

**Thermal and Behavioral relationships in the Eastern
Massasauga Rattlesnake, *Sistrurus c. catenatus*.**

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SUMMARY

The body temperatures (T_b) of ectothermic vertebrates are constrained within boundaries of microclimates they inhabit. The operable temperatures they encounter often dictate their physiology, activity, and behavior. Therefore, a thorough understanding of an organisms' thermal biology is a key component of its ecology. The eastern massasauga rattlesnake, *Sistrurus c. catenatus* has declined range-wide. Conservation strategies to reduce unnatural mortality should be based on a firm understanding of the organism's ecology. The information on the thermal ecology of snakes is increasing; however, many species such as *S. c. catenatus* have received no attention. In this study, we determined the variation and relationships in T_b of free-ranging snakes to seasonal, diel, environmental, and behavioral variation. Snake T_b s were variable among individuals although not different by sex/reproductive state. The T_b s massasauga are functionally tied to seasonal and diel fluctuations in environmental temperatures. We detected little differentiation between sex/reproductive states in terms of thermoregulatory behavior. Snakes sought warmer microclimates and garnered heat through their posture, exposure to the sun, and visibility. Massasaugas remained close to the average temperature available with no difference between sex/reproductive states. Although models in open habitats predicted massasaugas could readily achieve greater than 35°C there were only a few instances where this occurred with the radiolocated massasaugas. The variation surrounding the date of entrance into winter dormancy is narrower compared to the date of emergence suggesting the timing of entrance is more fixed. Overall, snakes maintained a T_b of 9.8°C during the winter dormancy period although there were periods in mid winter where T_b s were much lower. It remains unknown as to how snakes maintained a warmer T_b relative to the soil thermal profile while remaining visible throughout the winter. From our data, we recommend the cessation of potentially fatal management practices in or near massasauga habitat during the active season. We do not recommend the termination of necessary management practices to preserve ecosystem functionality, but instead recommend the use of our functional equation to delineate when activity should be conducted in or near massasauga habitat.

INTRODUCTION

Throughout the course of an activity season, the T_b of ectotherms fluctuates with and is related to environmental temperatures (T_e). In some instances T_e may exceed the boundaries of species' physiologically manageable temperatures, thus ectothermic organisms are required to precisely regulate their body temperature (T_b) to optimize physiological processes. All ectotherms innately possess and behaviorally maintain a preferred T_b (Avery, 1982) which potentially could exhibit regional differentiation. During periods where T_e s are below or above the preferred T_b , many reptile species exhibit thermoregulatory behaviors ranging from shuttling, basking, perching, breezing, and postural changes (Heatwole and Taylor, 1987). When thermal gradients shift such that preferred T_b cannot be maintained, reptiles slowly enter into a period of dormancy. However, even within this dormancy period T_b is still behaviorally regulated, but is substantially lower than during the active period (Sexton and Hunt, 1980; Sexton and Marion, 1981). Once a minimum T_e is attained, the activity of ectothermic organisms again increases signaling the onset of the activity period (Sexton and Hunt, 1980; Sexton and Marion, 1981). The knowledge of the thermal ecology of a species allows us to delineate the onset of winter dormancy, the emergence from winter dormancy, and the times of peak activity within a year

(Peterson *et al.*, 1993). From a land manager's standpoint, knowing the timing of these events or how to predict them can lead to a reduction in mortality as a result of management practices (i.e. burning, mowing, and clearing).

The eastern massasauga rattlesnake (*Sistrurus catenatus catenatus*) has declined range-wide (Szymanski, 1998). For example, of the 24 *S. c. catenatus* localities reported by Smith (1961) for Illinois, only six to eight may remain extant (Beltz, 1992) with the Carlyle Lake population having the greatest likelihood of viability (Phillips *et al.*, 1999a,b). Potential negative impacts to the population include habitat destruction and unnatural mortality. Similar to most pit-vipers, *S. c. catenatus* is an ambush predator often selecting an ambush point and remaining therefor several days. Further, they often occupy relatively open habitats with a low amount of overstory canopy cover at Carlyle (Phillips *et al.*, 1999a,b). Thus, *S. c. catenatus* may face more extreme fluctuations in T_b related diel and seasonal fluctuations in T_e . Unfortunately, little information is available on the thermal ecology of snakes, especially *S. c. catenatus*. The objectives of this study are to:

- 1) provide a qualitative description of the range of operable T_b s
- 2) determine environmental and seasonal variation in T_b
- 3) determine if behavioral differentiation is present with respect to T_b
- 4) determine the selected thermal habitats
- 5) determine the T_b maintained during winter dormancy related to the T_e gradient of the soils

MATERIALS AND METHODS

Study Sites

This study was conducted at Carlyle Lake, Clinton County, Illinois (Plate 1). The study sites of Eldon Hazlet State Park (EHSP; ca. 3,000 acres), located on a peninsula along the western shoreline, and South Shore State Park (SSSP; ca. three miles long), located along the southeastern shoreline, are managed by the Illinois Department of Natural Resources (IDNR). The remaining sites are recreation areas managed by the US Army Corp of Engineers (USACE): Dam East Recreation Area (DERA), Dam West Recreation Area (DWRA), James Hawn Access Area (JHAA), Coles Creek Recreation Area (CCRA), Carrigan Access Area (CAA), and Keysport Access Area (KAA).

Data Acquisition

We made initial captures of snakes through visual encounter surveys (Heyer *et al.*, 1994) in suitable habitats during the spring and used snakes encountered by the USACE or IDNR. Temperature sensitive radio-transmitters were surgically implanted into (49 snakes over three-years) snakes (Reinert and Cundall, 1982) such that transmitters never constituted > 6% of the snake's mass. We define the active period as the time when snakes emerge from crayfish burrows after dormancy and commence terrestrial activity and the dormant period as the time when snakes remain semi-active in crayfish burrows and activity is subterranean. During the active period, we radiolocated snakes daily (in a few instances snakes were located every other day) with the time of tracking rotated between morning (0700–1059), afternoon (1100–1459), and early evening (1500–1859) periods. The pulse rate, time interval between radio pulses, was recorded using a stopwatch and equated to T_b using factory calibration curves provided by the

radio-transmitter manufacturer (HOLOHIL). During the dormant period, we radiolocated snakes once to twice per week during the warmest part of the day.

Upon each visual location, we recorded whether the snake was above or below ground. If the snake was above ground, we record the following behavioral categories: posture (coiled, looped, or straight; Plate 2), visibility (fully, partially, or not), exposure (full sun, partial sun/shade, or full shade), and whether the snake was still or moving. If snakes were below ground, we visually inspected burrows with a flashlight to determine if massasaugas were visible from the burrow entrance, recorded the presence or absence of visible water, and identified the presence of additional snakes. Finally, we recorded shaded air temperature (SAT - °C), and substrate temperature (SUB - °C). The number of daylight hours was summarized from calendars for the entire study period. To make time of day a continuous variable we converted it to decimal hours (e.g. 0615 = 6.25).

We determined the range of possible environmental temperatures (T_e) a snake could occupy, using 27 biophysical snake models constructed from copper pipe (Bakken and Gates, 1975). Each model measured 60 cm long with a 7.5 cm in circumference with a copper cap sealing the distal end. Because of the relative inflexibility of the pipe, we only used a curved body posture representing a semi s-shape (Plate 3). Models were first painted with a gray Krylon primer coat, then with a base coat of flat medium olive green, then we painted 30 – 35 saddles consisting of a base layer of black and a second layer of a flat rust brown on each model to mimic the patterning of *S. c. catenatus*. A 235 ml Rubbermaid ServingSaver™ container was affixed to the open end of the model with clear epoxy then silicone for waterproofing. A HOBO® thermistor cable was sent midway up the model and we wrapped the cable in foam posterior to the thermistor probe to prevent the probe from contacting the pipe. A HOBO® H8 series data logger was then launched to read in ½ hour intervals and placed inside the container. Gross locations for models were selected randomly from UTM grid coordinates of the site but on the finer scale, we attempted to place models as many microhabitats as possible. Because our radiolocations were not necessarily congruent with when the dataloggers recorded temperature, we reconverted time and grouped it into ½ hr categories. Each snake location was then corresponded to a ½ hr interval for that day.

A single model was chosen for calibration with a recently deceased adult massasauga. We placed the deceased *S. c. catenatus*, with a thermistor probe inside the body cavity, into multiple thermal environments ranging from 5° C to 30° C along with one of the constructed models (Plate 4). Both model temperature and snake T_b were recorded simultaneously every minute for four hours (20 minutes in 12 microhabitats). The final microhabitat was a cool-down in a refrigerator where model and snake temperatures were recorded every half hour until they both stabilized. Because of tissue decay, we could not calibrate each model so we must assume the thermodynamics of all models are the same and that the deceased snake's pigmentation was representative of the entire population. We then natural log transformed model and snake temperatures to remove non-linearity. Finally, we regressed model temperature versus snake temperature after 20 min of exposure in a microhabitat and the final reading from the refrigerator to derive a prediction equation.

During winter dormancy, we placed 15 sets comprised of three HOBO® H8 series data loggers in the soil to record the over-winter thermal profile. Holes were dug with a gas-powered auger near sites where radio-located massasaugas had chosen for dormancy. We placed loggers at the 60 cm, 30 cm, and surface (just below the surface) depths. Loggers were launched to read in ½ hr intervals and sealed in 235 ml Rubbermaid ServingSaver™ containers with silicon.

Data Analysis

General Variation. We constructed histograms of T_b for each snake to determine modal temperatures throughout year. To determine if mean T_b differed by sex we summarized the data for all sexes then used t-test assuming unequal variances. Snakes were then divided into three states: males, non-gravid females, and gravid females to test for physiological and behavioral differences between these groups. This division is maintained throughout the remainder of the analysis. We used ANOVA to test for gross differentiation in mean T_b among sex/reproductive state.

Environmental and Temporal Variation. We plotted snake temperature versus day of the year to visually inspect fluctuations in T_b across season. We expected to observe and quantify four periods using the daily graphs: 1) a period of low T_b and low variance (winter dormancy), 2) a period of increasing T_b and variance (egress), 3) a period of a higher stable T_b and variance (primary activity period), and 4) a period of decreasing T_b and variance (ingress). We related each snake's T_b to SAT, SUB, photoperiod, and time of day using multiple regression to determine which factors most influence T_b . To provide a general perspective of the environmental and temporal variation in T_b , we averaged T_b , SAT, SUB, and time of day for each day across each sex/reproductive state. We then used multiple regression to determine if average daily T_b was related to average SAT, SUB, photoperiod, and time of day. Finally, to determine if average daily T_b differed between sex/reproductive states, we performed an ANCOVA with sex/reproductive state as the category, average SAT, SUB, time, and photoperiod as the covariates, and average daily T_b as the response variable.

Behavioral Analysis. To determine if T_b s differed with respect to behavior, we first performed and ANCOVA with sex/reproductive state, visibility, exposure, posture, and movement as the class variables, SAT, SUB, photoperiod, and time of day as the covariates, and T_b as the response variable. If significant interactions are present between effects and covariates, we must remove the covariates from the analysis. To remove environmental and seasonal influences we used the residuals of T_b from a multiple regression using SAT, SUB, time of day, and photoperiod for all snakes pooled to generate a combined model. We then analyzed differences in residual T_b using ANOVA with behaviors and sex/reproductive state as the categories and residual T_e and the response variable.

Thermal Selection. We summarized the data from the snake models to determine the maximum, minimum, average, and standard error of potential T_e s across microhabitats sampled. We then obtained a deviance factor using the following equation: $T_{bdev} = (T_{bobs} - T_{bavg}) / ST_{bpot}$ where T_{bobs} is the observed T_b of snake through radiotelemetry, T_{bavg} is the mean potential T_b from the thermal models, and ST_{bpot} is the standard error of potential T_b from the thermal models. The deviance factor is explained whereby positive values are warmer than potential average and negative values are cooler than potential average. Because the deviance factor is scaled as the number of standard errors from the potential mean, values greater 2 or -2 would be significantly different from the potential mean. We then repeated the environmental, seasonal, and behavior analyses using the deviance factor as a variable.

Dormancy Temperatures. We plotted the thermal profiles for the surface, 30cm, and 60cm loggers along with the T_b of the radiolocated snakes in the burrows. We then averaged the winter dormancy temperatures for each individual snake and compared sexes using a t-test assuming unequal variances. Next, we averaged the thermal profiles across logger sites to obtain average thermal profiles for the surface, 30cm, and 60cm depths.

RESULTS

General Variation. Overall, snakes rarely exceeded 35°C and several modes were present (Figure 1). The upper modal temperature appears to be between 30 – 34°C, and the lower modal temperature occurs between 6 – 10 °C (Figure 1). Mean T_b throughout the duration of the tracking period showed variation among individuals (Table 1). Mean T_b for 7524 locations of 40 *S. c. catenatus* was 22.2°C ($s = 3.7^\circ\text{C}$, 95% C.I. = $21.1^\circ\text{C} \leq T_b \leq 23.4^\circ\text{C}$: Table 1). Mean male T_b (mean = 22.4°C, $s = 3.8^\circ\text{C}$, 95% C.I. = $20.3^\circ\text{C} \leq T_b \leq 23.9^\circ\text{C}$, $n = 21$: Table 1), was not significantly different ($T_{\text{stat}} = 0.229$, d.f. = 37, $p = 0.820$) from mean female T_b (mean = 22.1°C, $s = 3.6^\circ\text{C}$, 95% C.I. = $20.7^\circ\text{C} \leq T_b \leq 24.0^\circ\text{C}$, $n = 19$: Table 1). However, this includes overall data from the winter dormancy period and low T_b s during winter dormancy will negatively influence the mean T_b . Focusing on the active period, variation among individuals was still present (Table 2). Mean T_b for 6034 locations of 39 *S. c. catenatus* (one individual was monitored mainly through the winter dormancy period only) during the active period was 24.3°C ($s = 2.2^\circ\text{C}$, 95% C.I. = $23.6^\circ\text{C} \leq T_b \leq 25.0^\circ\text{C}$: Table 2). Again, average male T_b (mean = 24.3°C, $s = 2.2^\circ\text{C}$, 95% C.I. = $23.3^\circ\text{C} \leq T_b \leq 25.3^\circ\text{C}$, $n = 21$: Table 2) was not significantly different ($T_{\text{stat}} = 0.421$, d.f. = 36, $p = 0.676$) from average female T_b (mean = 24.2°C, $s = 2.2^\circ\text{C}$, 95% C.I. = $23.1^\circ\text{C} \leq T_b \leq 25.3^\circ\text{C}$, $n = 19$: Table 2). As stated previously because gravid females could exhibit differences in physiological processes and behavior we then partitioned females into gravid and non-gravid categories and repeated the comparisons of mean T_b during the activity season (Table 2). There was no significant difference ($F_{\text{stat}} = 0.101$, $df = 38$, $p = 0.904$) in overall mean T_b between males (mean = 24.3°C, $s = 2.2^\circ\text{C}$, 95% C.I. = $23.3^\circ\text{C} \leq T_b \leq 25.3^\circ\text{C}$, $n = 21$: Table 2) and gravid (mean = 24.2°C, $s = 2.2^\circ\text{C}$, 95% C.I. = $22.5^\circ\text{C} \leq T_b \leq 25.9^\circ\text{C}$, $n = 9$: Table 2) and nongravid females (mean = 24.0°C, $s = 2.3^\circ\text{C}$, 95% C.I. = $22.4^\circ\text{C} \leq T_b \leq 25.7^\circ\text{C}$, $n = 10$: Table 2).

Temporal and Environmental Variation. When graphed by day, T_b appears to follow a sin-wave function with the trough occurring during the dormant period and a peak from June – mid-September (Figure 2). Figure 2 depicts the apparent four-period trend; there is a stable minimum T_b and constant variance (winter dormancy: late November – late February), increasing T_b and variance (egress: late February-May), high stable T_b with constant variance (primary activity season: June – Mid. September) and decreasing T_b and variance (ingress: Mid. September - November). Photoperiod and time of day explained a significant amount of T_b variation among individuals (Table 3). Overall, 59% (55% males, 52% nongravid females, and 59% gravid females) of the variation in individual T_b was explained by photoperiod and time of day (Table 3). However, there are differences in the response of individuals' T_b to these variables. For example, snake 132 exhibited a significant response in T_b to the time of day but not to photoperiod and snake 231 exhibited the converse responses (Table 3). Gravid females did not significantly respond to photoperiod whereas nongravid females and males did respond (Table 3). When including the effects of SAT and SUB, on average 85% (86% males, 82% non gravid females, and 86% gravid females) of the individual variation in T_b during the active period was

explained (Table 4). However, the overall effects of SUB, photoperiod, and time of day are encompassed within the variation in SAT (Table 4). When we pool the data and examine average daily T_b by sex/reproductive state, the cyclicity of T_b is exacerbated, however it appears that gravid females increase more rapidly in T_b early in the year and decrease more rapidly in T_b at the end of the season (Figure 3). They cyclical nature of snake T_b closely follows the cyclicity in SAT and SUB (Figure 4). Using multiple regression we found that the average daily T_b of all sex/reproductive states significantly responds to SAT, SUB, photoperiod, and time of day when considering the active period only (Table 5). In this circumstance, 86% of the variation is explained (89% males, 84% nongravid females, and 87% gravid females) regarding sex/reproductive state (Table 5). However, when considering the combined effects of SAT, SUB, photoperiod, and time of day, there are no differences in T_b with respect to sex/reproductive state (Table 5). ANCOVA using the average T_b to control for the effects of SAT, SUB, photoperiod, and time of day revealed a difference in sex/reproductive state only during the active period (Table 6). During the study SAT and SUB interact with sex/reproductive state (Figures 5 and 6). Nongravid females were the warmest at lower SATs and SUBs but as SATs and SUBs increase, the order flips such that males are the warmest at higher SATs and SUBs followed by gravid females, then nongravid females (Figure 5). When considering only the active period, Nongravid females remain the warmest at lower SATs and SUBs, but at higher SATs males are the warmest (Figure 6). At higher SUBs, gravid females are the warmest (Figure 6).

Behavioral Variation. ANCOVA showed that T_b for posture, visibility, and movement were significantly different (Table 7). Snakes that were straight, moving, and in partial sun/shade were the warmest whereas snakes that were coiled, lying still, and not visible were the coolest (Figure 7). Only SUB was not a significant covariate and it was removed from the model (Table 7). The covariates of SAT and time of day significantly interacted with sex/reproductive state, posture, exposure, and visibility (Table 7). Males were the coolest at lower SATs but the warmest at higher SATs whereas nongravid females were the warmest at lower SATs and the same as gravid females at higher SATs (Figure 8). Nongravid female T_b increased slower in response to time of day whereas male T_b increased faster (Figure 8). Snakes that were straight were the warmest at lower SATs followed by looped, then coiled snakes but the reverse order was observed for higher SATs (Figure 9). Coiled snakes were the coolest earlier in the day whereas looped snakes were the warmest, however later in the day the order was reversed (Figure 9). Snakes in the full sun remained warmer than snakes in the full shade at all SATs and times of day (Figure 10). Snakes in the partial sun/shade increased from being as cool as snakes in the full shade at lower SATs and earlier times to being as warm as snakes in the full sun at higher SATs and later times (Figure 10). Snakes that were fully visible remained warmer at all SATs compared to snakes that were not visible (Figure 11). Snakes that were partially visible were as cool as snakes that were not visible at lower SATs and as warm as snakes that were fully visible at higher SATs (Figure 11). Snakes that were partially visible earlier in the day were cooler than snakes that were fully visible, however later in the day the order was reversed (Figure 11). Posture and visibility significantly interacted with sex/reproductive state (Table 7). Nongravid females had the lowest T_b with respect to posture and sex/reproductive state (Figure 12). With respect to visibility, nongravid females had the lowest T_b s when partially and fully visible (Figure 12).

Because of interactions with the covariates, the actual differences in the effect variables may be the result of nonhomogenous slopes. Thus, we had to remove the effects of SAT, SUB, photoperiod, and time of day by obtaining residuals (see methods). Posture, movement, exposure, and visibility were all significantly different in residual T_b (Table 8). Snakes that were in full sun, fully visible, and moving had higher T_b s on average compared to snakes in full shade, not visible, and lying still (Figure 13). Although there appears to be no difference between postures (Figure 13), the difference observed by the ANOVA is due to significant interactions with other behaviors (Table 8). Nongravid females had higher T_b s than average for all postures (Figure 14). All sex/reproductive states converge when straightened out (Figure 14). Male and nongravid female snakes were equally higher than average in T_b when not visible (Figure 14). Males and nongravid females were higher than average in T_b compared to gravid females when not visible (Figure 14). All sex/reproductive states converge when partially visible and males were higher than average in T_b compared to females when fully visible (Figure 14).

Thermal Preference and Selection. After twenty minutes of exposure, model temperatures were significantly related to snake T_b s (Figure 15). The relationship of using pure temperatures was significant ($r^2 = 0.858$, $p < 0.001$, $df = 12$) and resulted in the subsequent prediction equation: Snake $T_b = 0.861(\text{Model Temp.}) + 3.552$. Natural log transforming both model and snake temperatures significantly increased ($r^2 = 0.987$, $p < 0.001$, $df = 12$) the predictive capability of the relationship resulting in the following prediction equation: $\ln(\text{Snake } T_b) = 0.713\ln(\text{Model Temp.}) + 0.412$. Thus to equate model temperature to potential snake T_b s, we used the natural log transformed equation. Typical thermal daily thermal profiles sometimes predicted that snakes in certain environments could potentially exceed 40°C , however T_b s rarely deviated beyond the average potential (Figure 16). The difference between snake T_b and the average potential snake T_b (deviance factor) was not significantly related ($r^2 = 0.059$, $p = 0.404$, $df = 1170$) to SAT, SUB, photoperiod, or time of day. Because no relationship was observed, we proceeded with an ANOVA using sex/reproductive state, visibility, exposure, movement, and posture as categories and the deviance factor as the dependent variable. ANOVA results indicated visibility was the only significant main effect and only visibility and exposure interacted in terms of deviation from potential average T_b (Table 9). Snakes that were fully visible showed a greater deviation from potential average T_b compared to snakes partially or not visible (Figure 17). Snakes that were partially visible showed a greater deviation from potential T_b compared to snakes not visible (Figure 17). Snakes that were in full sun showed a greater deviation from potential average T_b compared to snake either in partial sun/shade or in full shade (Figure 17). In full sun, snakes that were partially visible showed a greater deviation from average potential T_b followed by snakes that were fully visible then snakes that were not visible (Figure 18). In partial sun/shade, snakes that were fully visible and partially visible showed a greater deviation from average potential T_b , but were equal, compared to snakes that were not visible (Figure 18). In full shade, there was no difference in deviation from potential average T_b for all visibility categories (Figure 18).

Winter Dormancy. Snakes entered the winter dormancy period from 27 September to 23 October but over the three years of study entrance into dormancy centered around 11 October (Table 10). Entrance temperatures were variable but average approximately 17°C SAT and 13°C SUB (Table 10). Snakes emerged from winter dormancy from 7 March to 30 April and centered around 2 April (Table 10). Emergence temperatures were variable but averaged approximately

20.2°C SAT and 18.4°C SUB. Snakes spent on average 174 days dormant or 47.6% of the year (Table 10). Winter dormancy T_b s ranged from 1.6°C to 24.9°C but averaged 9.8°C for 19 individuals radiolocated (Table 11). Some individuals did come to the surface during winter and were able to attain relatively warm T_b s (Table 11). Mean winter dormancy T_b s were not significantly different between sex/reproductive states ($F = 0.136$, $p = 0.873$, $df = 18$). Although T_b s mimicked the general thermal profile trend, visual inspection revealed snakes maintained higher T_b s than the thermal profile at 60 cm (Figures 19 and 20). On average snakes were 5°C warmer compared to all profiles (Table 11) and this difference is not related to photoperiod (Figure 20).

