pm0.3^{\circ}$ C when snakes were inactive (t=2.41, df=87, P=0.018). Average ambient ground temperature was $25.1\pm0.7^{\circ}$ C when snakes were active and $23.3\pm0.3^{\circ}$ C when they were inactive (t=2.49, df=87, P=0.015).

We had expected that results from the dusk and dawn locations designed to measure site-to-site movement would show the same pattern of seasonal variation as our nocturnal remote locations. However, this was not the case. Instead, site-to-site movement was highest in May and June, with lower levels in July and August (Fig. 6). While this trend was not significant ($\chi 2=0.70$, df=1, P=0.4), the data clearly stand in stark contrast to the nocturnal activity data gathered remotely (Fig. 4).

DISCUSSION

Both types of transmitter enabled us to gather data unattainable using more conventional techniques. While temperature-sensitive transmitters are now frequently used with snakes, we urge wider use of motion-sensitive transmitters. Circadian activity

patterns of most snakes remain unknown, and nocturnal tracking by conventional means is difficult, time-consuming, and can easily result in disturbance of the animal.

Temperature-sensitive transmitters

Being active at higher body temperatures should be advantageous for a snake because muscle efficiency increases with temperature. Quick muscle response is vital to an active snake, both in hunting prey and in escaping predators. When inactive at lower temperatures, snakes stayed well hidden in retreat sites or under heavy cover.

Our data showed evidence of behavioral thermoregulation. Inactive snakes kept body temperatures at moderate levels relative to fluctuating ambient temperatures (Fig. 1). In particular, snakes showed thermoregulation in circadian (Fig. 2) and seasonal patterns (Fig. 3). An apparent thermoregulatory mechanism is the selection of resting or retreat sites. Remaining inside a log, tree cavity, pile, or underground cavern insulates snakes from outside temperature fluctuations. Resting on the ground under cover may serve the same function. Of course, additional factors – such as protection from predators – would be expected to contribute to snakes' selection of retreat sites.

Temperature-sensitive transmitters can be used to undertake focal studies of individuals. For example, we monitored body temperature of two snakes as they sought retreat sites during a prescribed burn conducted by the Forest Service. We found that snakes can survive fires of low intensity by seeking sheltered underground sites where body temperature is not affected by flames passing above on the surface (Withgott 1994).

Increasingly, studies of thermoregulation utilize artificial models of the animal (Bakken 1992, Peterson et al. 1993). These models, containing thermistors, are placed near an animal's retreat site in order to measure body temperatures the animal could potentially have attained. Our method of measuring shaded air temperature gave us adequate results, but more intensive studies should ideally attempt to use such models. Motion-sensitive transmitters

Data from our motion-sensitive transmitters showed that nocturnal activity in rat snakes peaked in the hot months of summer. This contrasts with data showing diurnal activity peaking in May and falling in the summer. Variables measured during nocturnal locations suggest that temperature drives snake activity on any particular night, and presumably may drive the diurnal-nocturnal seasonal shift in activity.

The fact that nocturnal site-to-site movement did not follow the same seasonal pattern as nocturnal activity is curious. It seems to indicate that on summer nights snakes move about actively but do not advance from one site to another. Perhaps they make looping forays, returning before dawn to the retreat site they left. This is interesting, for we have not detected such behavior during the daytime. We have no clear explanation for this pattern, and small sample size requires that it be interpreted cautiously. However, we emphasize that without motion-sensitive transmitters we would never have been aware of this situation. Had we only been using conventional methods of radiotracking (i.e., dusk-dawn locations), we would have been forced to conclude that snakes were most active nocturnally during May and June, paralleling the diurnal pattern. Use of motion-sensitive transmitters gave us insight into an unanticipated complexity in behavior.

The drawback of motion-sensitive transmitters is ambiguity. Our data include as "active" any snake registering a change in pulse rate during the 10-min. listening period. While most snakes registered many changes, some registered only one or two. Such cases may represent snakes moving very slowly, moving over very level ground, or moving up

or down steep inclines. Alternatively, they may represent resting snakes that adjust position and tip the mercury switch. Such ambiguity is inevitable with remote sensing, and the investigator will need to establish arbitrary threshholds for activity. However, our results suggest that choice of a threshhold will probably not affect patterns perceived. Using our data on seasonal patterns in nocturnal activity, we compared distributions resulting from threshholds of one, two, and three pulse rate changes per 10 min., and none were significantly different (Kolmogorov-Smirnov test, $D \le 0.43$, $n_1 = n_2 = 7$, $P \ge 0.5$). One can minimize ambiguity in signal interpretation, as done by Grothe (1992), by carefully calibrating snake movement and signal behavior in the lab.

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