DISCUSSION

General Variation. Snake T_b s were variable among individuals although not different by sex/reproductive state. This is interesting because gravid females have been previously reported to maintain a higher T_b through the gestation period (Seigel, 1986). One possibility for this difference is based on the range of microclimates available. Females from more northern populations select specific basking sites where thermal requirements can be met (Szymanski, 1998; C. Parent pers com). This is because the range of thermal habitats available which meet the requirements to successfully gestate embryos are in relatively lower abundance following the general temperature decrease with increasing latitude. At the southern range limit of the massasaugas, Carlyle, it is quite possible that the thermal requirements for gravid females are alleviated and thus there is no requirement for differential selection of specific gestation sites or habitats. This poses some difficulty in terms of management as specific habitats for gestation may not be present and gravid females may gestate throughout the entire open grassy habitat. This can be further supported if there is a parallel lack of habitat differentiation between sex/reproductive states.

Temporal and Environmental Variation. The T_b s massasauga are functionally tied to seasonal and diel fluctuations in environmental temperatures. Although there was individual variation in the responses, there was an overall functional response to SAT, SUB, photoperiod, and time of day. Again, gravid females responded no differently compared to males and nongravid females further substantiating the lack of thermal selection for specific gestation sites. The functional relationship provides an excellent framework for predicting massasauga T_b and in turn activity. This predictive equation is further explored below and can be used by land managers to time burns or other activities near hibernacula or suitable habitat. Generally, days with shorter photoperiods, lower SATs and SUBs, and earlier in the day are the most suitable for management activities in suitable habitat.

Behavioral Variation. We detected little differentiation between sex/reproductive states in terms of thermoregulatory behavior. However, we did find certain behaviors resulted in warmer T_b s. Snakes sought warmer microclimates and garnered heat through their posture, exposure to the sun, and visibility. Snakes early in the morning and at cooler SATs were warmer when they were straightened out, in full sun, and fully exposed. Snakes are most likely straightened out and more visible in the mornings because these two behaviors act in concert to increase heat transfer. As the day progresses, the coiled posture is warmer. This is most likely due to heat conservation since a coiled snake has less surface area than one either looped or straightened out

(Ayers and Shine, 1997). From the standpoint of management, this data suggests that activities within massasauga habitat should be minimized early and late in the season, as most snakes will exhibit positive thermoregulation. Because snakes are more visible, exposed, and straightened out at earlier times and are cooler, their locomotor abilities are not optimum thus their ability to evade disturbance is hindered. Furthermore, we have observed numerous occasions where massasaugas were perched on top of clumps of vegetation, sometimes 6 inches from the ground. Thus, mowing in or near the massasauga habitat early and late in the season can prove more fatal than previously thought. Other manicuring activities, such as weed-eating, can prove fatal to massasaugas during the warmer periods because they do not overtly bask but remain concealed.

Thermal Preference and Selection. Massasaugas remain close to the average temperature available with no difference between sex/reproductive states. This suggests all sex/reproductive states are exhibiting thermoregulatory behaviors in a similar fashion, and snakes are exhibiting thermophobia and thermophilia to maintain T_b . Snakes in the full sun and visible were warmer than snakes in partial sun/shade and full shade, and partially and not visible but they never deviated too far from their average potential T_b . Although models in open habitats predicted massasaugas could readily achieve greater than 35°C there were only a few instances where this occurred with the radiolocated massasaugas.

Winter Dormancy. The variation surrounding the date of entrance into winter dormancy is narrower compared to the date of emergence suggesting the timing of entrance is more fixed. We have not exhaustively analyzed the data but we perceive that entrance into and emergence from dormancy is a response to current and previous climactic patterns. Although the average date when snakes enter dormancy appears as an easy measure to assess when management activities can commence in massasauga habitat, there are numerous occasions when snakes emerged from burrows on favorable days during the winter. Furthermore, throughout much of the winter, snakes remained visible from their entrance of the burrow perhaps using cues to determine favorable days. Overall, snakes maintained a T_b of 9.8°C during the winter dormancy period although there were periods in mid winter where T_b s were much lower. It remains unknown as to how snakes maintained a warmer T_b relative to the soil thermal profile while remaining visible throughout the winter.

MANAGEMENT RECOMMENDATIONS. From our data, we recommend the cessation of potentially fatal management practices in or near massasauga habitat during the active season. Unnatural mortality can occur early and late in the season because of the requirement of snakes to thermoregulate. Thus, their behavior can conflict with certain management practices such as mowing or prescribed burning. During the primary activity season, unnatural mortality from management practices can occur because snakes exhibit thermophobia (remaining cool) by becoming less visible. Moreover, the interface between entrance and emergence into dormancy and winter dormancy is a critical period when a snake's pattern of surface activity is unpredictable and they lack the locomotor ability for flight from potential hazards.

We do not recommend the termination of necessary management practices to preserve ecosystem functionality, but instead recommend the use of our functional equation to delineate when activity should be conducted in or near massasauga habitat. From Table 5 the overall regression equation over the entire season could predict 89% of the variation in T_b . Thus a land manager can simply input the SAT, SUB, photoperiod, and time of day (in decimal hours) to

obtain a predicted snake T_b before the onset of a management activity. For instance, let us assume a land manager at Carlyle Lake wants to conduct a prescribed burn. The date is 3 February 2002 (photoperiod for this day is 10.3 hrs), the time is 9.5 hrs (09:30), and SAT is 16.5 °C and SUB is 6.5°C. Putting this into the following equation:

$$\text{Snake } T_b = 0.61(\text{SAT}) - 0.08(\text{SUB}) + 1.56(\text{Photoperiod}) + 0.26(\text{Time of Day}) - 13.45, \text{ or} \\ 0.61(16.5) - 0.08(6.5) + 1.56(10.3) + 0.26(9.5) - 13.45,$$

yields a predicted snake T_b of 14.6°C. Although using average winter temperature (9.8°C) might seem intuitive as a demarcation line for activity, it is biased by cooler temperatures during the coldest period of winter. Thus, we recommend using the lower 95% confidence limit of maximum winter dormancy T_b (12.0°C). The lower confidence limit was chosen because the mean and upper confidence limit are influenced by snakes opportunistically basking during the winter. In our example, snakes could potentially be on the surface and the land manager should choose to forgo burning in massasauga habitat because of the potential for snakes to exhibit surface activity, even though it is during the winter. Following this protocol will account for aberrant surface activity during the winter whereas simply using a range of dates when snakes have previously entered hibernation does not.

USE OF NON-GAME WILDLIFE AWARD

Funding was used to defray the costs of travel for a field assistant during the critical fall ingression period. The materials for the biophysical models were purchased out of pocket by the primary author (MJD) because they needed to be constructed and placed into the environment before the grant was awarded. While onsite, data was collected on snake body temperatures utilizing already implanted temperature sensitive radio transmitters and was recorded in tandem with radiolocations of the snakes. In addition, body temperatures were recorded using an infrared thermometer when snakes were visible above ground. Finally, during this ingression period several 60cm deep holes were dug near hibernacula sites of the radiolocated snakes and temperature data loggers were buried in the holes to record the thermal profile of the soil over-winter. The field assistant aided in general data collection of snake body temperatures, aided in recovering the biophysical models placed in the spring and downloading and organizing their data, and finally in the construction and placement of temperature data loggers used to monitor over-wintering temperatures.

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Table 1: Mean, standard deviation, 95% C.I. and sample size of T_b for 40 radiolocated *S. c.*

catenatus at Carlyle Lake, Clinton County, Illinois from Spring 2000 to Spring 2003.

Females					Males				
Snake	\bar{X}_{T_b}	S_{T_b}	95% C.I.	<i>n</i>	Snake	\bar{X}_{T_b}	S_{T_b}	95% C.I.	<i>n</i>
13	21.1	7.3	$20.2 \leq T_b \leq 22.1$	218	34	28.9	4.5	$28.0 \leq T_b \leq 29.8$	102
24	24.5	7.2	$23.5 \leq T_b \leq 25.6$	187	39	27.3	4.5	$26.3 \leq T_b \leq 28.3$	86
41	26.4	5.9	$25.4 \leq T_b \leq 27.4$	149	50	24.1	5.8	$22.8 \leq T_b \leq 25.4$	75
52	24.0	6.3	$23.2 \leq T_b \leq 24.8$	224	51	25.0	7.2	$24.0 \leq T_b \leq 25.9$	224
54	20.7	9.0	$19.7 \leq T_b \leq 21.7$	307	76	22.5	7.9	$21.9 \leq T_b \leq 23.1$	613
63	28.3	4.8	$29.7 \leq T_b \leq 27.0$	52	81	22.2	7.1	$20.8 \leq T_b \leq 23.5$	106
80	26.6	5.9	$25.3 \leq T_b \leq 28.0$	77	86	23.0	6.9	$21.5 \leq T_b \leq 24.5$	86
131	18.7	8.1	$17.7 \leq T_b \leq 19.8$	227	91	24.2	6.5	$23.3 \leq T_b \leq 25.1$	196
132	25.6	6.4	$27.1 \leq T_b \leq 24.1$	75	95	22.8	7.3	$21.8 \leq T_b \leq 23.8$	202
162	19.9	8.0	$19.0 \leq T_b \leq 20.7$	353	96	22.6	6.7	$21.6 \leq T_b \leq 23.5$	203
174	19.6	8.1	$18.5 \leq T_b \leq 20.7$	191	111	21.2	9.3	$20.2 \leq T_b \leq 22.3$	307
195	16.7	6.5	$15.9 \leq T_b \leq 17.6$	210	130	22.3	6.5	$20.1 \leq T_b \leq 24.5$	31
231	17.4	7.4	$16.2 \leq T_b \leq 18.5$	155	137	24.1	6.7	$23.1 \leq T_b \leq 25.2$	169
246	17.1	6.8	$15.9 \leq T_b \leq 18.2$	134	151	21.6	8.6	$20.8 \leq T_b \leq 22.4$	455
298	26.0	5.8	$24.8 \leq T_b \leq 27.2$	94	182	20.6	8.3	$19.6 \leq T_b \leq 21.6$	277
306	21.7	7.2	$20.6 \leq T_b \leq 22.8$	164	186	21.0	9.4	$19.9 \leq T_b \leq 22.1$	284
321	20.3	7.6	$19.2 \leq T_b \leq 21.4$	190	245	14.9	5.0	$13.9 \leq T_b \leq 15.8$	110
324	27.2	6.0	$26.2 \leq T_b \leq 28.3$	123	270	22.9	6.7	$22.0 \leq T_b \leq 23.9$	189
335	18.2	8.9	$16.7 \leq T_b \leq 19.6$	146	271	12.1	2.5	$11.6 \leq T_b \leq 12.5$	104
					303	24.5	9.0	$23.3 \leq T_b \leq 25.6$	225
					317	22.0	7.1	$21.1 \leq T_b \leq 23.0$	204

Table 2: Mean, standard deviation, 95% C.I. and sample size of T_b during the active period for 39 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from Spring 2000 to Spring 2003.

Females				Males					
Snake	\bar{X}_{T_b}	S_{T_b}	95% C.I.	n	Snake	\bar{X}_{T_b}	S_{T_b}	95% C.I.	n
Non-Gravid									
13	23.1	6.3	$22.1 \leq T_b \leq 24.0$	182	34	28.9	4.5	$28.0 \leq T_b \leq 29.8$	102
24	25.8	6.4	$24.8 \leq T_b \leq 26.7$	167	39	27.3	4.5	$26.3 \leq T_b \leq 28.3$	86
41	26.4	5.9	$24.4 \leq T_b \leq 27.4$	149	50	24.1	5.8	$22.8 \leq T_b \leq 25.4$	75
52	24.5	5.9	$23.7 \leq T_b \leq 25.3$	214	51	25.9	6.5	$25.0 \leq T_b \leq 26.8$	206
54	24.7	7.0	$23.8 \leq T_b \leq 25.6$	223	76	24.6	7.0	$24.0 \leq T_b \leq 25.2$	507
80	26.6	5.9	$25.3 \leq T_b \leq 28.0$	77	81	23.5	6.6	$22.1 \leq T_b \leq 24.9$	91
195	19.9	6.5	$18.8 \leq T_b \leq 21.1$	126	86	23.0	6.9	$21.5 \leq T_b \leq 24.5$	86
231	21.5	6.8	$20.0 \leq T_b \leq 23.1$	76	91	25.0	5.9	$24.2 \leq T_b \leq 25.9$	181
246	22.0	6.2	$20.3 \leq T_b \leq 23.7$	53	95	24.0	6.7	$23.0 \leq T_b \leq 25.0$	181
298	26.0	5.8	$24.8 \leq T_b \leq 27.2$	94	96	23.4	6.2	$22.5 \leq T_b \leq 24.3$	188
					111	25.7	6.4	$24.8 \leq T_b \leq 26.5$	223
Gravid									
					130	22.3	6.5	$20.1 \leq T_b \leq 24.5$	36
					137	24.1	6.7	$23.1 \leq T_b \leq 25.2$	169
63	28.3	4.8	$27.0 \leq T_b \leq 29.7$	52	151	24.3	7.4	$23.5 \leq T_b \leq 25.0$	365
131	22.8	6.9	$21.7 \leq T_b \leq 23.9$	150	182	24.6	6.6	$23.6 \leq T_b \leq 25.5$	192
132	25.6	6.4	$24.1 \leq T_b \leq 27.0$	75	186	25.5	7.2	$24.5 \leq T_b \leq 26.5$	199
162	22.7	7.2	$21.9 \leq T_b \leq 23.6$	263	245	18.3	5.9	$16.5 \leq T_b \leq 20.0$	47
174	23.5	7.1	$22.2 \leq T_b \leq 24.7$	121	270	23.1	6.6	$22.2 \leq T_b \leq 24.1$	185
306	22.6	6.8	$21.5 \leq T_b \leq 23.7$	151	303	27.8	5.9	$26.9 \leq T_b \leq 28.7$	182
321	22.9	6.3	$21.9 \leq T_b \leq 23.9$	151	317	23.1	6.5	$22.2 \leq T_b \leq 24.1$	185
324	27.2	6.0	$26.2 \leq T_b \leq 28.3$	123					
335	22.4	7.3	$21.0 \leq T_b \leq 23.9$	101					

Table 3: Regression coefficients (r^2), df, p , and parameter estimates for a multiple regression analysis on the effects of photoperiod and time of day on T_b for 39 *S. c. catenatus* radiolocated from Spring 2000 to Spring 2003 at Carlyle Lake, Clinton County, Illinois. Snakes are treated individually and are grouped by sex/reproductive condition.

Snake	r^2	p	F	df	Photoperiod Estimate	p	Time Estimate	p	Intercept Estimate	p
Non-gravid Females										
13	0.52	<0.001	33.29	179	2.28	<0.001	0.393	<0.001	-13.06	0.004
24	0.61	<0.001	47.31	164	2.50	<0.001	0.431	<0.001	-13.12	0.002
41	0.59	<0.001	38.59	146	2.39	<0.001	0.425	<0.001	-11.35	0.011
52	0.44	<0.001	25.44	211	1.95	<0.001	0.318	<0.001	-5.52	0.201
54	0.68	<0.001	95.08	219	3.74	<0.001	0.602	<0.001	-33.78	<0.001
80	0.43	<0.001	8.31	74	2.05	0.003	0.410	0.011	-5.00	0.573
195	0.54	<0.001	25.95	123	2.56	<0.001	0.684	<0.001	-22.38	<0.001
231	0.59	<0.001	19.99	73	4.80	<0.001	0.224	0.334	-39.36	<0.001
246	0.41	0.010	5.04	50	3.54	0.005	0.236	0.414	-22.51	0.117
298	0.43	<0.001	10.37	91	2.99	0.066	0.666	<0.001	-25.91	0.264
Gravid Females										
63	0.45	0.004	6.20	49	0.04	0.990	0.567	<0.001	20.20	0.667
131	0.59	<0.001	39.24	147	3.06	<0.001	0.435	<0.001	-23.69	<0.001
132	0.33	0.017	4.31	72	1.49	0.286	0.522	0.007	-2.63	0.896
162	0.70	<0.001	122.71	260	2.60	<0.001	0.655	<0.001	-33.04	<0.001
174	0.58	<0.001	29.29	118	2.86	<0.001	0.330	0.030	-18.88	<0.001
306	0.69	<0.001	68.28	148	3.03	<0.001	0.491	<0.001	-24.55	<0.001
321	0.71	<0.001	74.32	148	2.88	<0.001	0.547	<0.001	-23.05	<0.001
324	0.44	<0.001	14.01	120	1.49	<0.001	0.639	<0.001	-1.71	0.784
335	0.86	<0.001	135.47	98	3.79	<0.001	0.634	<0.001	-35.85	<0.001

Table 3: Cont.

Snake	r ²	p	F	df	Photoperiod		Time		Intercept	
					Est.	p	Est.	p	Est.	p
Males										
34	0.27	0.024	3.89	99	-0.37	0.670	0.310	0.007	30.14	0.018
39	0.33	0.008	5.06	83	2.01	0.135	0.342	0.006	-6.31	0.746
50	0.54	<0.001	14.45	72	8.16	<0.001	0.116	0.519	-96.05	0.001
51	0.52	<0.001	38.23	203	2.18	<0.001	0.599	<0.001	-10.93	0.016
76	0.59	<0.001	137.76	504	2.92	<0.001	0.473	<0.001	-20.43	<0.001
81	0.68	<0.001	36.99	88	3.79	<0.001	0.314	0.188	-27.57	0.001
86	0.59	<0.001	21.72	83	11.08	<0.001	0.283	0.134	-141.85	<0.001
91	0.59	<0.001	47.11	177	2.24	<0.001	0.479	<0.001	-11.11	0.004
95	0.61	<0.001	53.41	178	2.77	<0.001	0.448	<0.001	-19.33	<0.001
96	0.62	<0.001	58.78	185	2.73	<0.001	0.414	<0.001	-18.96	<0.001
111	0.66	<0.001	83.35	220	3.12	<0.001	0.629	<0.001	-24.95	<0.001
130	0.14	0.733	0.31	33	-0.71	0.618	0.137	0.665	30.26	0.160
137	0.49	<0.001	25.82	166	2.21	<0.001	0.633	<0.001	-14.06	<0.001
151	0.61	<0.001	107.93	362	3.33	<0.001	0.579	<0.001	-27.89	<0.001
182	0.68	<0.001	80.04	189	3.37	<0.001	0.569	<0.001	-27.88	<0.001
186	0.63	<0.001	62.90	196	3.52	<0.001	0.698	<0.001	-30.88	<0.001
245	0.74	<0.001	27.26	44	7.25	<0.001	0.311	0.148	-71.40	<0.001
270	0.50	<0.001	30.48	181	1.89	<0.001	0.625	<0.001	-10.64	0.022
303	0.64	<0.001	63.53	179	2.52	<0.001	0.554	<0.001	-13.44	<0.001
317	0.58	<0.001	47.15	182	2.52	<0.001	0.449	<0.001	-16.84	<0.001

	r ²	p	Photoperiod		Time		Intercept	
			Estimate	p	Estimate	p	Estimate	p
Males	0.55	0.038	3.33	0.071	0.45	0.083	-26.51	0.048
Females	0.56	0.002	2.63	0.071	0.48	0.042	-17.64	0.185
Non-gravid	0.52	0.002	2.88	0.007	0.44	0.076	-19.20	0.117
Gravid	0.59	0.002	2.36	0.142	0.54	0.004	-15.91	0.261
Overall	0.55	0.021	2.99	0.071	0.47	0.063	-22.19	0.115

Table 4: Regression coefficients (r^2), df, p , and parameter estimates for a multiple regression analysis on the effects of shaded air temperature (SAT), substrate temperature (SUB) photoperiod, and time of day on T_b during the active season for 38 *S. c. catenatus* radiolocated from Spring 2000 to Spring 2003 at Carlyle Lake, Clinton County, Illinois. Snakes are treated individually and are grouped by sex/reproductive condition.

Snake	r^2	p	F	df	SAT		SUB		Photoperiod		Time		Intercept	
					Est.	p	Est.	p	Est.	p	Est.	p	Est.	p
Non-gravid Females														
13	0.79	<0.001	72.35	175	0.61	<0.001	0.02	0.400	0.64	0.017	0.14	0.113	-3.43	0.304
24	0.90	<0.001	163.07	162	0.50	<0.001	0.52	<0.001	0.07	0.754	0.07	0.280	4.50	0.092
41	0.86	<0.001	101.30	144	0.47	<0.001	0.43	<0.001	0.07	0.810	0.09	0.201	6.58	0.073
52	0.72	<0.001	55.18	209	0.78	<0.001	-0.22	<0.001	1.11	<0.001	0.16	0.428	-6.56	0.092
54	0.87	<0.001	162.75	214	0.35	<0.001	0.34	<0.001	1.60	<0.001	0.21	0.005	-15.89	<0.001
80	0.87	<0.001	53.91	72	0.71	<0.001	0.04	0.784	-1.13	0.018	0.22	0.018	21.10	<0.001
195	0.77	<0.001	41.96	118	0.50	<0.001	0.12	0.474	0.92	0.082	0.32	0.025	-9.44	0.150
231	0.84	<0.001	43.38	71	0.20	0.210	0.58	0.005	0.52	0.537	-0.16	0.331	2.85	0.770
246	0.81	<0.001	23.06	48	0.39	0.035	0.82	0.002	-4.37	0.004	-0.02	0.897	52.23	<0.001
298	0.79	<0.001	37.30	89	0.70	<0.001	0.20	0.104	-1.05	0.372	0.21	0.107	14.82	0.371
Gravid Females														
63	0.87	<0.001	35.51	45	-0.06	0.231	0.92	<0.001	1.10	0.546	0.13	0.186	-7.55	0.781
131	0.82	<0.001	74.71	145	0.30	0.044	0.44	0.002	0.97	0.004	0.10	0.290	-8.38	0.062
132	0.89	<0.001	66.97	70	-0.23	0.256	1.23	<0.001	-1.20	0.091	0.14	0.138	16.98	0.091
162	0.86	<0.001	181.22	256	0.37	<0.001	0.34	<0.001	1.21	<0.001	0.26	<0.001	-12.81	<0.001
174	0.87	<0.001	90.73	116	0.32	0.034	0.66	<0.001	-0.35	0.379	-0.04	0.672	7.11	0.162
306	0.89	<0.001	139.73	141	0.31	<0.001	0.39	<0.001	1.07	<0.001	0.19	0.023	-9.77	0.001
321	0.85	<0.001	97.02	146	0.18	0.073	0.52	<0.001	0.62	0.036	0.20	0.024	-4.66	0.175
324	0.73	<0.001	32.88	116	0.30	0.014	0.46	0.005	-0.18	0.648	0.23	0.097	7.71	0.138
335	0.93	<0.001	161.24	95	0.34	<0.001	0.20	0.077	1.71	<0.001	0.33	<0.001	-17.89	<0.001

Table 4: Cont.

Snake r^2	p	F	df	SAT		SUB		Photoperiod		Time		Intercept		
				Est.	p	Est.	p	Est.	p	Est.	p	Est.	p	
Males														
34	0.77	<0.001	35.99	96	0.68	<0.001	0.30	0.003	-0.63	0.337	-0.05	0.545	15.19	0.116
39	0.77	<0.001	29.95	80	0.73	<0.001	0.25	0.008	1.10	0.265	-0.01	0.928	-11.25	0.435
50	0.82	<0.001	33.87	68	0.41	<0.001	0.59	<0.001	1.24	0.405	-0.12	0.367	-15.68	0.441
51	0.87	<0.001	148.71	200	0.80	<0.001	-0.07	0.367	0.64	0.116	0.36	<0.001	-5.35	0.120
76	0.86	<0.001	363.66	499	0.82	<0.001	-0.02	0.169	0.72	<0.001	0.16	0.001	-5.95	<0.001
81	0.91	<0.001	108.20	86	0.44	<0.001	0.44	0.001	0.69	0.053	0.08	0.310	-1.26	0.758
86	0.85	<0.001	51.07	76	0.79	<0.001	0.30	0.055	0.26	0.865	0.04	0.750	-7.30	0.731
91	0.89	<0.001	161.90	175	0.63	<0.001	0.08	0.274	0.21	0.434	0.23	<0.001	2.74	0.434
95	0.86	<0.001	120.96	174	0.36	<0.001	0.44	<0.001	0.39	0.162	0.14	0.097	-1.80	0.577
96	0.82	<0.001	94.24	181	0.32	<0.001	0.43	<0.001	0.46	0.106	0.11	0.176	-1.39	0.672
111	0.87	<0.001	166.28	213	0.20	0.008	0.52	<0.001	0.78	0.000	0.23	0.001	-4.95	0.091
137	0.84	<0.001	98.56	164	0.28	0.029	0.65	<0.001	-0.62	0.060	0.15	0.094	8.63	0.051
151	0.86	<0.001	258.59	259	0.47	<0.001	0.37	<0.001	0.70	<0.001	0.270	<0.001	-8.00	0.002
182	0.89	<0.001	186.27	186	0.59	<0.001	0.17	0.103	1.01	<0.001	0.090	0.202	-7.56	0.027
186	0.88	<0.001	163.96	193	0.38	<0.001	0.48	<0.001	0.91	0.002	0.23	0.007	-8.87	0.022
245	0.87	<0.001	32.15	42	0.16	0.479	0.56	0.089	2.01	0.267	0.10	0.535	-19.37	0.342
270	0.85	<0.001	116.12	176	0.73	<0.001	0.04	0.683	-0.08	0.723	0.30	<0.001	1.61	0.586
303	0.90	<0.001	186.94	175	0.59	<0.001	0.07	0.426	0.46	0.145	0.19	0.003	2.61	0.258
317	0.88	<0.001	155.21	178	0.40	<0.001	0.38	<0.001	0.25	0.266	0.18	0.013	-1.16	0.661

Table 4: Cont.

Averages	r^2	p	SAT Est.	p	SUB Est.	p	Photoperiod Est.	p	Time Est.	p	Intercept Est.	p
Males	0.86	<0.001	0.51	0.027	0.31	0.115	0.55	0.221	0.14	0.212	-3.64	0.333
Females	0.84	<0.001	0.37	0.047	0.42	0.098	0.17	0.226	0.15	0.202	1.98	0.172
NonGravid	0.82	<0.001	0.52	0.025	0.29	0.177	-0.16	0.259	0.12	0.240	6.68	0.185
Gravid	0.86	<0.001	0.20	0.072	0.57	0.009	0.55	0.189	0.17	0.159	-3.25	0.157
Overall	0.85	<0.001	0.44	0.037	0.37	0.106	0.36	0.224	0.14	0.207	-0.83	0.252

Table 5: Regression coefficients (r^2), df, p , and parameter estimates for a multiple regression analysis on the effects of average daily shaded air temperature (SAT), average daily substrate temperature (SUB), photoperiod, and time of day on the average daily T_b of gravid female, nongravid female, and male *S. c. catenatus* radiolocated from Spring 2000 to Spring 2003 at Carlyle Lake, Clinton County, Illinois. The upper analysis represents the entire study whereas the lower set of analyses represents only the active season. The bottom set of both analyses is the test of sex/reproductive condition class.

Entire Season																
	r^2	p	F	df	SAT		SUB		Photoperiod		Time		Sex		Intercept	
					Est.	p	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p
Non-gravid Females	0.88	<0.001	607.58	680	0.66	<0.001	-0.18	<0.001	1.55	<0.001	0.26	<0.001			-12.34	<0.001
Gravid Females	0.90	<0.001	535.90	532	0.34	<0.001	0.18	0.003	1.64	<0.001	0.29	<0.001			-14.49	<0.001
Males	0.91	<0.001	902.45	722	0.67	<0.001	-0.05	0.174	1.37	<0.001	0.24	<0.001			-12.02	<0.001
Sex/Reproductive	0.89	<0.001	1529.81	1943	0.61	<0.001	-0.08	0.003	1.56	<0.001	0.26	<0.001	-0.02		0.841-13.45	<0.001
Active Season Only																
Non-gravid Females	0.84	<0.001	371.18	598	0.72	<0.001	-0.24	<0.001	1.53	<0.001	0.26	<0.001			-12.21	<0.001
Gravid Females	0.87	<0.001	342.63	461	0.39	<0.001	0.21	0.002	1.69	<0.001	0.25	<0.001			-16.63	<0.001
Males	0.89	<0.001	609.30	641	0.73	<0.001	-0.12	0.002	1.27	<0.001	0.24	<0.001			-10.77	<0.001
Sex/Reproductive	0.86	<0.001	951.50	1709	0.68	<0.001	-0.14	0.003	1.55	<0.001	0.26	<0.001	0.11		0.267-13.83	<0.00

Table 6: ANCOVA results for sex/reproductive state differences in average daily Tb with photoperiod, average time of day, average shaded air temperature, and average substrate temperature for 40 *S. c. catenatus* radiolocated between Spring 2000 to Spring 2003 at Carlyle Lake, Clinton County, Illinois. Results on the right represent the entire study period whereas results on the left represent only the active season. Significant results are highlighted in bold.

Source of Variation	Entire Tracking Period					Active Season Only				
	SS	df	MS	F	<i>p</i>	SS	df	MS	F	<i>p</i>
Total	116394.30	1948	59.75			77825.12	1714	45.41		
Model	94022.29	14	6715.88	580.57	<0.001	58622.91	14	4187.35	370.71	<0.001
Sexcode	16.20	2	8.10	0.70	0.497	75.04	2	37.52	3.32	0.036
Potoperiod	5107.50	1	5107.50	441.53	<0.001	4395.08	1	4395.08	389.10	<0.001
Time	1046.30	1	1046.30	90.45	<0.001	902.77	1	902.77	79.92	<0.001
Shaded Air Temp.	6371.32	1	6371.32	550.78	<0.001	6570.56	1	6570.56	581.70	<0.001
Substrate Temp.	4.40	1	4.40	0.38	0.538	30.16	1	30.16	2.67	0.102
Sexcode x Photoperiod	29.92	2	14.96	1.29	0.275	57.99	2	28.99	2.57	0.077
Sexcode x Time	5.09	2	2.55	0.22	0.803	0.88	2	0.44	0.04	0.962
Sexcode x Shaded Air Temp.	396.36	2	198.18	17.13	<0.001	354.06	2	177.03	15.67	<0.001
Sexcode x Substrate Temp.	293.67	2	146.84	12.69	<0.001	394.32	2	197.16	17.45	<0.001
Error	22372.02	1934	11.57			19202.21	1700	11.30		

Table 7: ANCOVA results for differentiation exposure to sun, visibility, posture, movement, and sex/reproductive state T_b with photoperiod, time of day, shaded air temperature, and substrate temperature as covariates for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2000 and the spring of 2003. Three-, four-, and five-way interactions were insignificant and removed for simplicity. All significant results are in bold.

Source of Variation	SS	df	MS	F	p
Total	154530.40	3986	38.77		
Model	98273.79	53	1854.22	129.63	<0.001
Sex/Reproductive State	48.26	2	24.13	1.69	0.185
Posture	110.11	2	55.06	3.85	0.021
Movement	79.02	1	79.02	5.52	0.019
Exposure	49.52	2	24.76	1.73	0.177
Visibility	241.16	2	120.58	8.43	<0.001
Sex/Reproductive State x Posture	193.49	4	48.37	3.38	0.009
Sex/Reproductive State x Movement	9.86	2	4.93	0.34	0.708
Sex/Reproductive State x Exposure	48.73	4	12.18	0.85	0.492
Sex/Reproductive State x Visibility	395.25	4	98.81	6.91	<0.001
SAT	3525.26	1	3525.26	246.46	<0.001
Time	584.71	1	584.71	40.88	<0.001
Photoperiod	252.80	1	252.8	17.67	<0.001
Sex/Reproductive State x SAT	407.30	2	203.65	14.24	<0.001
Sex/Reproductive State x Time	326.37	2	163.18	11.41	<0.001
Sex/Reproductive State x Photoperiod	44.33	2	22.16	1.55	0.213
Posture x SAT	85.04	2	42.52	2.97	0.051
Posture x Time	362.91	2	181.45	12.69	<0.001
Posture x Photoperiod	8.90	2	4.45	0.31	0.733
Movement x SAT	35.16	1	35.16	2.46	0.117
Movement x Time	36.96	1	36.96	2.58	0.108
Movement x Photoperiod	7.70	1	7.70	0.54	0.463
Exposure x SAT	235.13	2	117.57	8.22	<0.001
Exposure x Time	246.03	2	123.01	8.60	<0.001
Exposure x Photoperiod	61.30	2	30.65	2.14	0.118
Visibility x SAT	402.58	2	201.29	14.07	<0.001
Visibility x Time	255.07	2	127.54	8.92	<0.001
Visibility x Photoperiod	49.93	2	24.96	1.75	0.175
Error	56256.61	3933	14.30		

Table 8: ANOVA results for differentiation exposure to sun, visibility, posture, movement, and sex/reproductive state in residual T_b while removing the effects of photoperiod, time of day, shaded air temperature, and substrate temperature for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2000 and the spring of 2003. Significant results are in bold.

Source of Variation	SS	df	MS	F	<i>p</i>
Total	66511.72	3962	15.08		
Model	7109.57	23	30.91	20.50	<0.001
Sex/Reproductive State	59.55	2	29.77	1.97	0.139
Posture	909.57	2	454.78	30.16	<0.001
Movement	649.21	1	649.21	43.05	<0.001
Exposure	854.60	2	427.30	28.33	<0.001
Visibility	3262.76	2	1631.38	108.18	<0.001
Sex/Reproductive State x Posture	207.59	4	51.90	3.44	0.008
Sex/Reproductive State x Movement	33.11	2	16.56	1.10	0.334
Sex/Reproductive State x Exposure	109.39	4	27.35	1.81	0.124
Sex/Reproductive State x Visibility	700.15	4	175.04	11.61	<0.001
Error	59402.15	3939	15.08		

TABLE 9: ANOVA results for differentiation exposure to sun, visibility, posture, movement, and sex/reproductive state to the difference in observed snake Tb from average potential snake Tb derived from calibrate snake models for 12 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2002 and the fall of 2002. Significant results are in bold.

Source	SS	df	MS	F	<i>p</i>
Total	10186.49	697			
Model	1956.07	40	48.90	3.90	<0.001
Posture	7.55	2	3.77	0.30	0.740
Visibility	77.35	2	38.68	3.09	0.046
Exposure	71.63	2	35.82	2.86	0.058
Movement	0.04	1	0.04	0.00	0.958
Sex/Reproductive State	5.93	2	2.96	0.24	0.789
Sex/Reproductive State x Movement	3.50	2	1.75	0.14	0.869
Sex/Reproductive State x Exposure	20.53	4	5.13	0.41	0.802
Sex/Reproductive State x Visibility	17.58	4	4.39	0.35	0.844
Sex/Reproductive State x Posture	42.78	4	10.70	0.85	0.491
Posture x Visibility	60.87	4	15.22	1.21	0.303
Posture x Exposure	16.76	4	4.19	0.33	0.855
Posture x Movement	3.00	1	3.00	0.24	0.625
Visibility x Exposure	134.72	4	33.68	2.69	0.030
Visibility x Movement	18.26	2	9.13	0.73	0.483
Exposure x Movement	44.25	2	22.12	1.77	0.172
Error	8230.41	657	12.53		
Total	10309.29	698			

Table 10: Dates, SAT, and SUB by which snakes entered and emerged from the winter dormant period and number of days dormant for 24 *S. c. catenatus* radiolocated from the spring of 2000 and spring of 2003 at Carlyle Lake, Clinton County, Illinois. Average date of entrance and emergence, time dormant, and temperatures are below.

Snake	Dates		Duration	Entrance		Emergence	
	Entrance	Emergence		SAT	SUB	SAT	SUB
Nongravid Females							
13	10/17/2002	3/20/2003	154	6.5	8.1	22.1	18.9
24	10/4/2000	3/7/2001	154	19.3	10.2	11.9	8.5
52	10/6/2000	4/5/2001	181	13.6	7.1	25.8	16.8
54	10/2/2001	4/11/2002	191	27.7	19.7	26.6	20.8
162	10/19/2002	4/3/2003	166	10.9	11.2	24	22.3
195	10/9/2001	4/11/2002	184	21.2	15	26.6	20.8
231	10/7/2001	3/28/2002	172	17.9	12.4	9	7.9
246	10/5/2001	3/20/2002	166	10	10.2	7	7.2
Gravid Females							
131	10/20/2001	2/22/2002	125	19.8	13.8	6.8	1.2
162	10/10/2001	4/12/2002	184	20.4	14.3	22.9	20.9
174	10/16/2001	4/15/2002	181	11.8	8.8	27.7	25.9
321	10/17/2002	4/5/2003	170	6.5	8.1	22.3	20.9
335	10/20/2002	4/30/2003	192	9.4	9	30.1	32
Males							
51	10/10/2000	3/23/2001	164	20.7	17.6	21.6	22.7
76	10/4/2001	4/6/2002	184	25.3	20.8	12.6	14.8
76	11/8/2002	4/11/2003	154	20.2	8.6	22.3	24
91	10/5/2000	4/7/2001	184	17.9	9.8	26.2	21.3
95	10/16/2002	4/4/2003	170	12	12.4	22.3	20.9
111	10/2/2001	4/30/2002	210	27.7	19.7	25.7	25.4
151	10/5/2001	4/11/2002	188	10	10.2	26.6	20.8
182	9/27/2001	4/8/2002	193	20.8	18.7	20.2	17.4
186	10/2/2001	4/9/2002	189	27.7	19.7	19.3	21.1
245	10/7/2001	4/1/2002	176	17.9	12.4	16.6	14.7
271	10/10/2001	3/16/2002	157	20.4	14.3	5.8	8.3
303	10/23/2002	3/22/2003	150	9.3	6.6	20.2	19.7
317	10/15/2002	4/12/2003	179	21.2	15.8	22.9	23
Mean	10/11	4/2	174	17.2	12.9	20.2	18.4
Stdev.	9	15	18	6.5	4.4	7.1	6.9

Table 11: Average, sample size, standard deviation, maximum and minimum winter dormancy T_b s for 19 *S. c. catenatus* radiolocated from the spring of 2000 to the spring of 2003 at Carlyle Lake, Clinton County, Illinois.

	Mean	<i>n</i>	Stdev.	Maximum	Minimum
Nongravid Females					
13	12.1	51	2.96	24.9	8.5
54	7.4	54	1.52	10.3	3.4
195	10.6	52	0.66	12.0	9.4
231	10.1	52	2.65	22.8	7.4
246	10.5	48	0.56	11.8	9.5
	10.2	257	1.71	24.9	3.4
Gravid Females					
131	9.5	40	0.44	10.6	8.9
162	9.7	28	0.43	10.6	9.1
174	9.2	29	1.64	11.0	4.0
321	11.2	60	1.86	16.9	7.6
335	9.2	58	1.90	11.9	6.2
	9.8	215	0.83	16.9	4.0
Males					
76	10.2	53	0.65	11.4	9.0
95	13.8	37	2.10	16.9	7.0
111	5.6	53	2.54	11.1	1.6
151	8.1	52	1.50	12.0	6.1
182	8.4	53	1.31	11.5	6.2
186	6.7	52	1.76	10.9	3.7
271	9.7	46	1.30	14.7	8.1
303	11.0	51	4.77	20.3	2.2
317	12.4	37	2.10	14.9	3.0
	9.5	434	2.66	20.3	1.6
Grand Mean	9.8	906	2.00	24.9	1.6

Table 12: Average differences in snake T_b compared to surface, 30 cm, and 60 cm average thermal profiles by day for 19 *S. c. catenatus* radiolocated over the winters of 2001-2002, and 2002-2003 at Carlyle Lake, Clinton County, Illinois.

	Surface	30cm	60cm
Nongravid Females			
Mean	6.1	5.9	5.5
Stdev.	3.19	3.23	3.86
<i>n</i>	114	114	114
Gravid Females			
Mean	5.3	4.7	4.0
Stdev.	3.77	3.40	3.46
<i>n</i>	93	93	93
Males			
Mean	4.4	4.3	4.1
Stdev.	3.08	3.31	4.23
<i>n</i>	123	123	123
Total			
Mean	5.2	4.9	4.5
Stdev.	3.45	3.41	3.96
<i>n</i>	330	330	330

FIGURE LEGENDS

- Figure 1: Histograms of T_b for 40 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from the spring of 2000 to the spring of 2003.
- Figure 2: Seasonal variation in snake T_b for 40 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from the spring of 2000 to the spring of 2003.
- Figure 3: Average daily T_b by sex/reproductive state for 40 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from the spring of 2000 to the spring of 2003.
- Figure 4: Average daily shaded air temperature and substrate temperature taken at individual radiolocation points for 40 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from the spring of 2000 to the spring of 2003.
- Figure 5: Regression graphs of nongravid female, gravid female, and male average daily body temperatures in response to average daily shaded air temperature and average daily substrate temperature during the entire study period for 40 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from spring 2000 to the spring of 2003.
- Figure 6: Regression graphs of nongravid female, gravid female, and male average daily body temperatures in response to average daily shaded air temperature and average daily substrate temperature during the active period for 39 radiolocated *S. c. catenatus* at Carlyle Lake, Clinton County, Illinois from spring 2000 to the spring of 2003.
- Figure 7: Box and whisker plots of significantly different behavior types with 95% confidence interval as the whisker, standard error as the box, and mean as the bar for T_b when controlling for the effects of photoperiod, time, shaded air temperature, and substrate temperature for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2000 and the spring of 2003.
- Figure 8: Regression graphs of nongravid female, gravid female, and male T_b in response to shaded air temperature and time of day for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois from spring 2000 to the spring of 2003.
- Figure 9: Regression graph of posture specific T_b s in response to shaded air temperature and time of day for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois from spring 2000 to the spring of 2003.
- Figure 10: Regression graphs of exposure specific T_b s in response to shaded air temperature and time of day for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois from spring 2000 to the spring of 2003.

- Figure 11: Regression graphs of visibility specific T_b s in response to shaded air temperature and time of day for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois from spring 2000 to the spring of 2003.
- Figure 12: Interaction graphs for posture and visibility specific T_b s with respect to sex/reproductive state for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2000 and the spring of 2003.
- Figure 13: Box and whisker plots of each behavior type with 95% confidence interval as the whisker, standard error as the box, and mean as the bar for the residual T_b when removing the effects of photoperiod, time, shaded air temperature, and substrate temperature for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2000 and the spring of 2003.
- Figure 14: Interaction graphs for posture and visibility with respect to sex/reproductive state for the residual T_b when removing the effects of photoperiod, time, shaded air temperature, and substrate temperature for 39 *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois between the spring of 2000 and the spring of 2003.
- Figure 15: Calibration plots for snake thermal models.
- Figure 16: Profile of potential T_b derived from biophysical snake thermal models for July 23 2002 with snake T_b s derived from radiotelemetry plotted as filled circles.
- Figure 17: Box and whisker plots for visibility and exposure with 95% confidence interval as the whisker, standard error as the box, and mean as the bar for the deviation from average potential T_b *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois in 2002.
- Figure 18: Interaction graphs for visibility with respect to exposure for the deviation from average potential T_b *S. c. catenatus* radiolocated during the active season at Carlyle Lake, Clinton County, Illinois in 2002.
- Figure 19: Winter thermal profiles of logger sites buried at the surface, 30 cm, and 60m, with snake T_b s plotted for snakes radiolocated over the winters of 2001-2002 and 2002-2003 at Carlyle Lake, Clinton County, Illinois.
- Figure 20: Average winter thermal profiles with snake T_b s plotted as small filled circles for snakes radiolocated over the winters of 2001-2002 and 2002-2003 at Carlyle Lake, Clinton County, Illinois.

Figure 21: Average winter thermal profiles with average sex/reproductive state T_b plotted for snakes radiolocated over the winters of 2001-2002 and 2002-2003 at Carlyle Lake, Clinton County, Illinois.

Figure 22: Relationship of difference in snake T_b to the temperatures at the surface, 30cm, and 60cm strata in relation to photoperiod for snakes radiolocated over the winters of 2001-2002 and 2002-2003 at Carlyle Lake, Clinton County, Illinois.

Figure 1

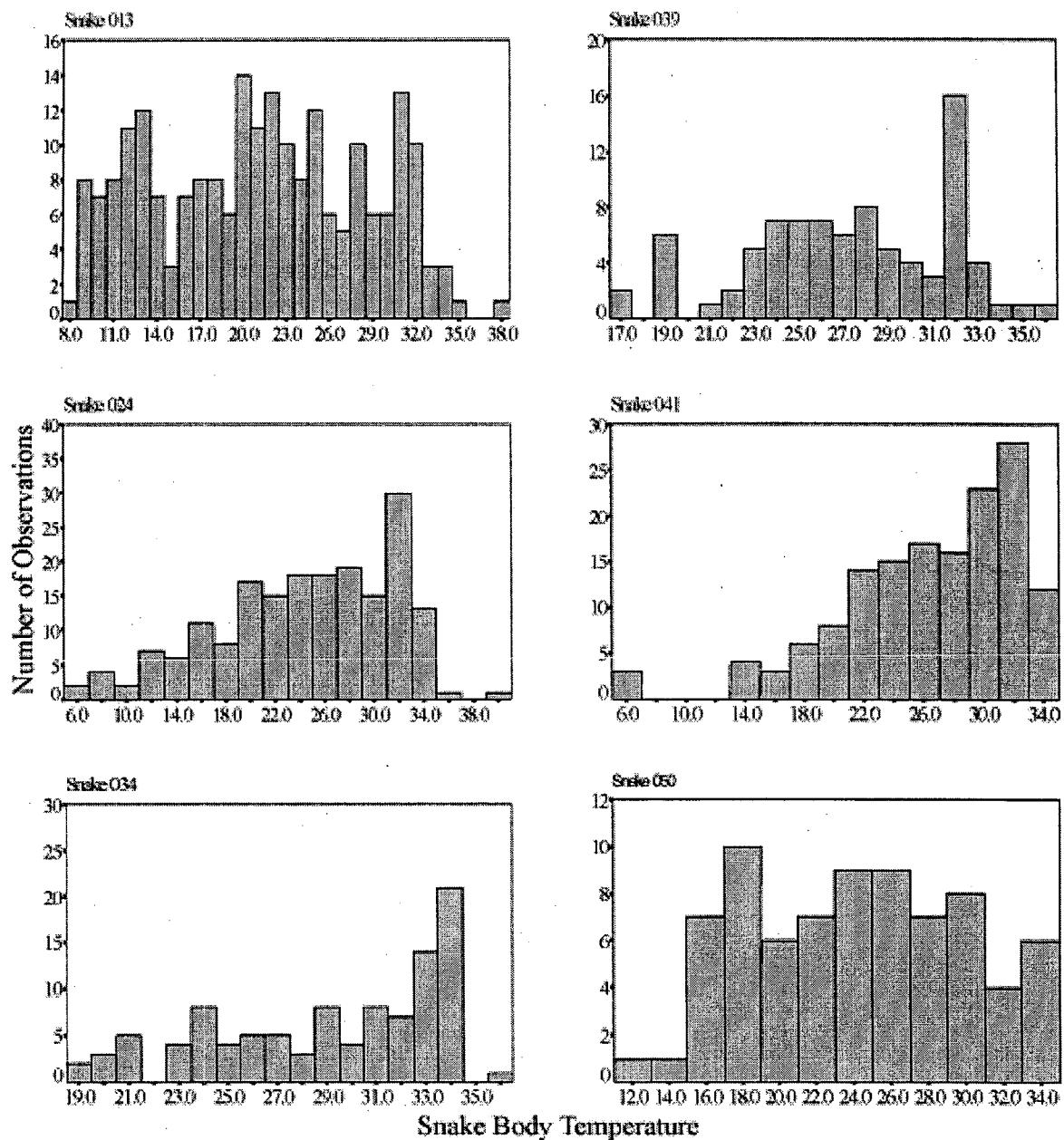


Figure 1 (Cont.)

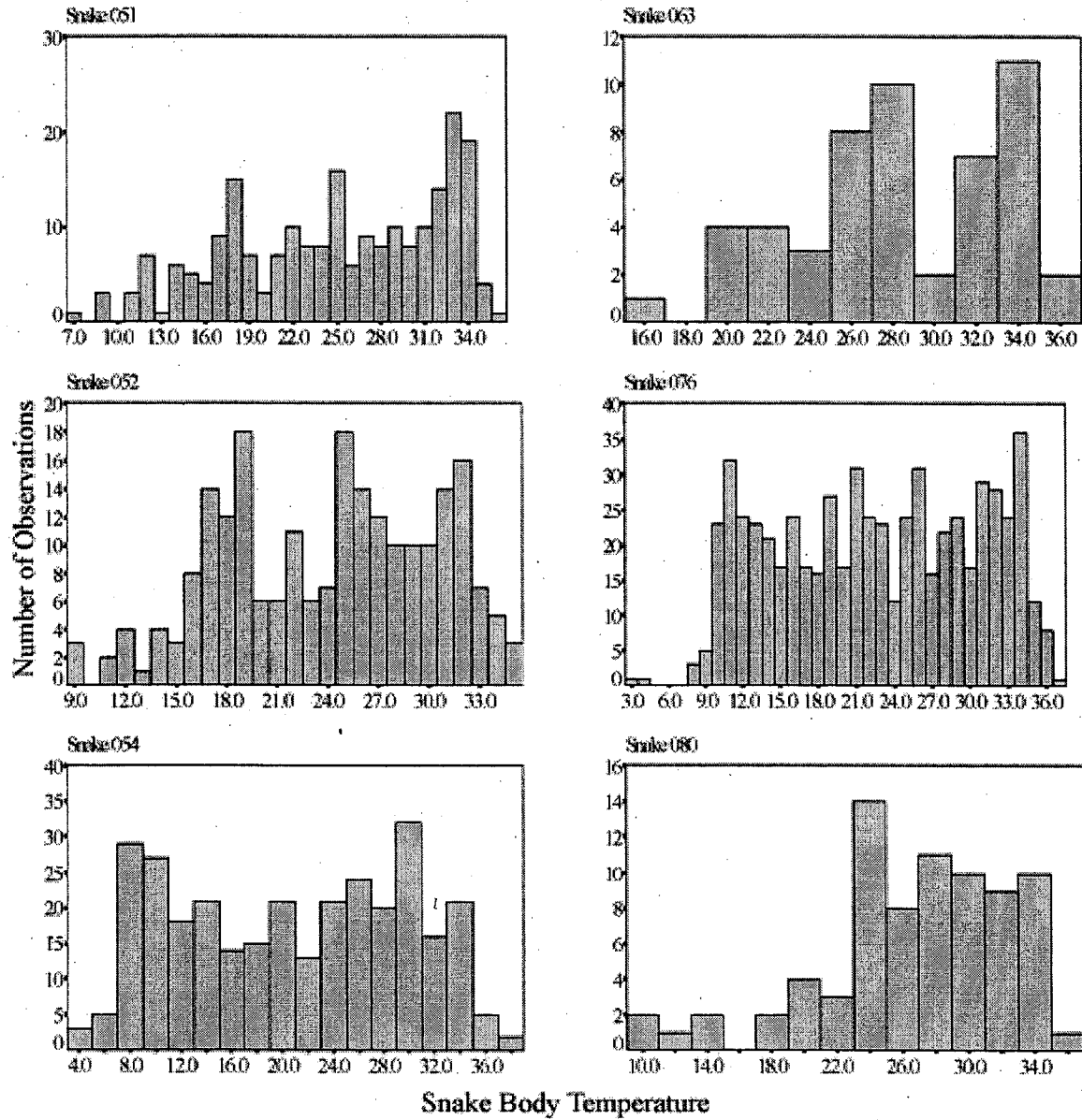


Figure 1 (Cont.)

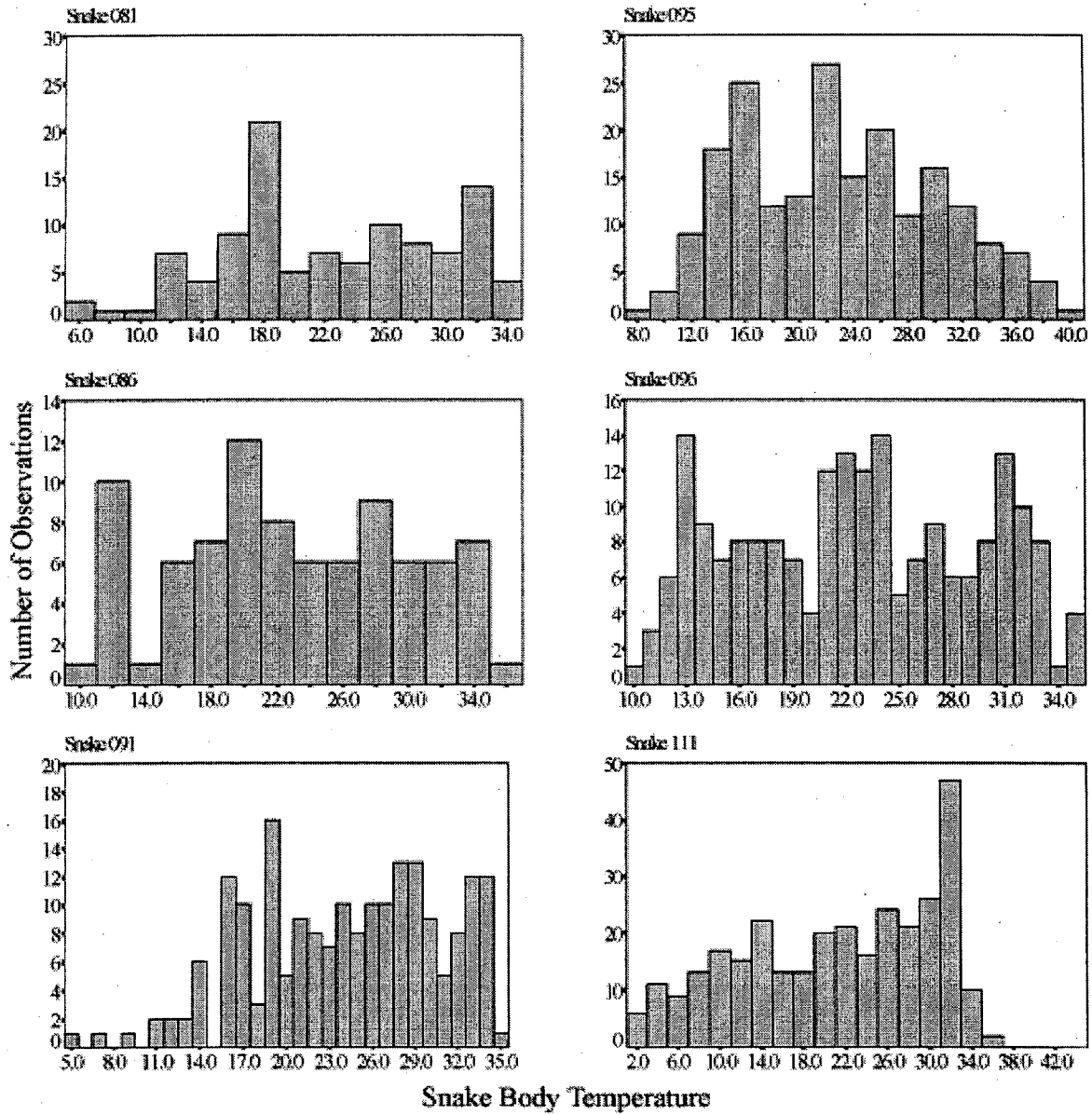


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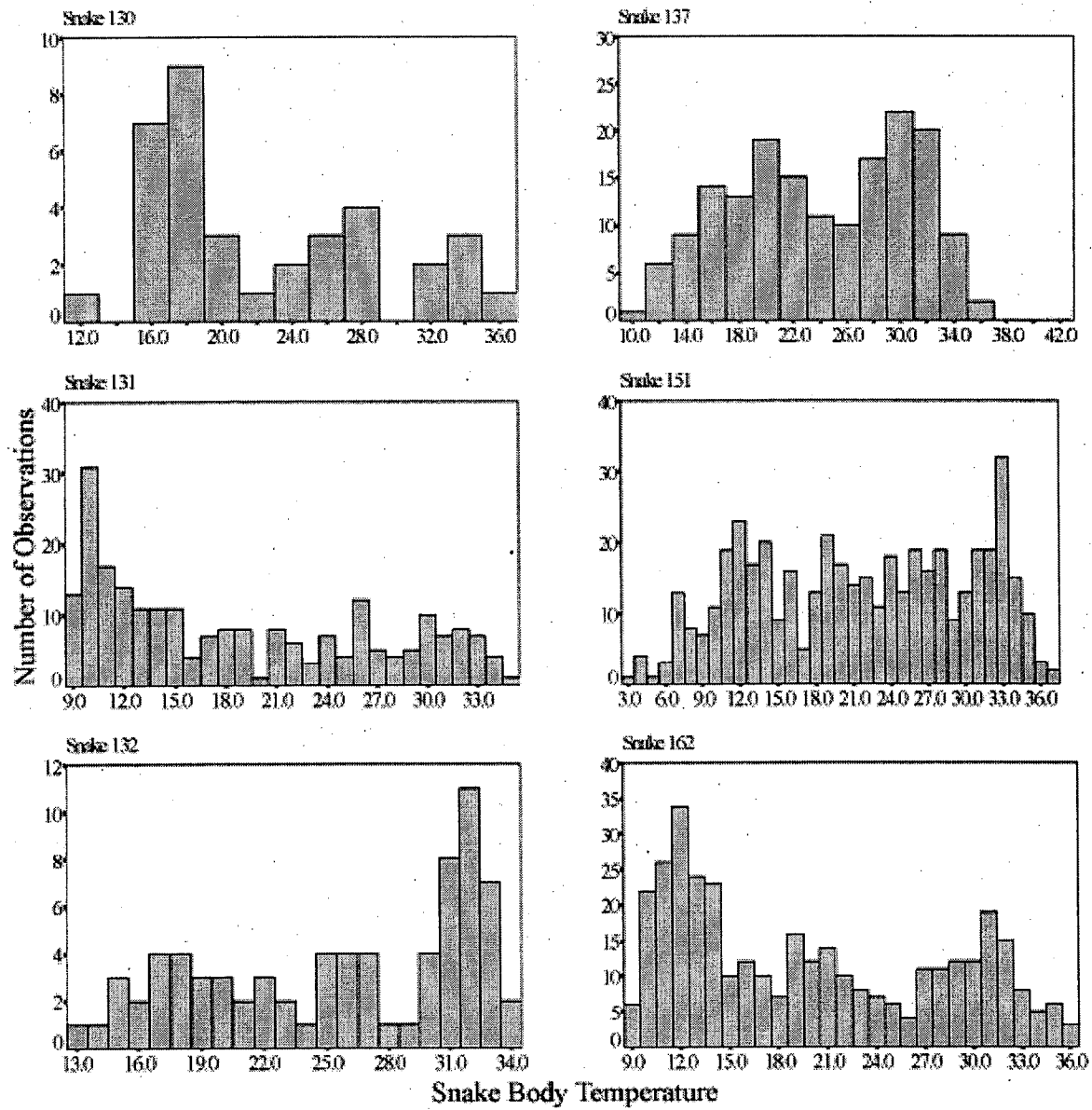


Figure 1 (Cont.)

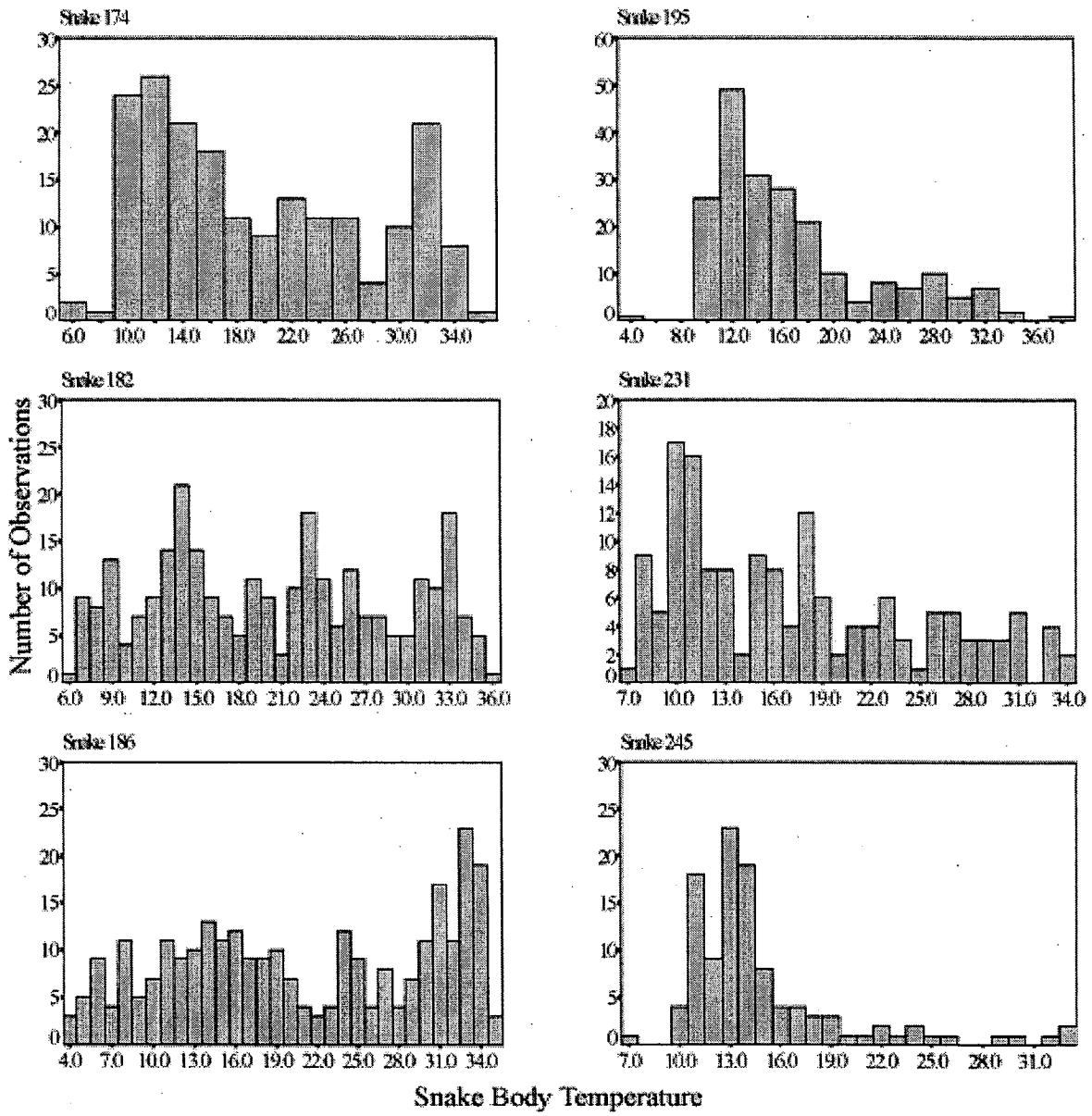


Figure 1 (Cont.)

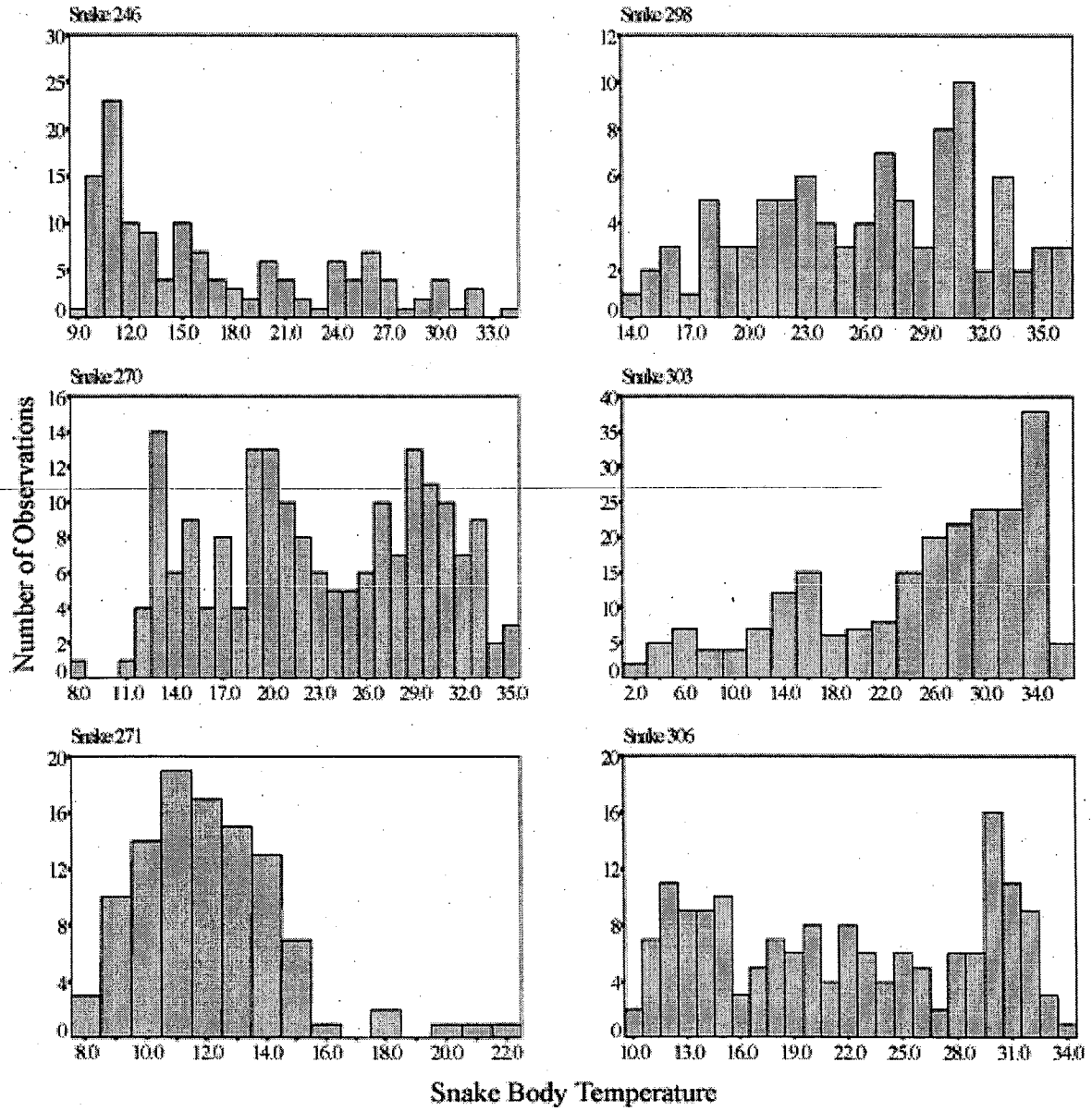


Figure 1 (Cont.)

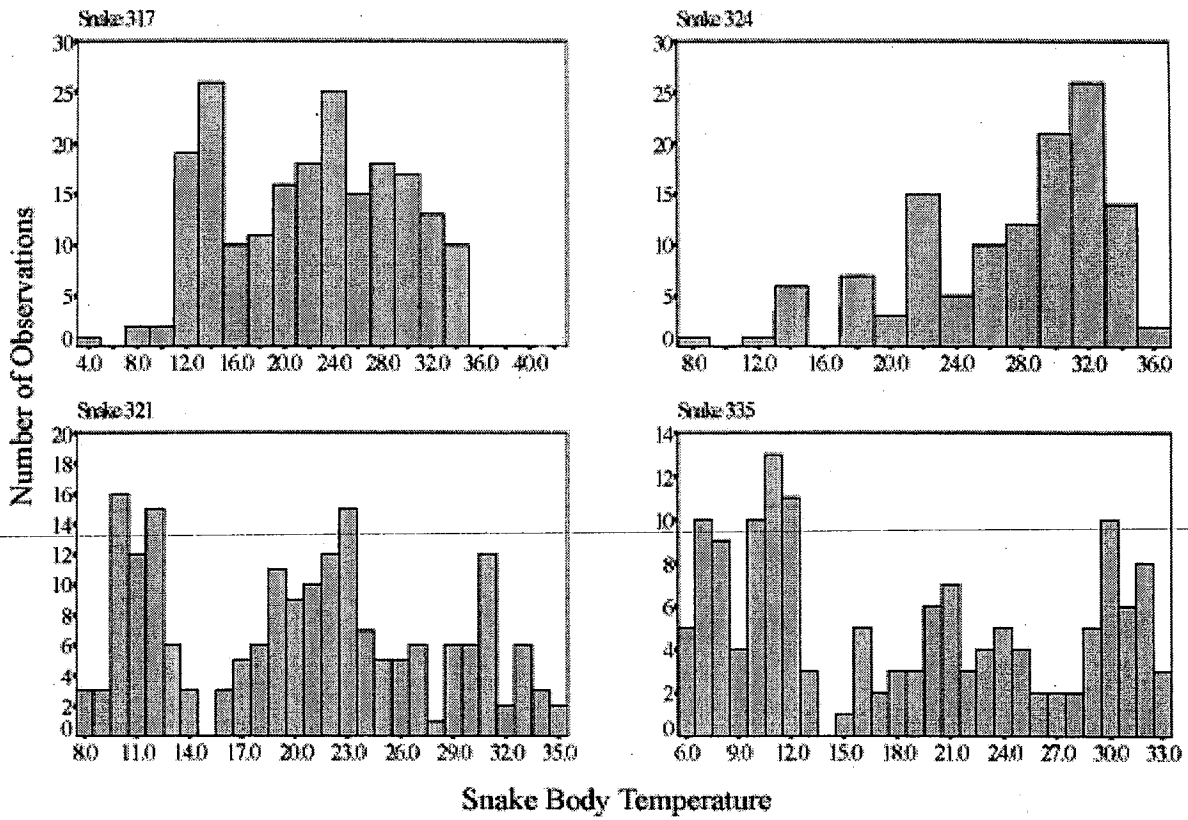


Figure 2

NONGRAVID FEMALES

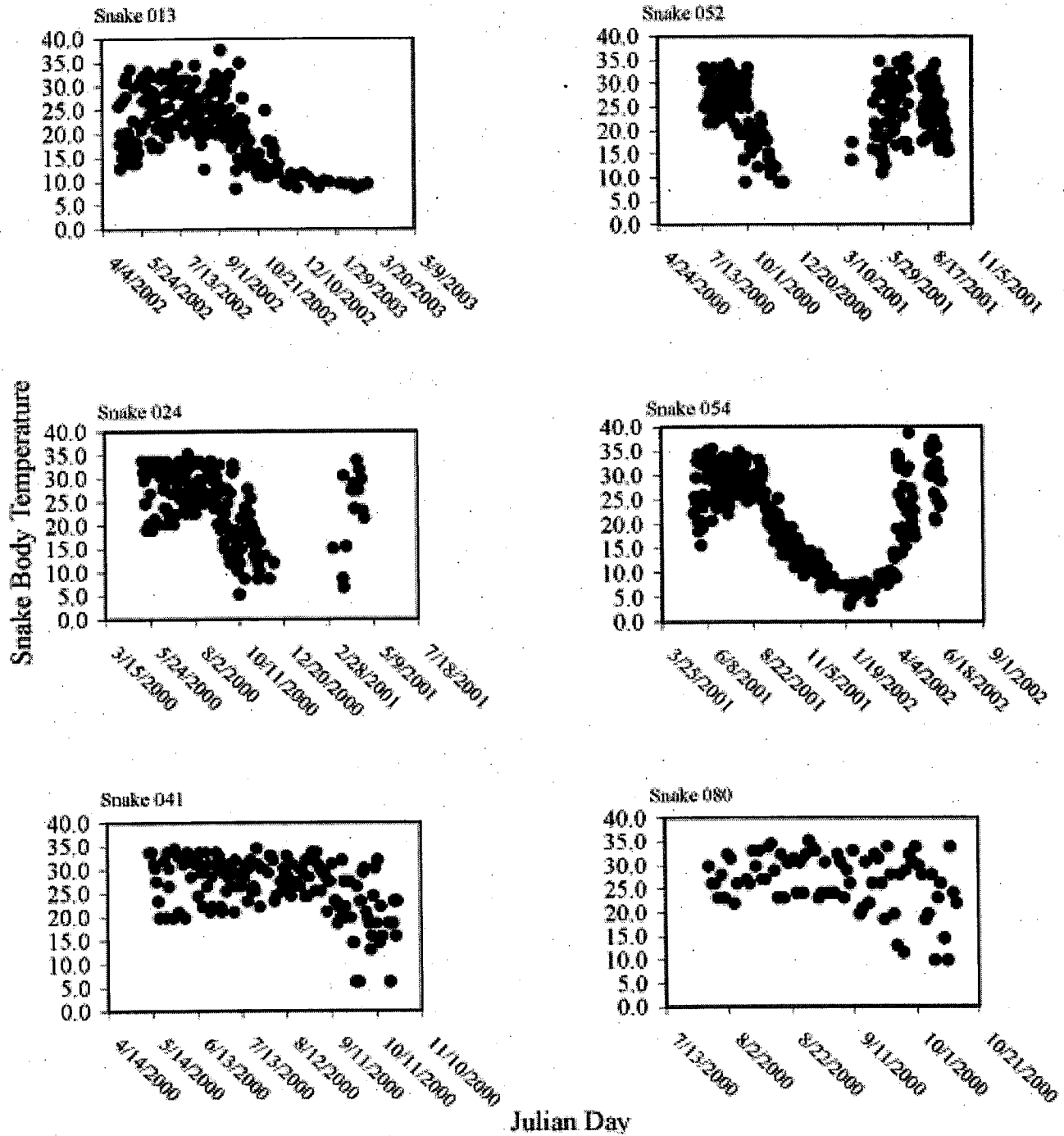


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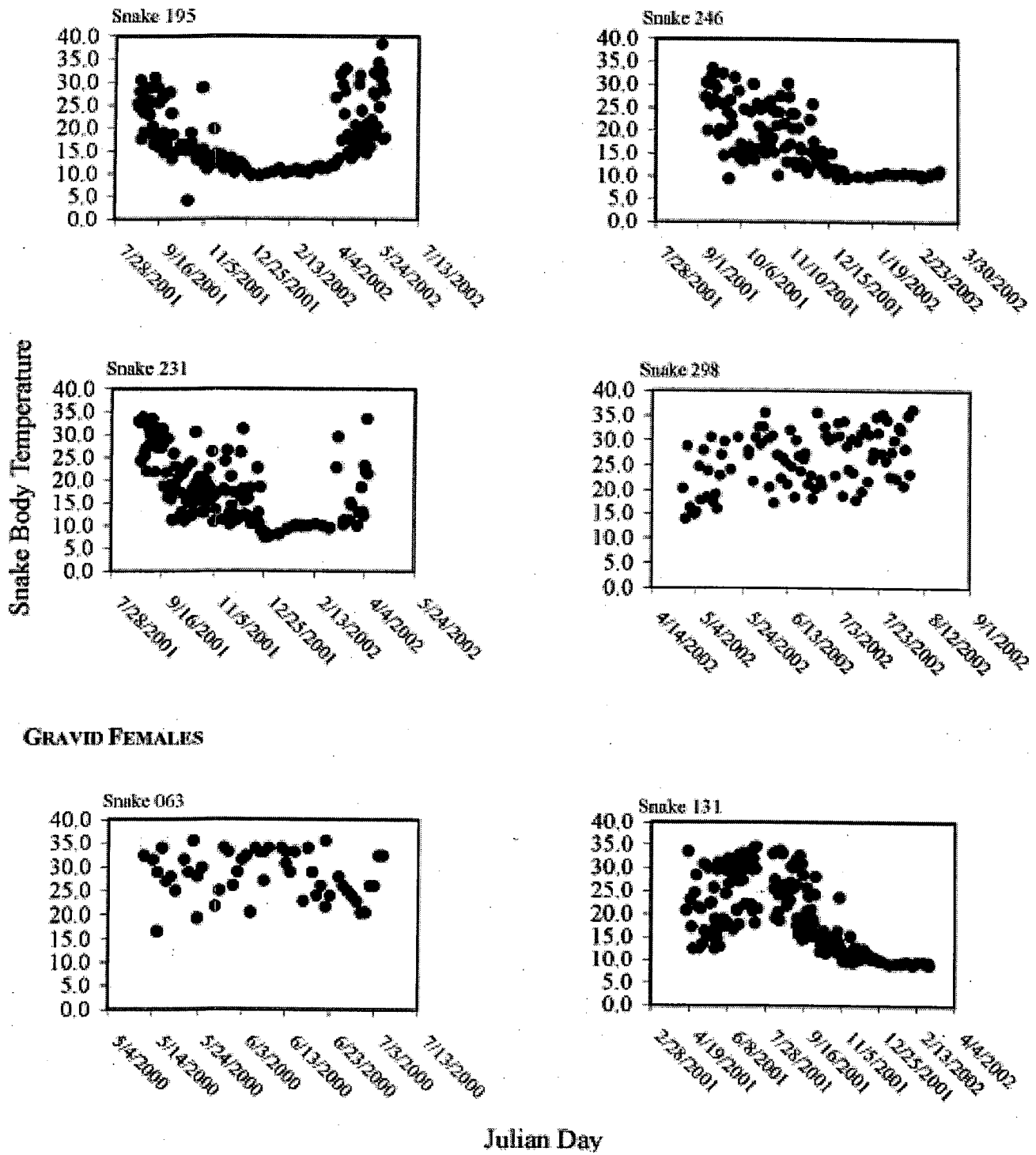


Figure 2 (Cont.)

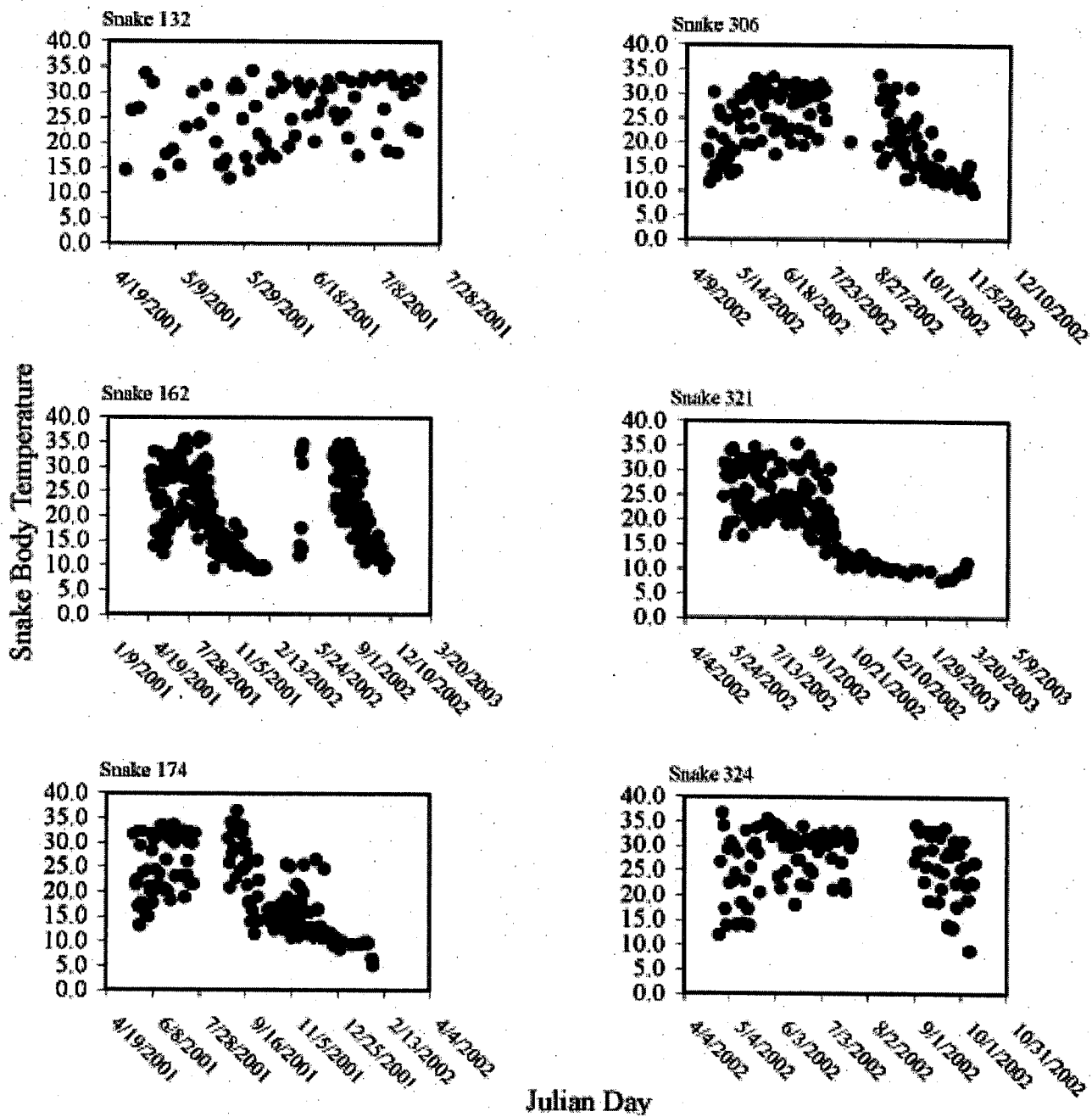
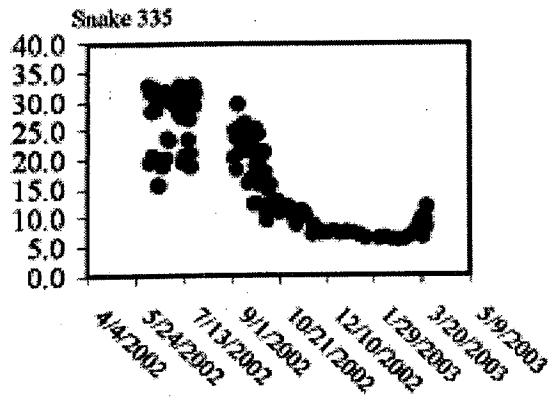
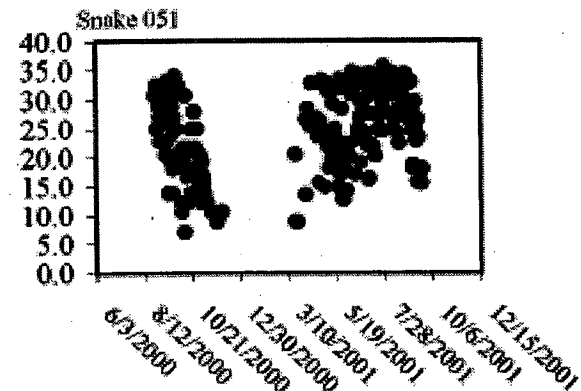
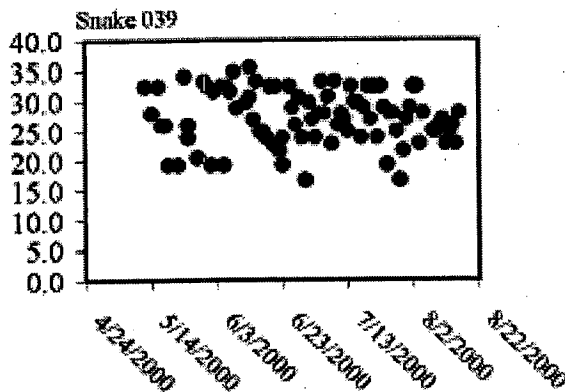
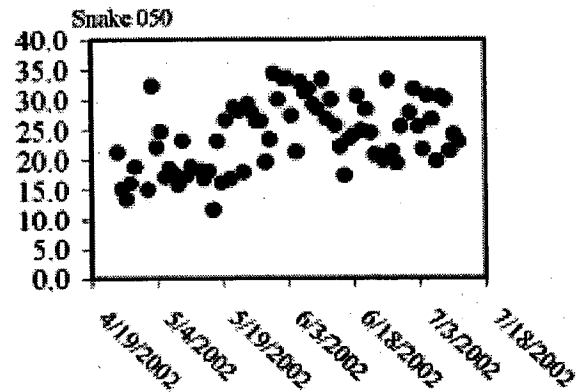
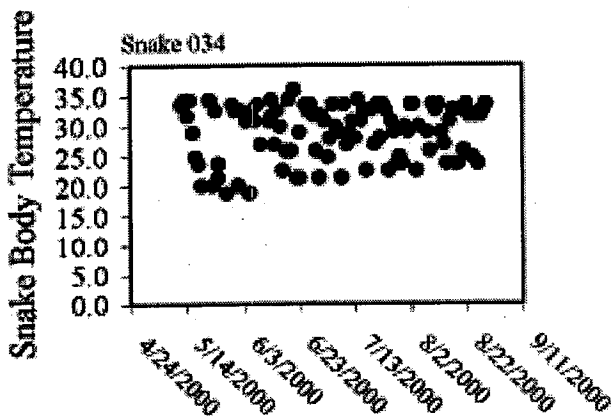


Figure 2 (Cont.)



MALES



Julian Day

Figure 2 (Cont.)

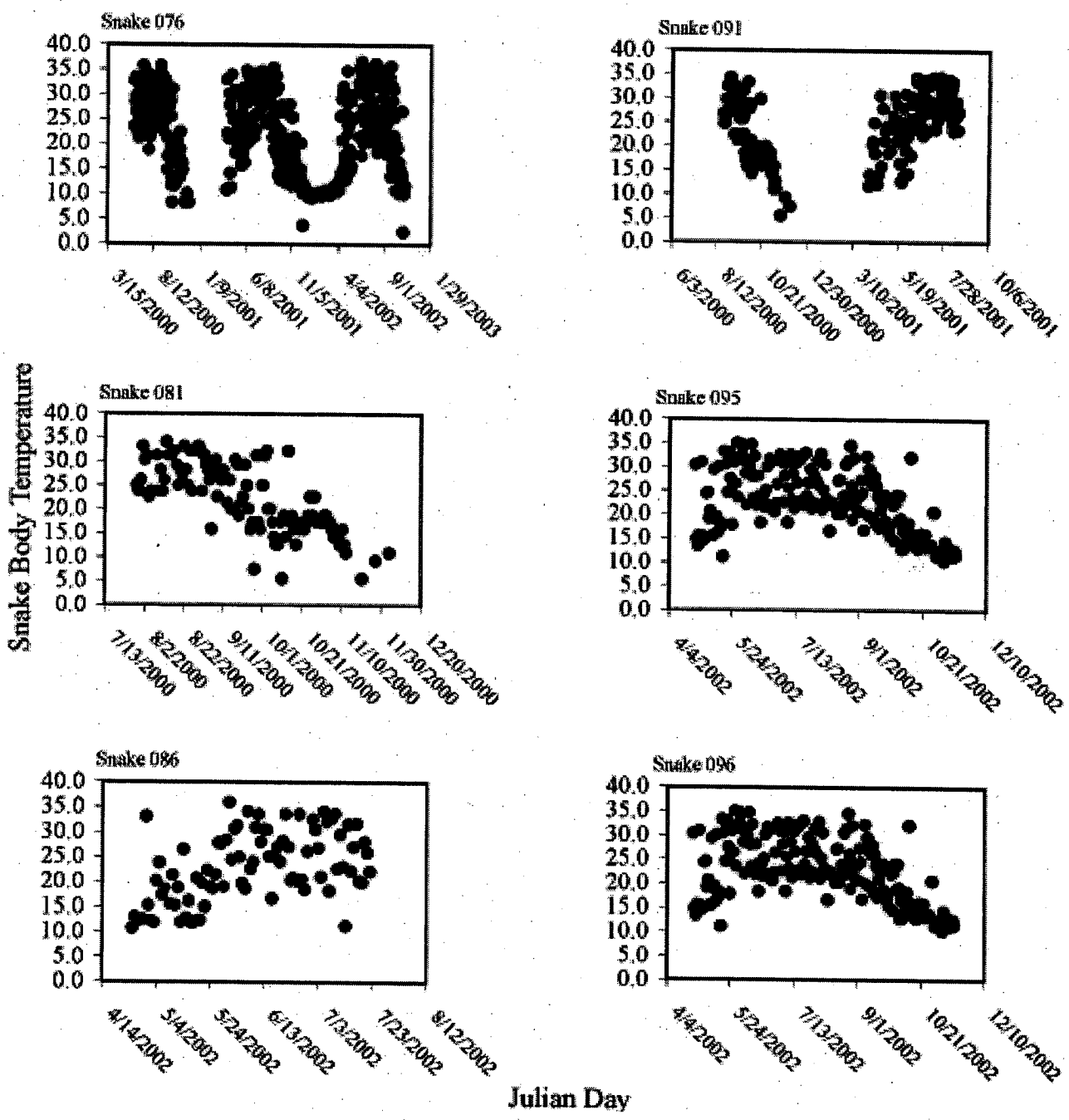


Figure 2 (Cont.)

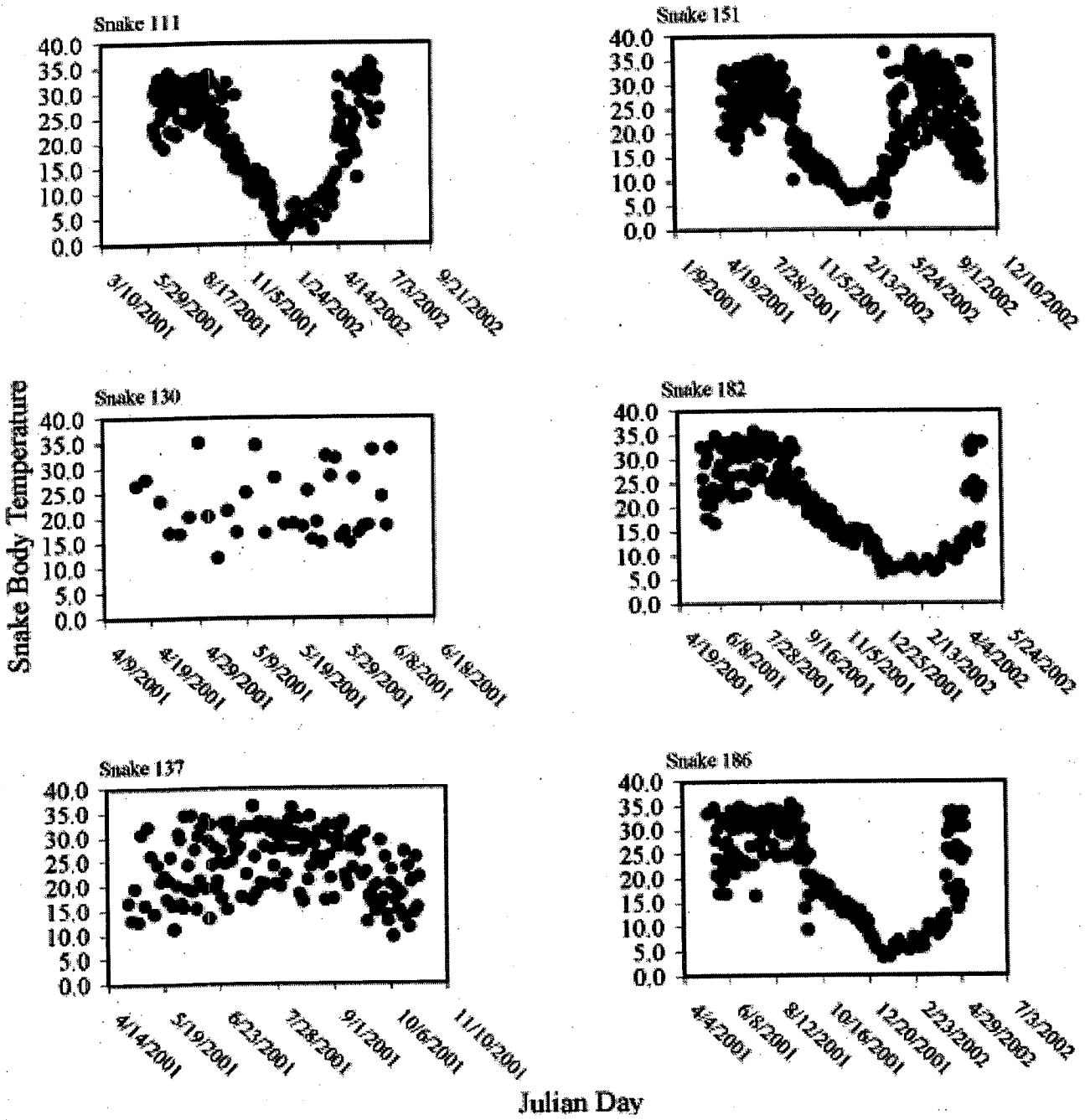


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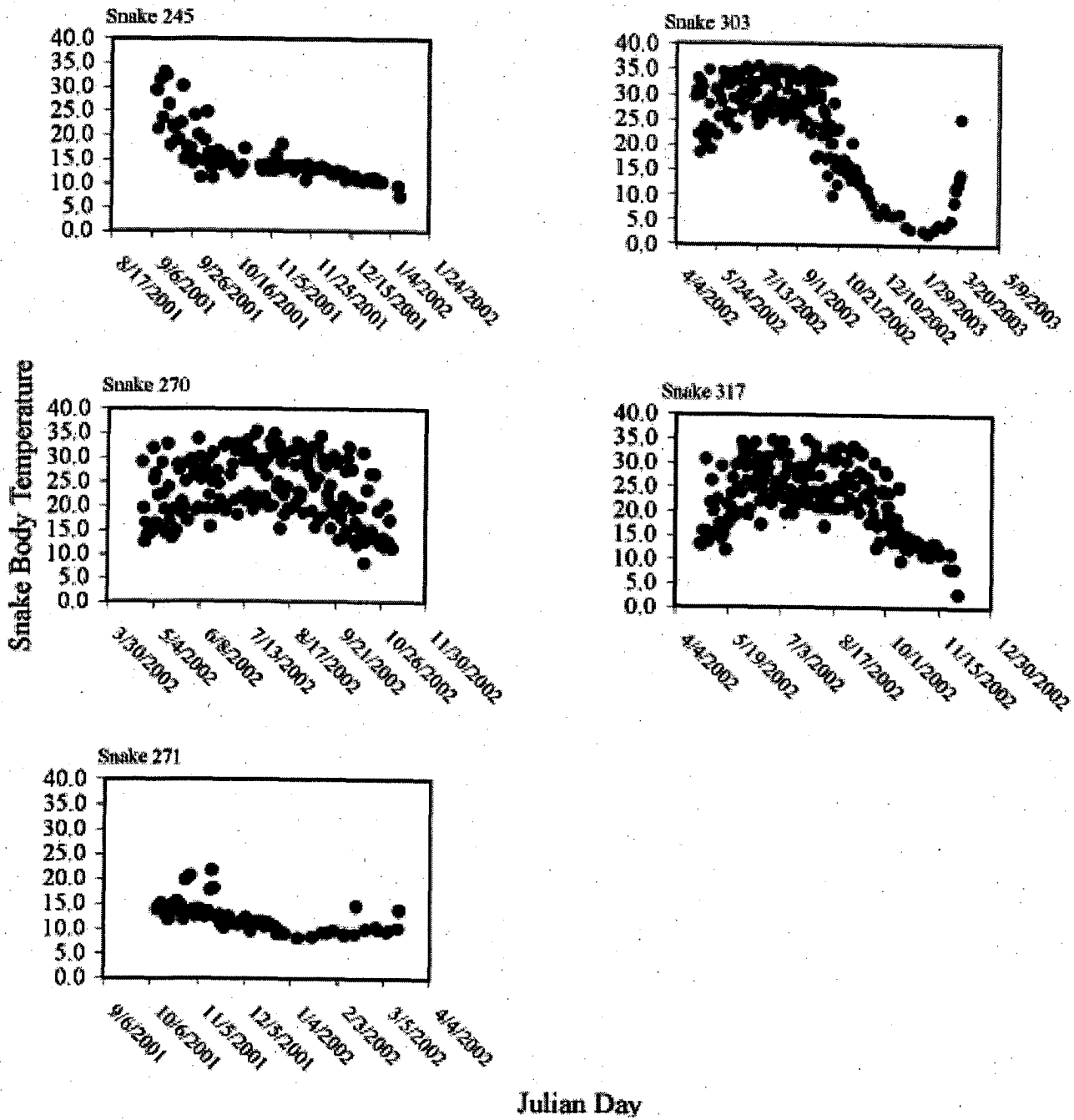


Figure 3

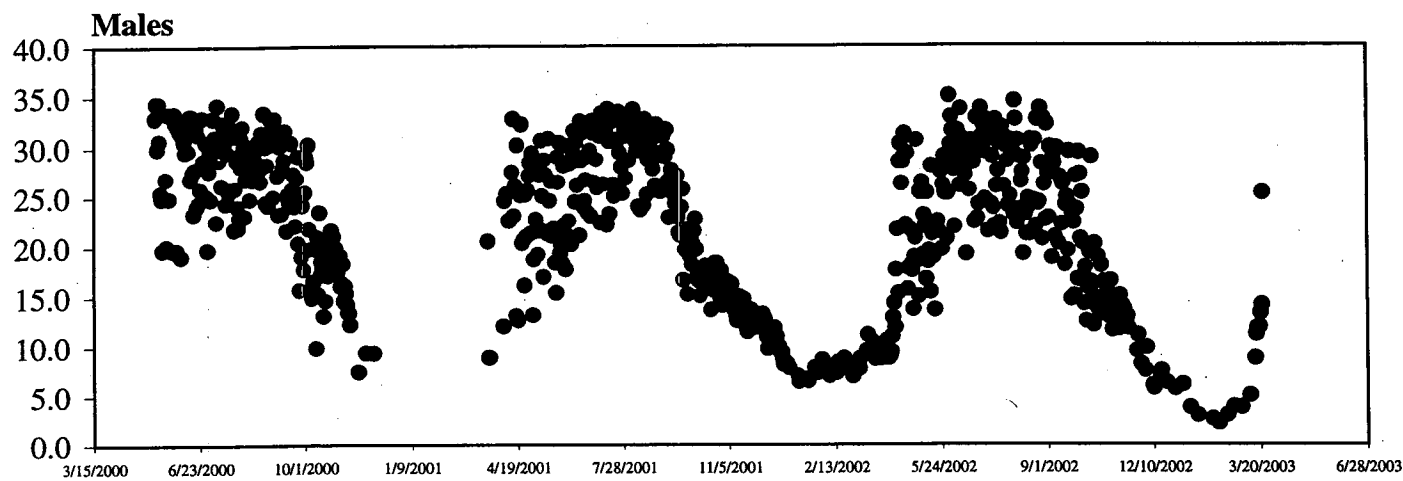
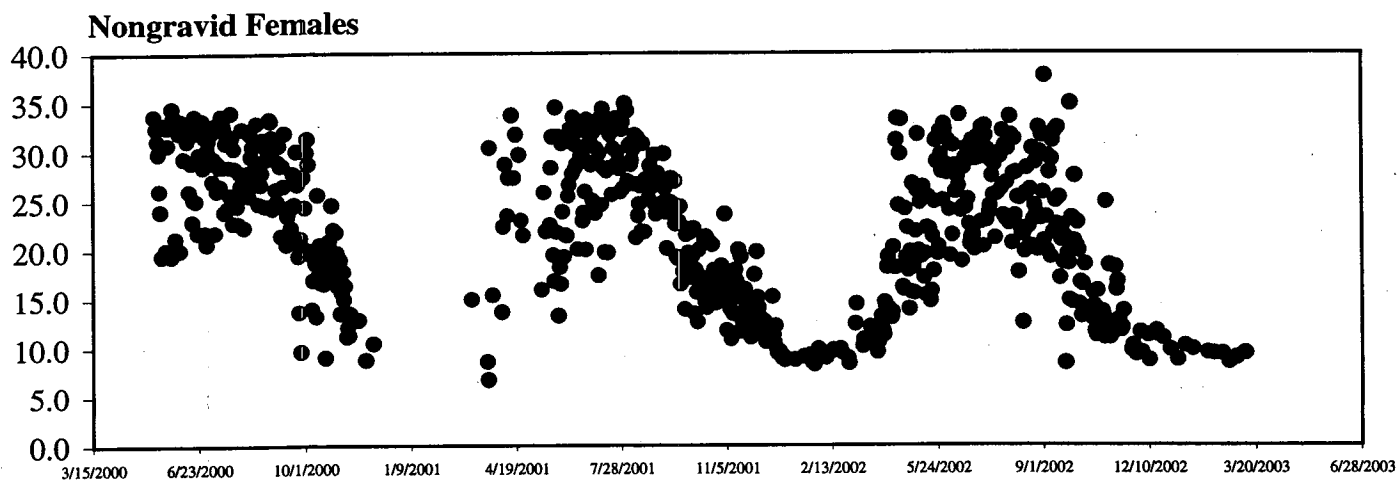
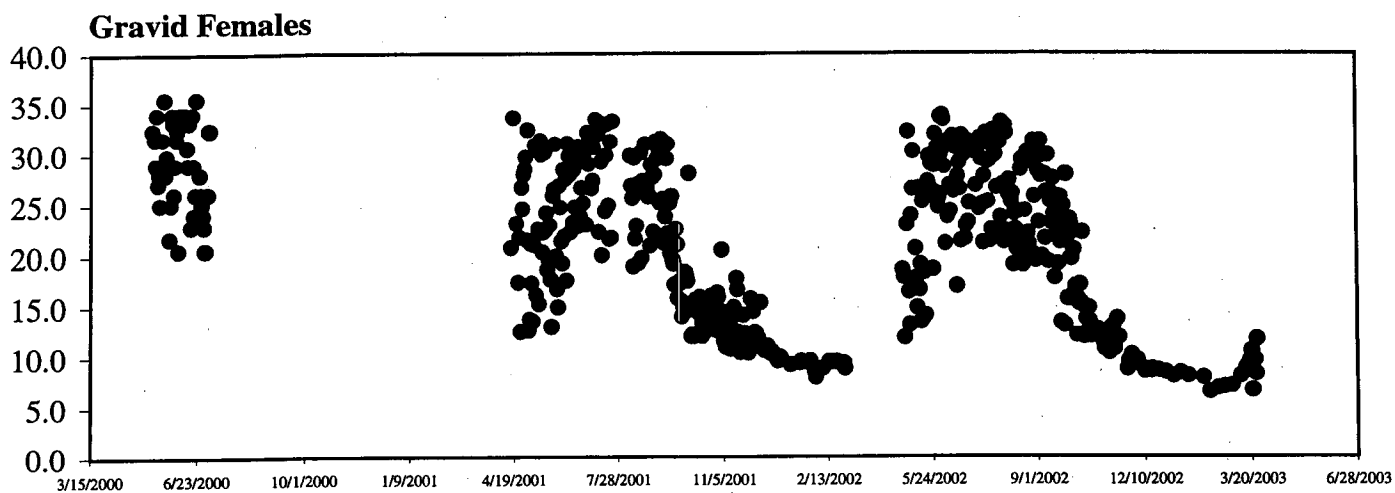


Figure 4

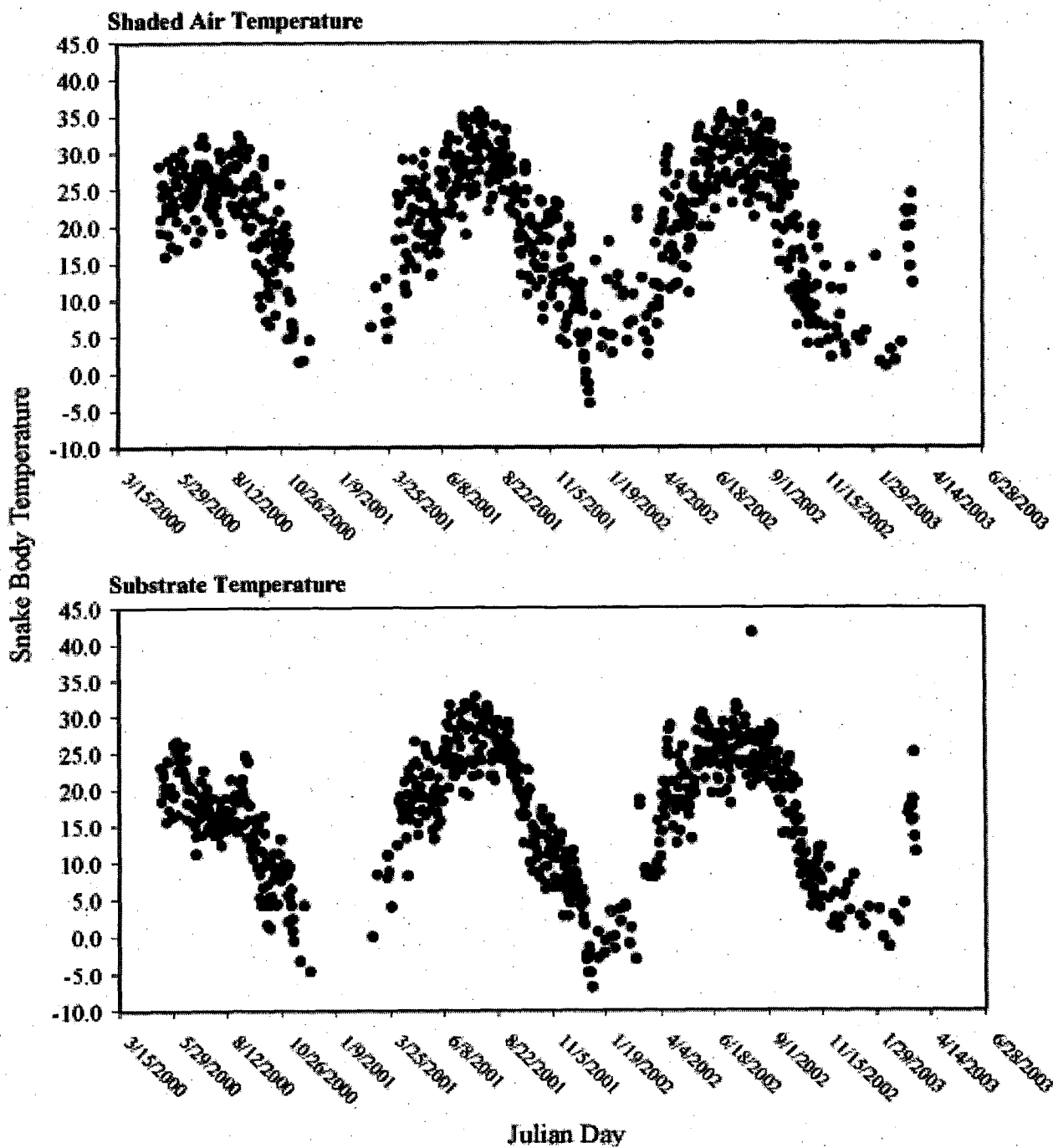


Figure 5

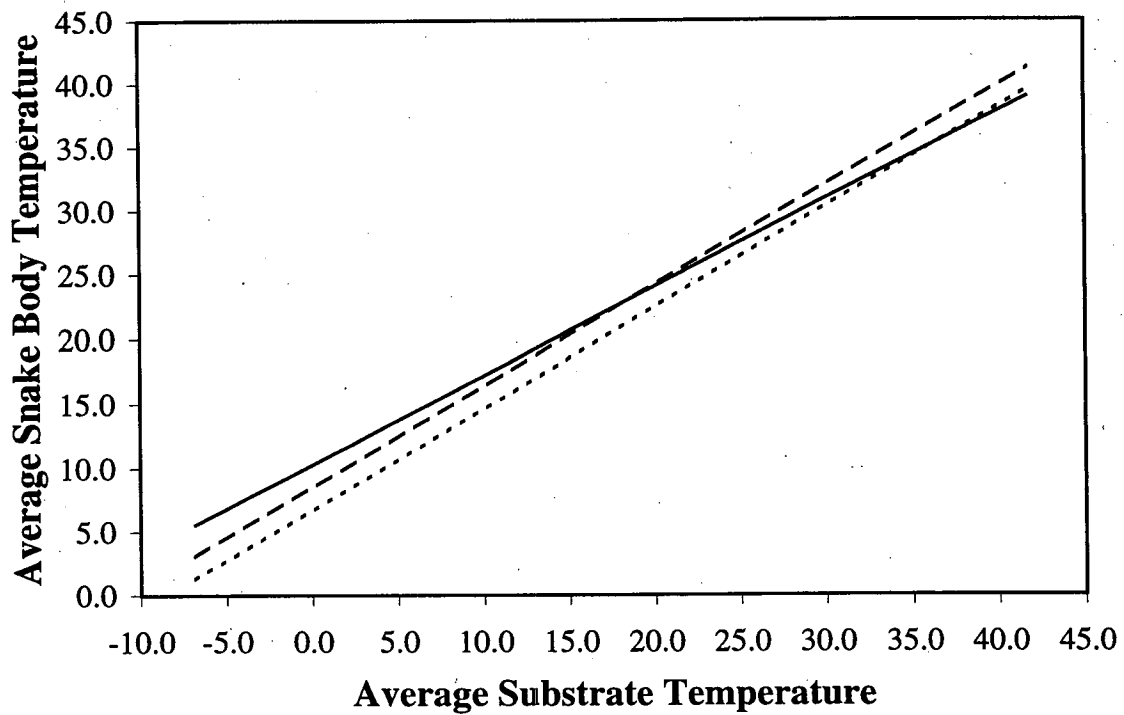
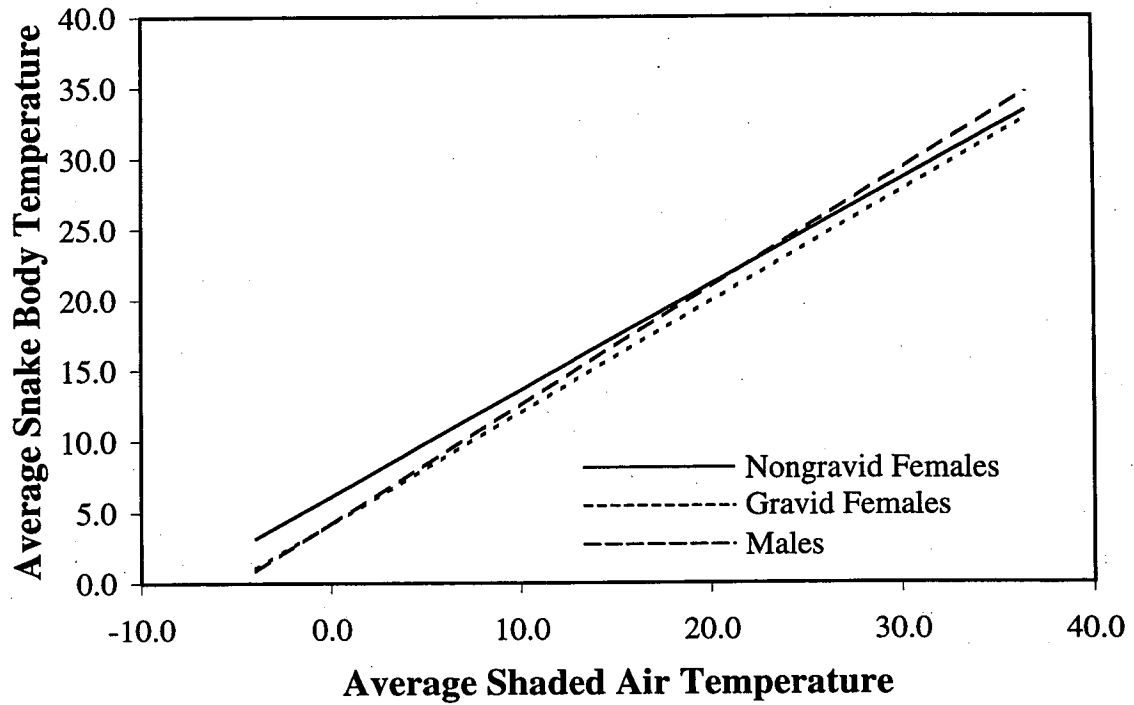


Figure 6

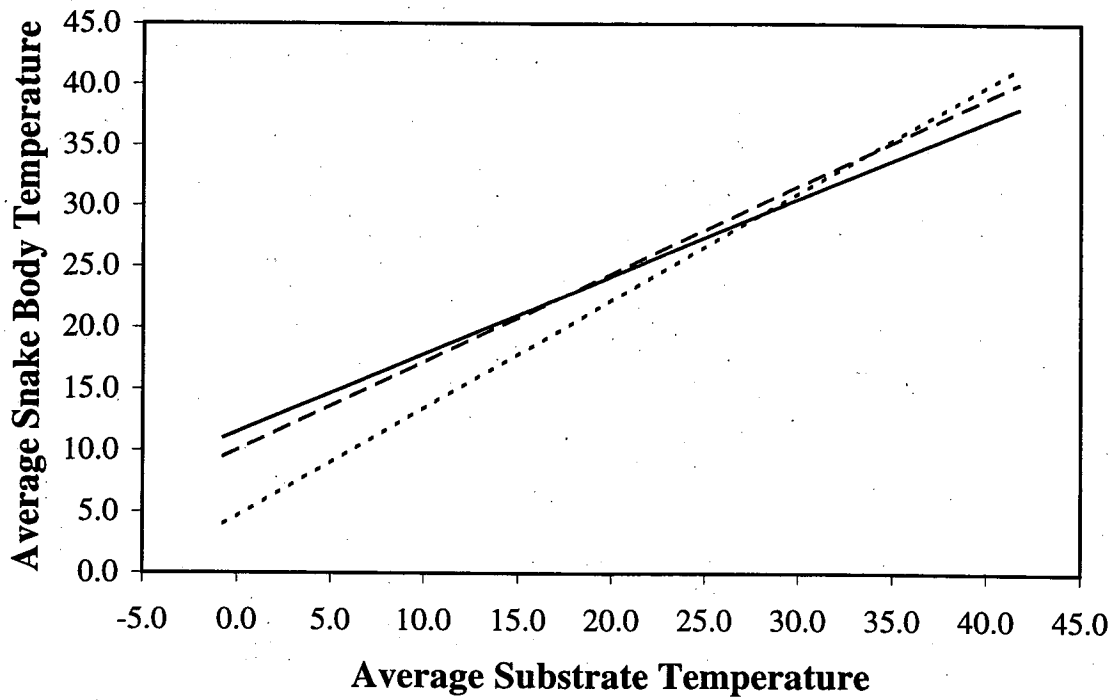
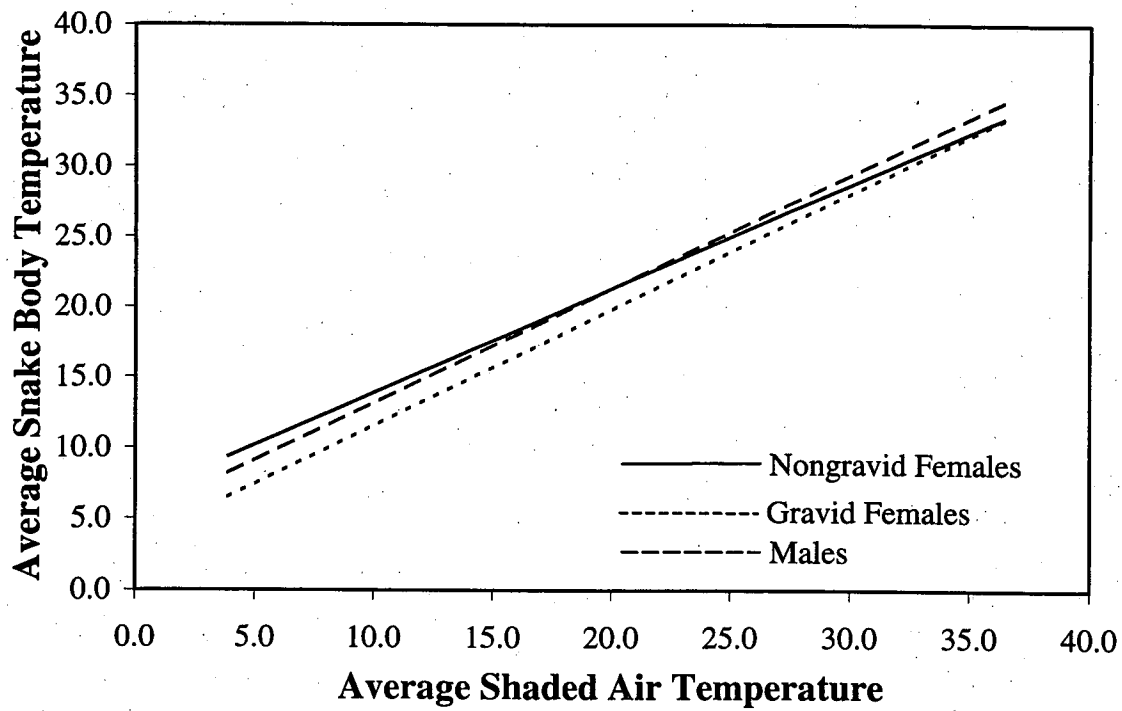


Figure 7

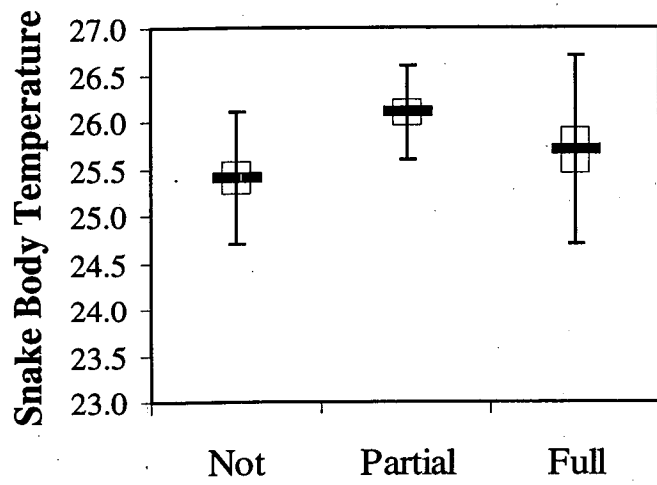
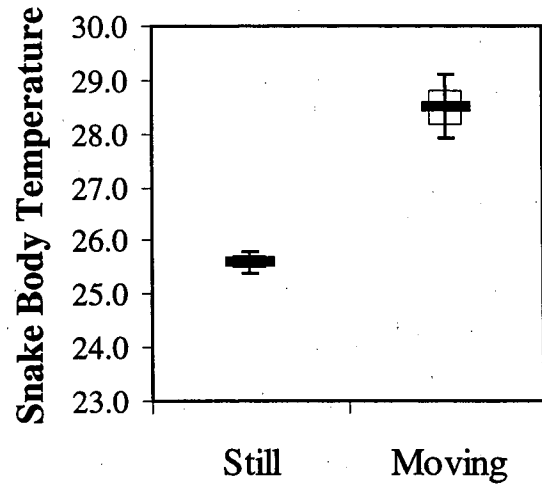
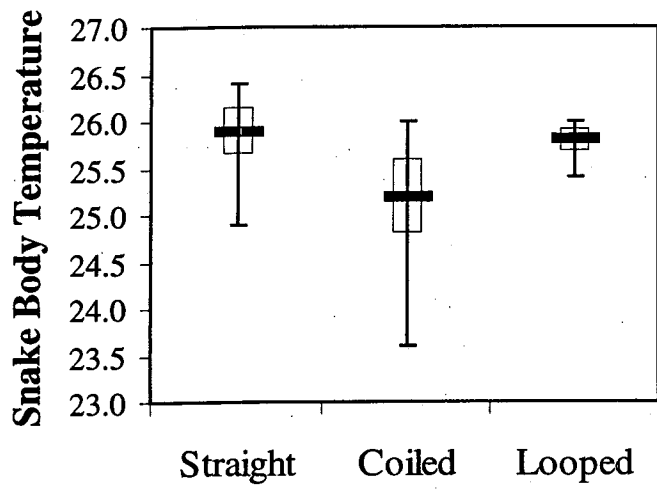


Figure 8

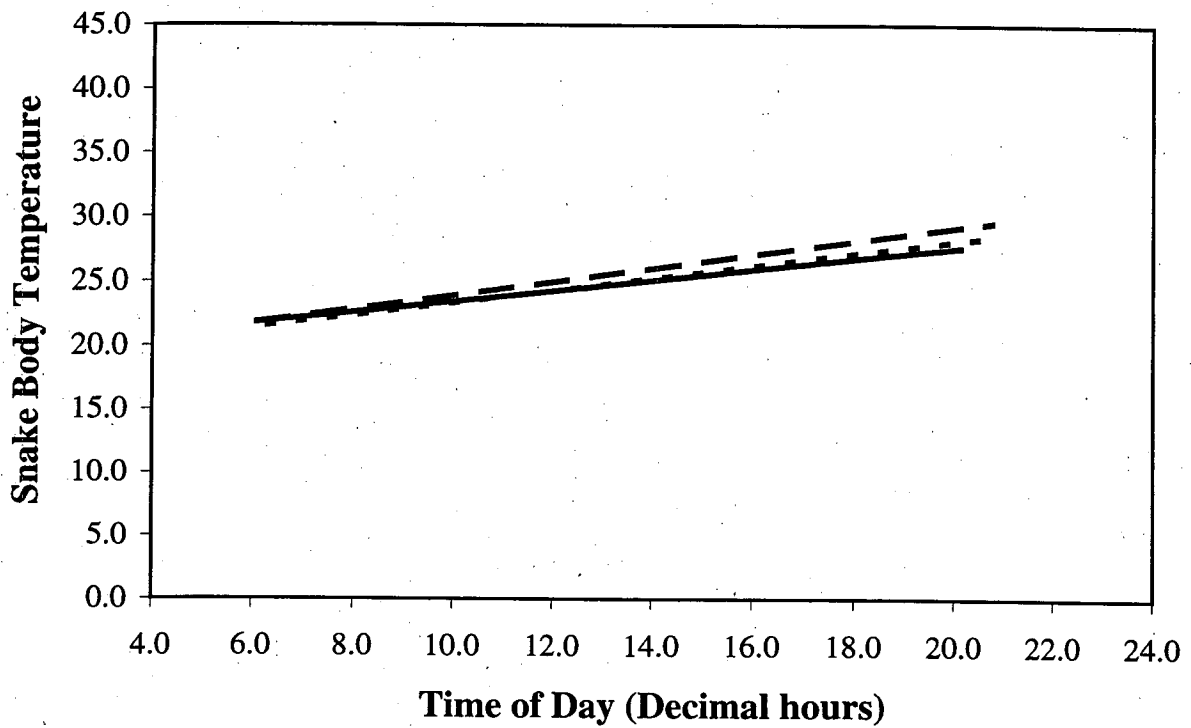
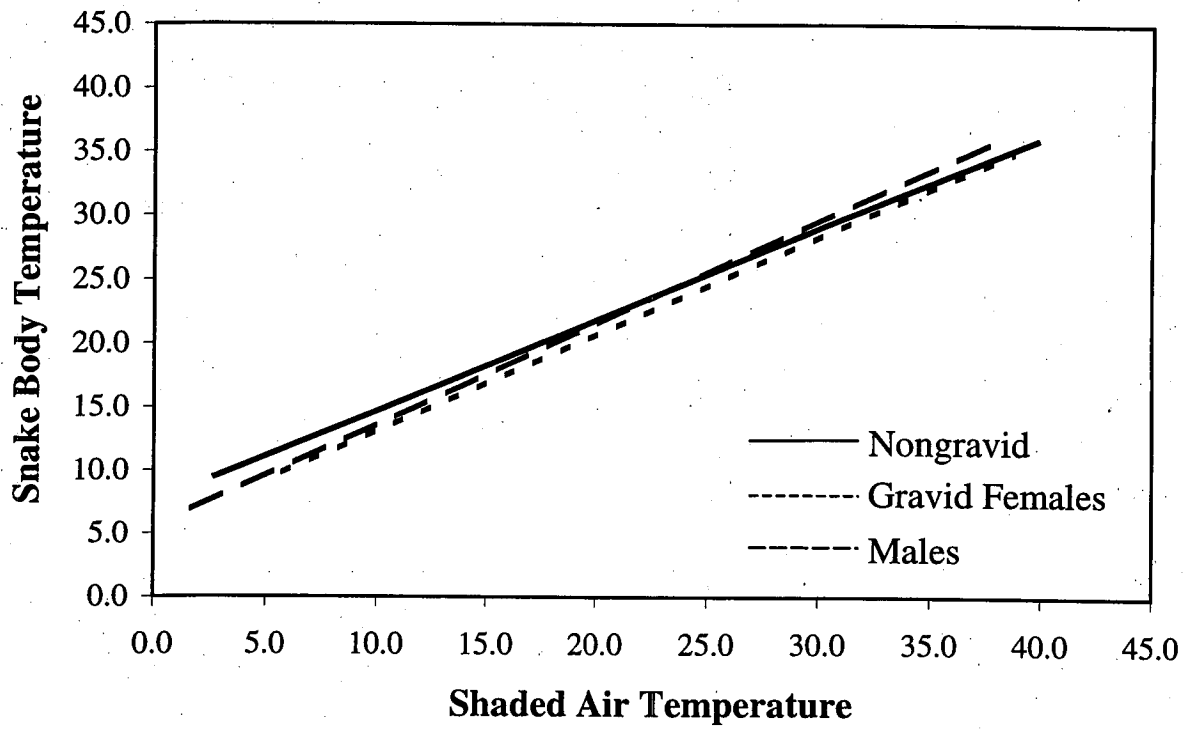


Figure 9

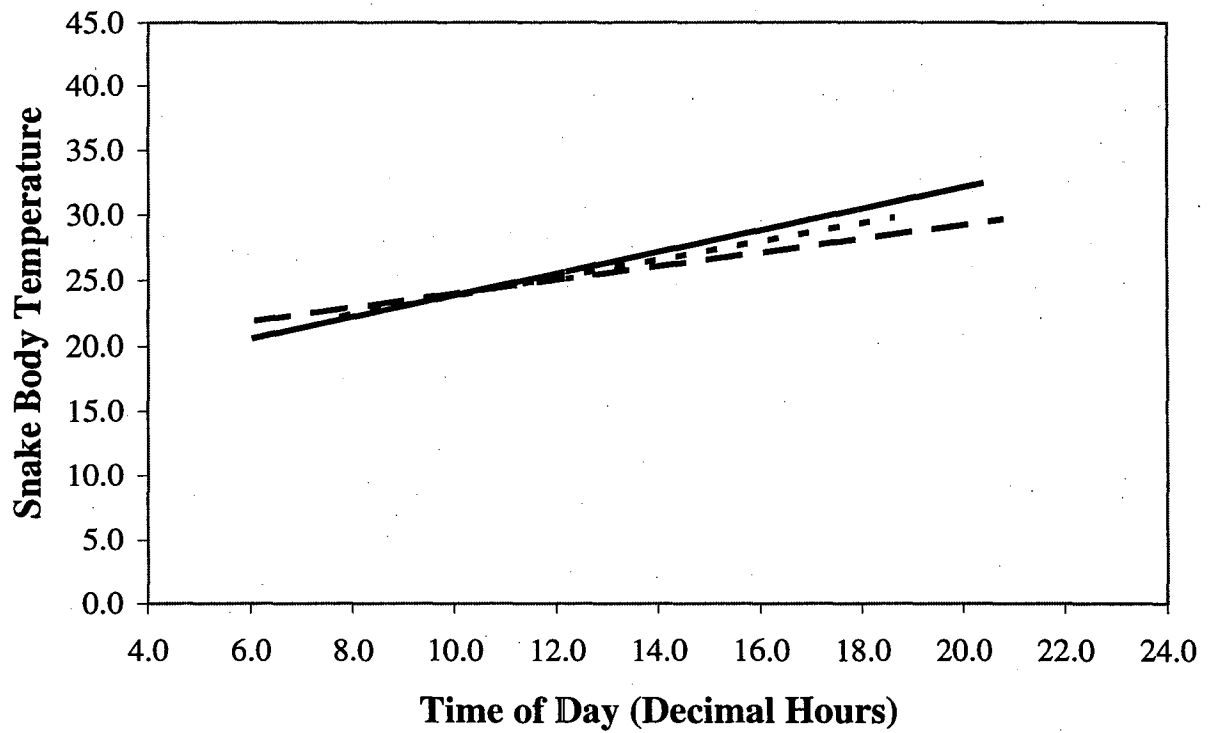
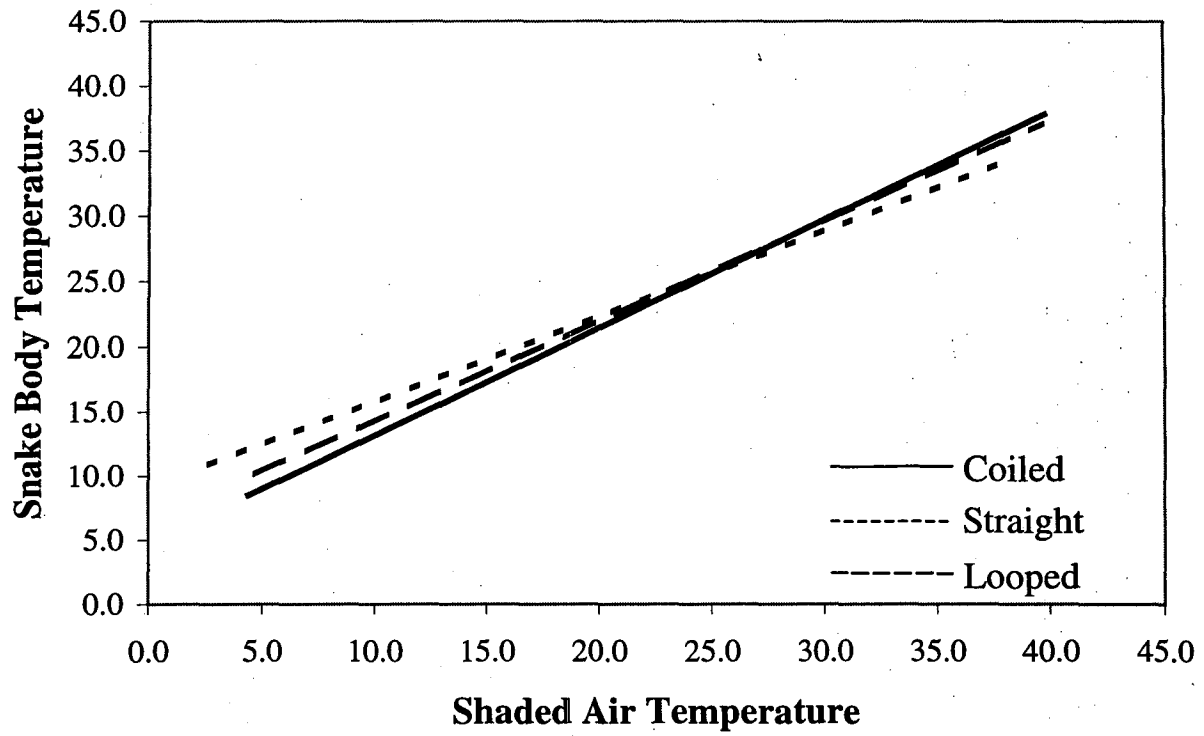


Figure 10

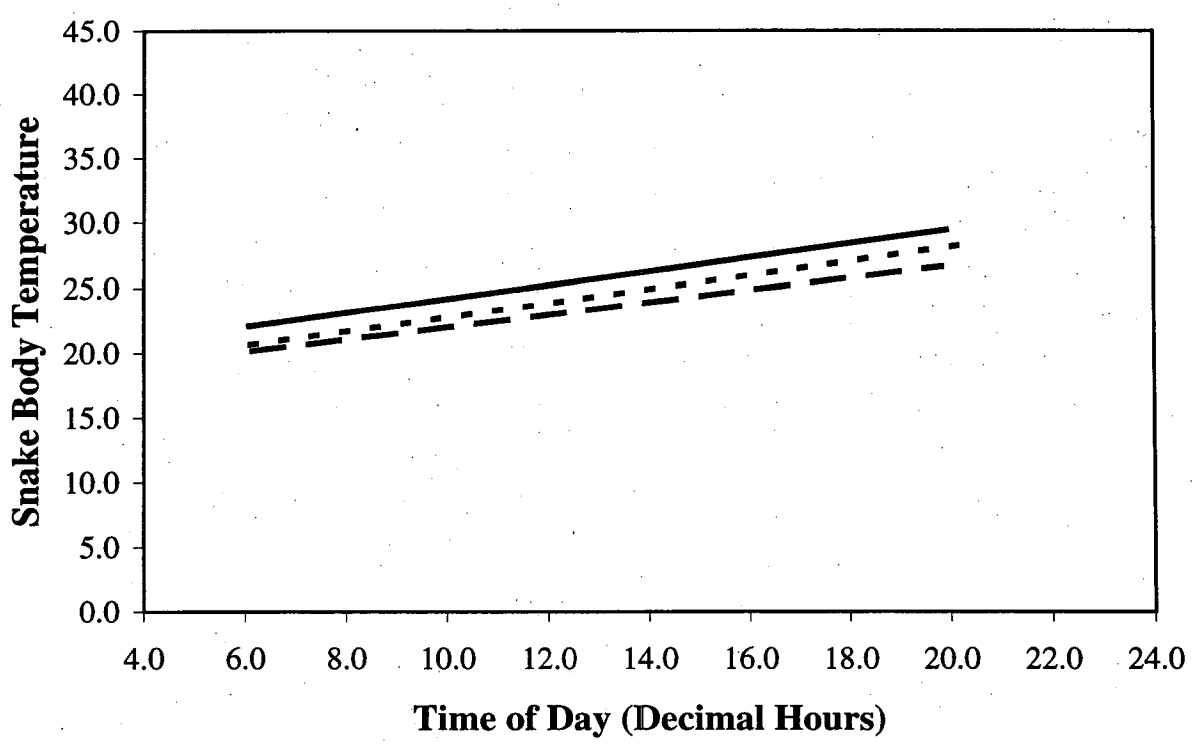
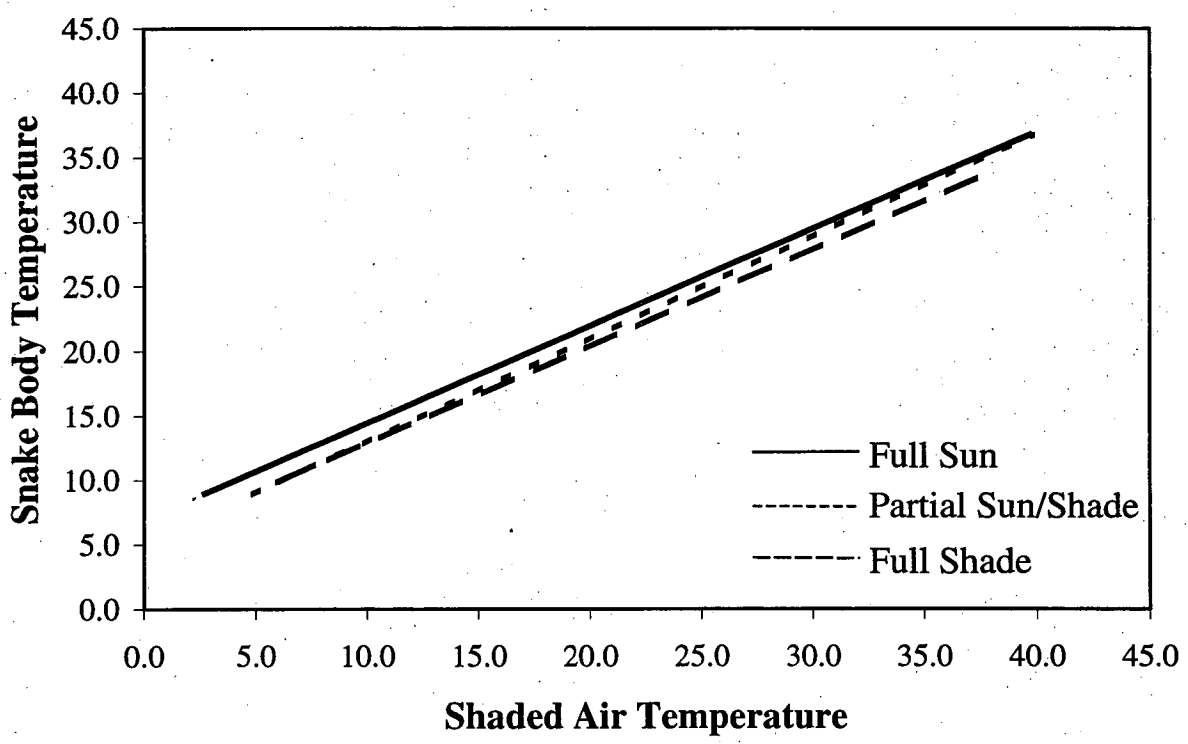


Figure 11

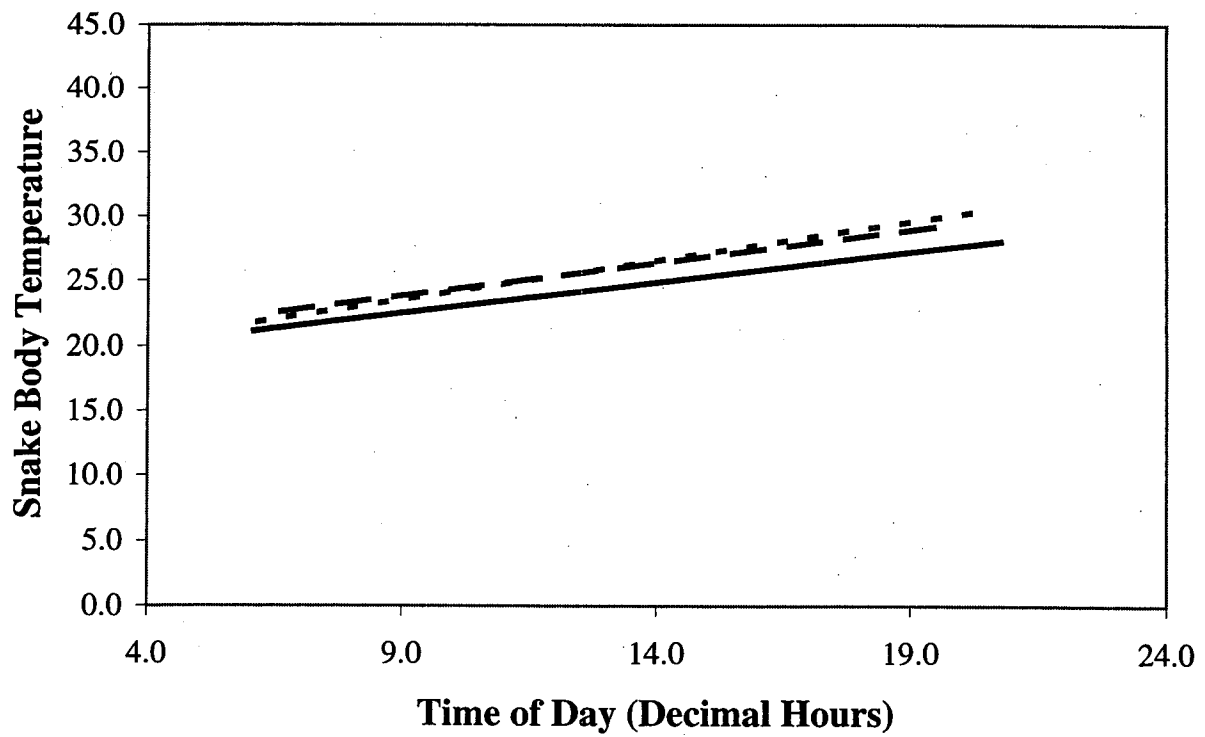
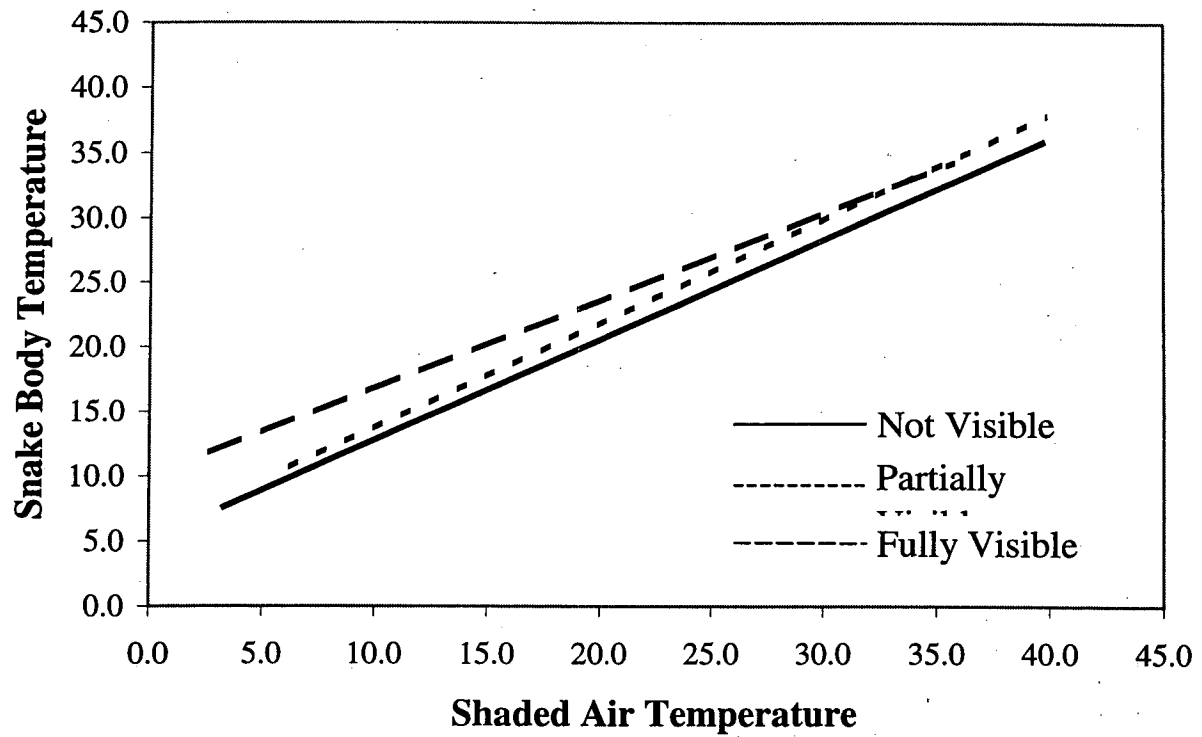


Figure 12

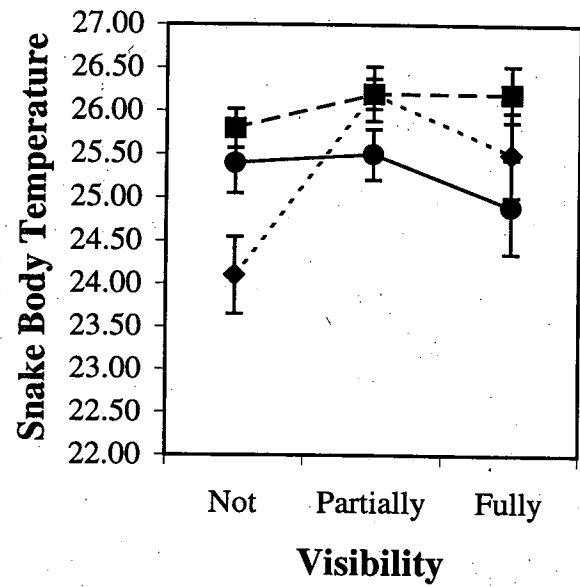
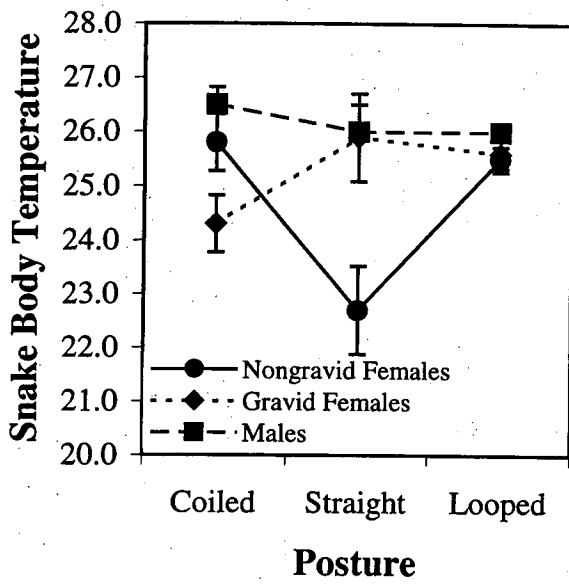


Figure 13

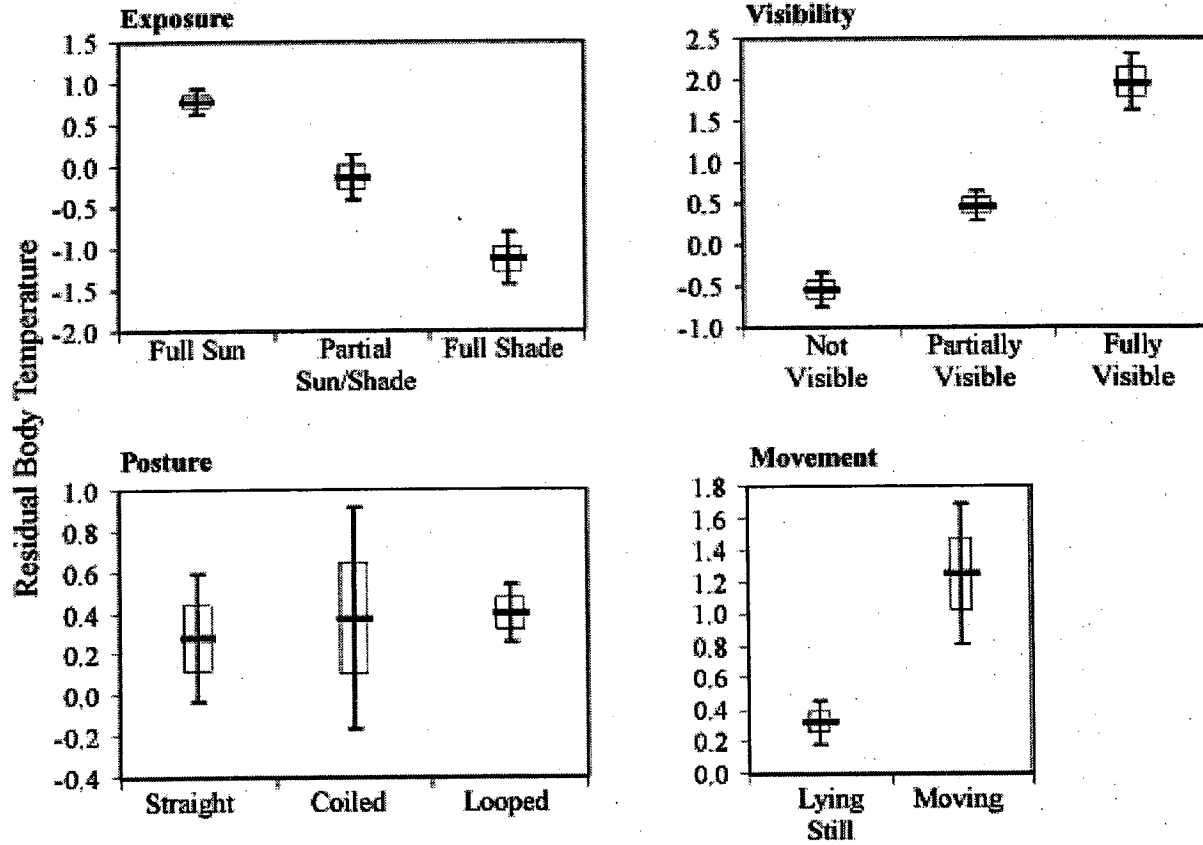


Figure 14

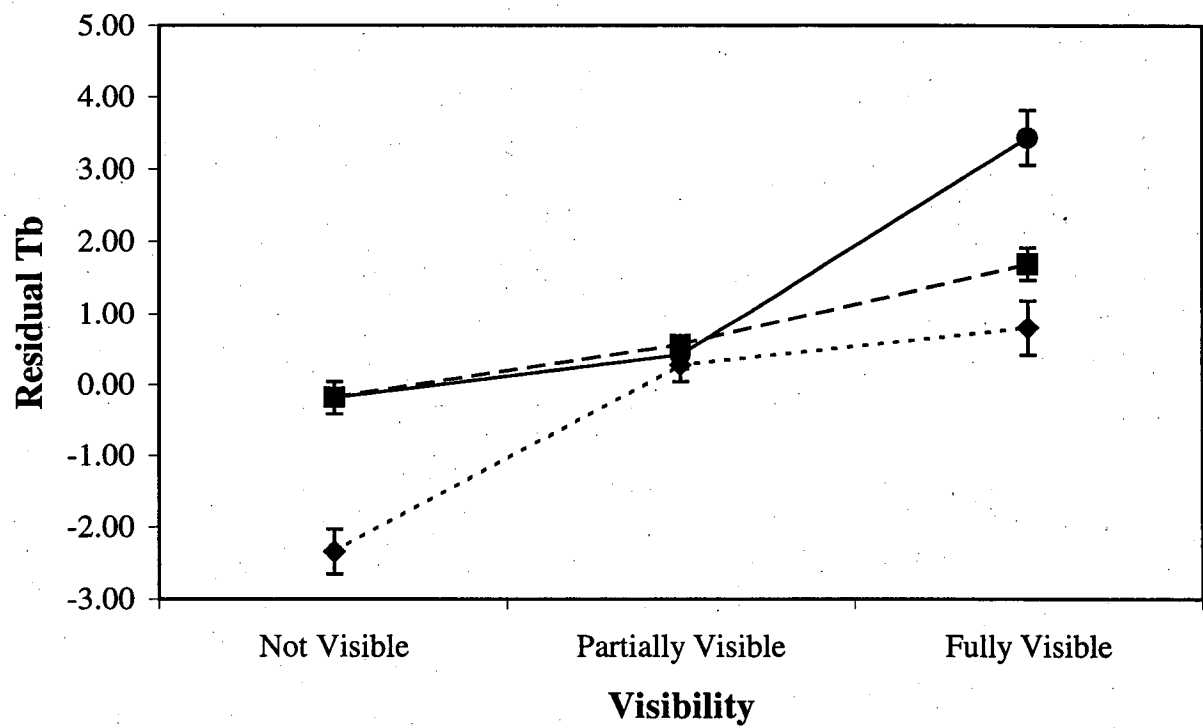
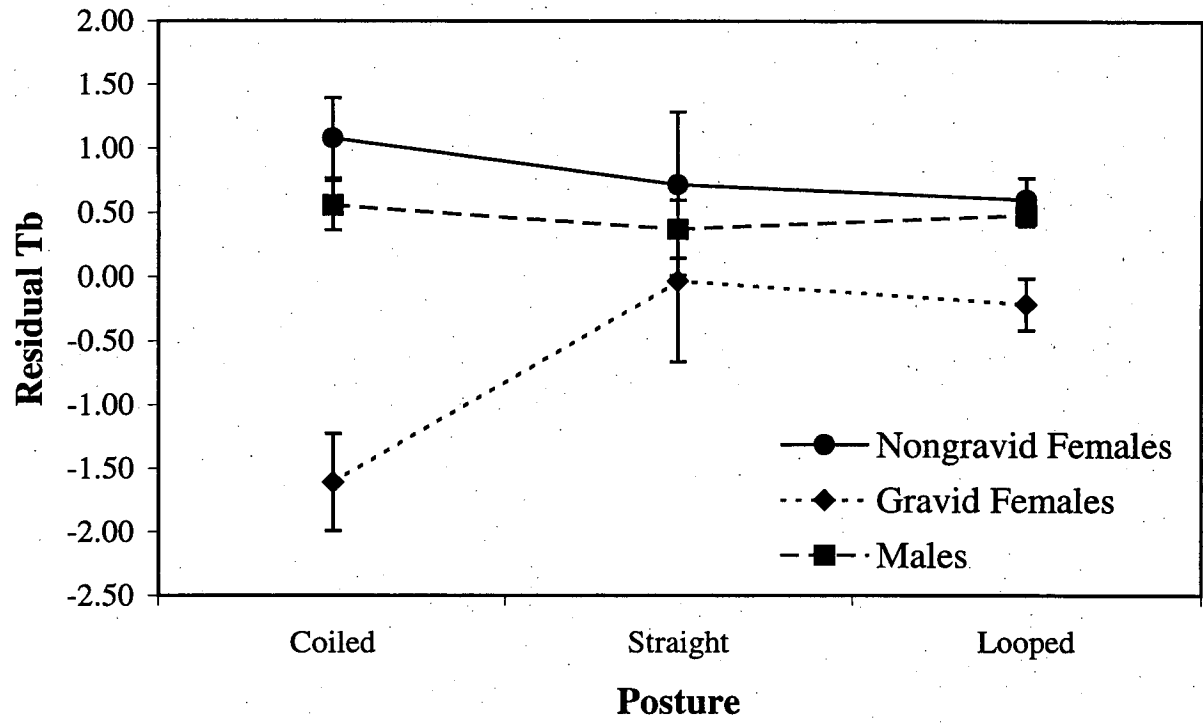


Figure 15

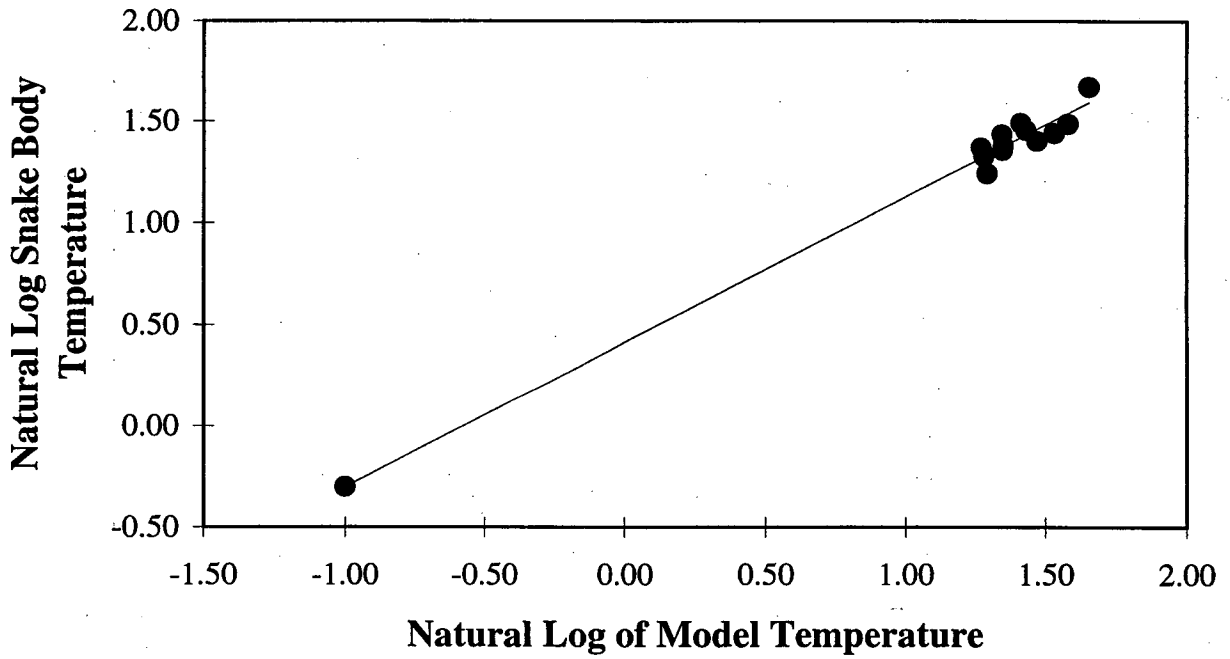
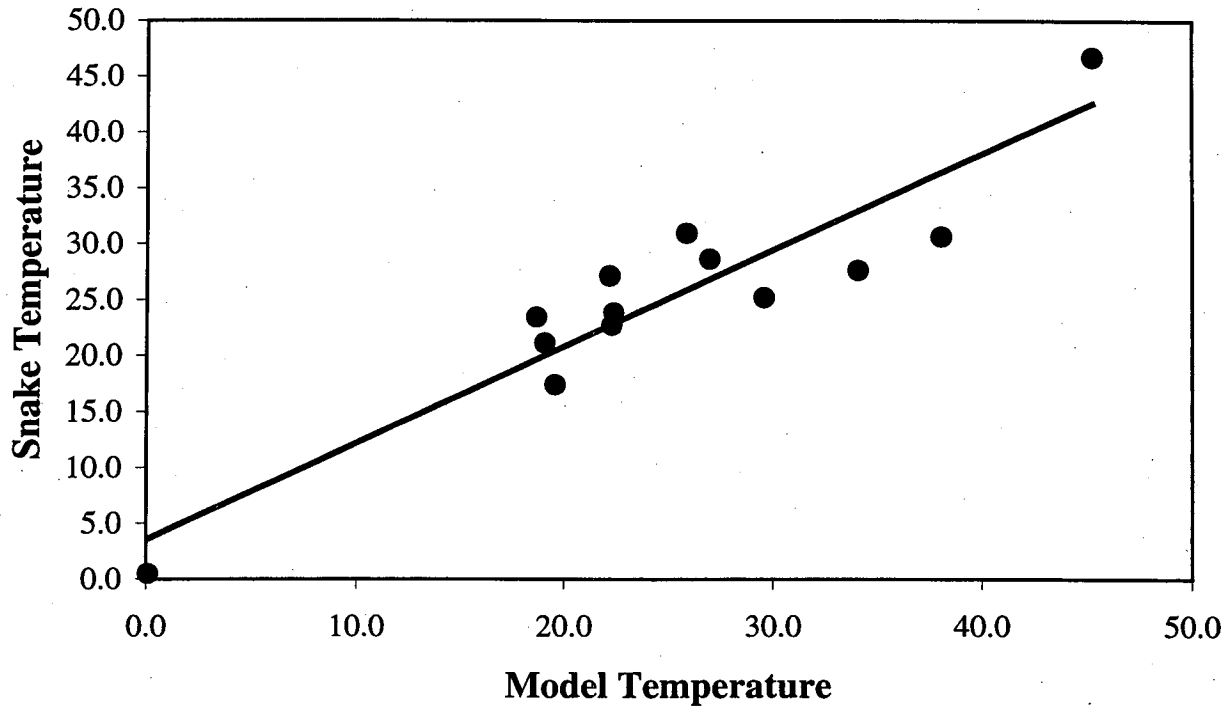


Figure 16

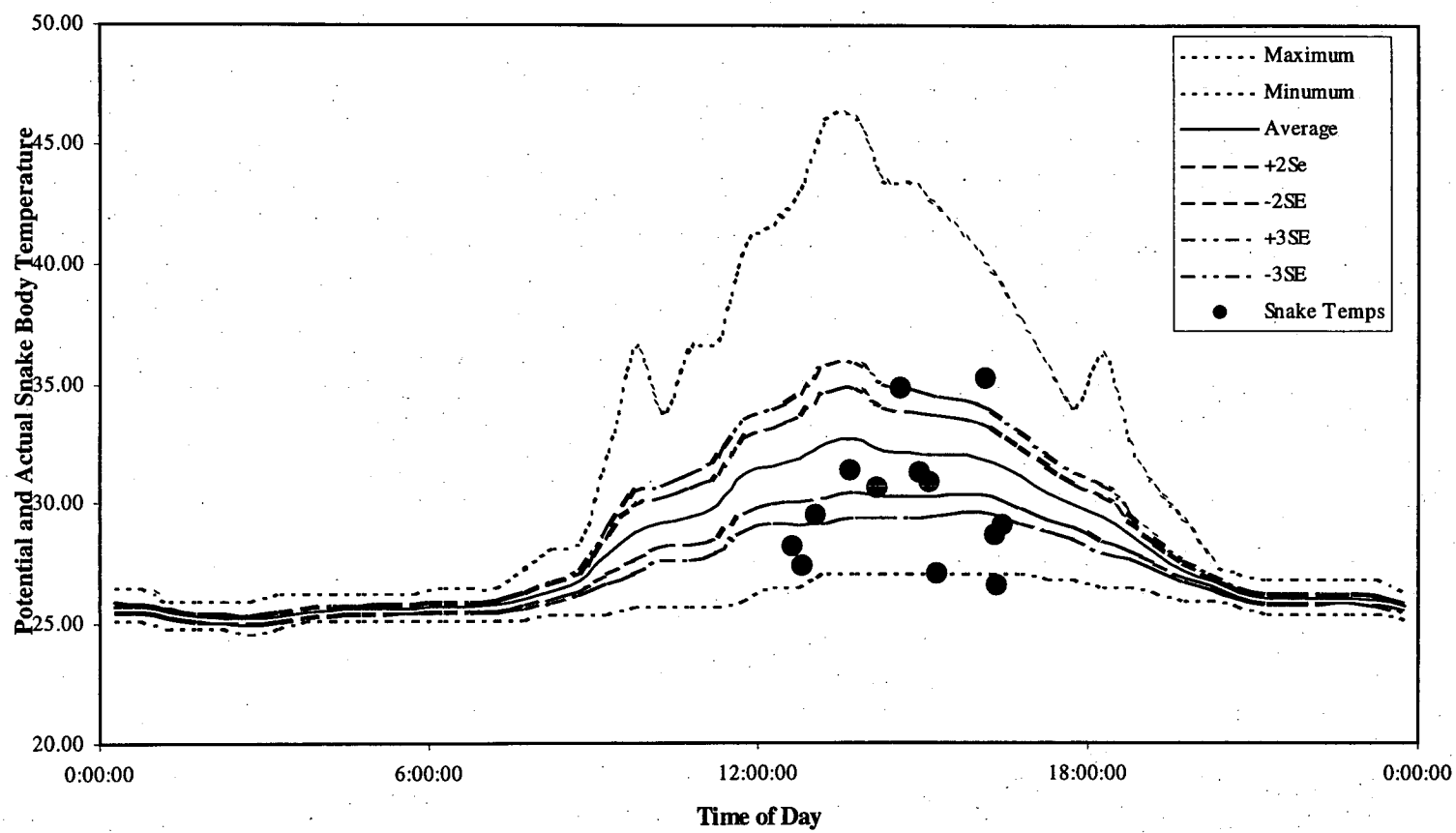


Figure 17

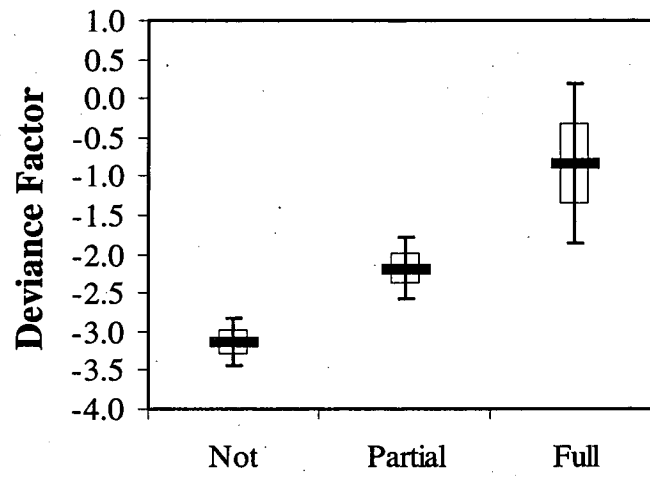
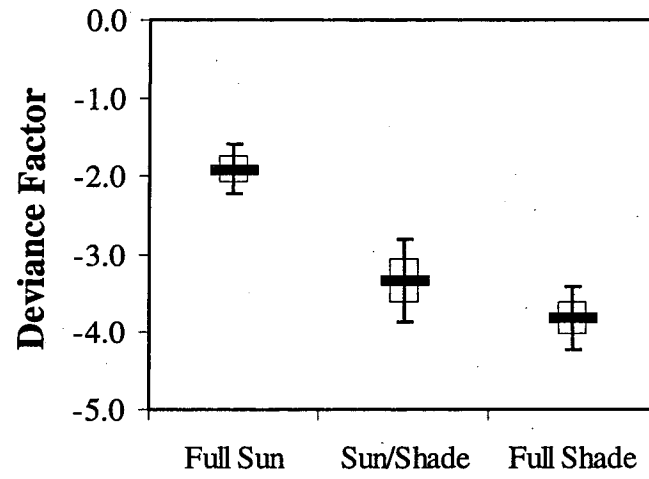


Figure 18

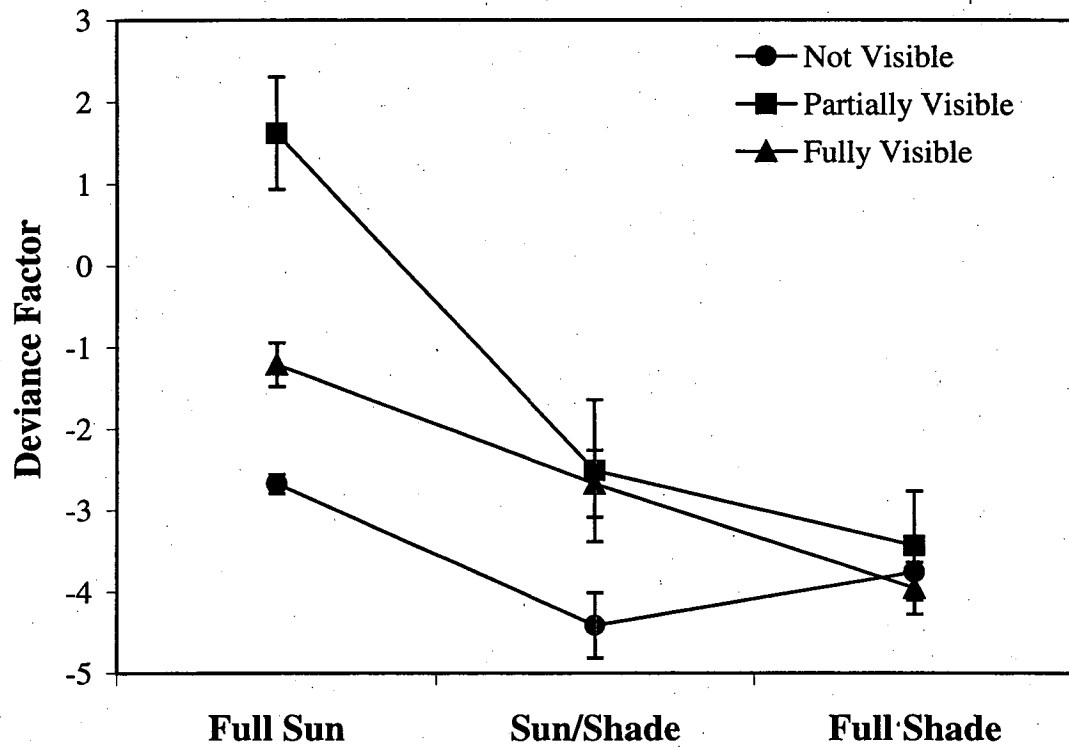


Figure 19

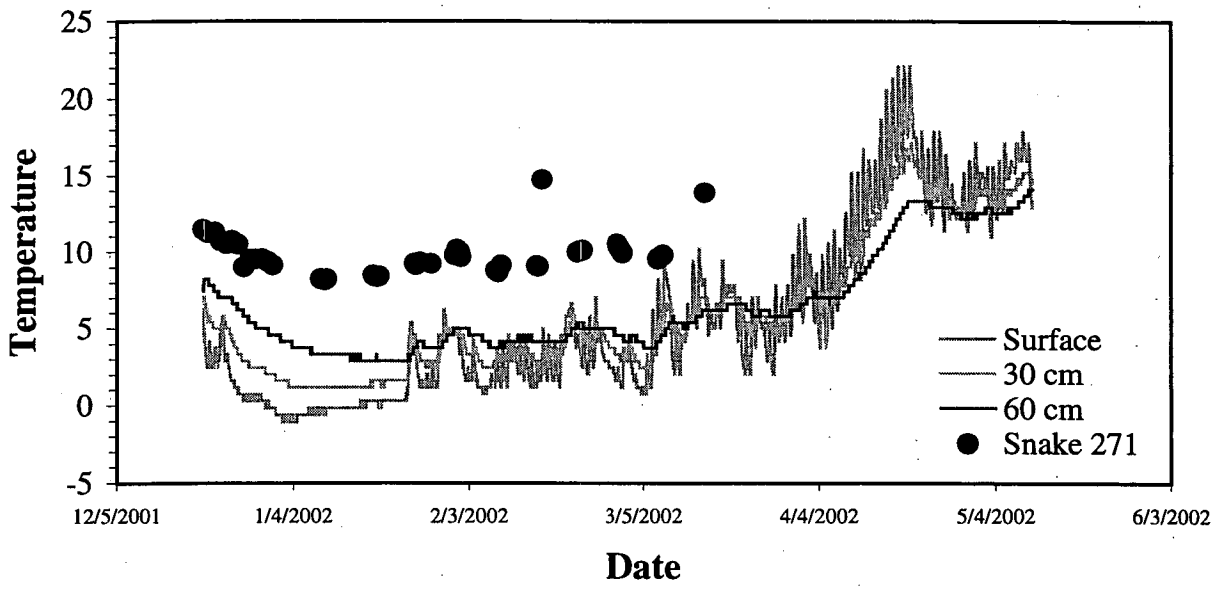
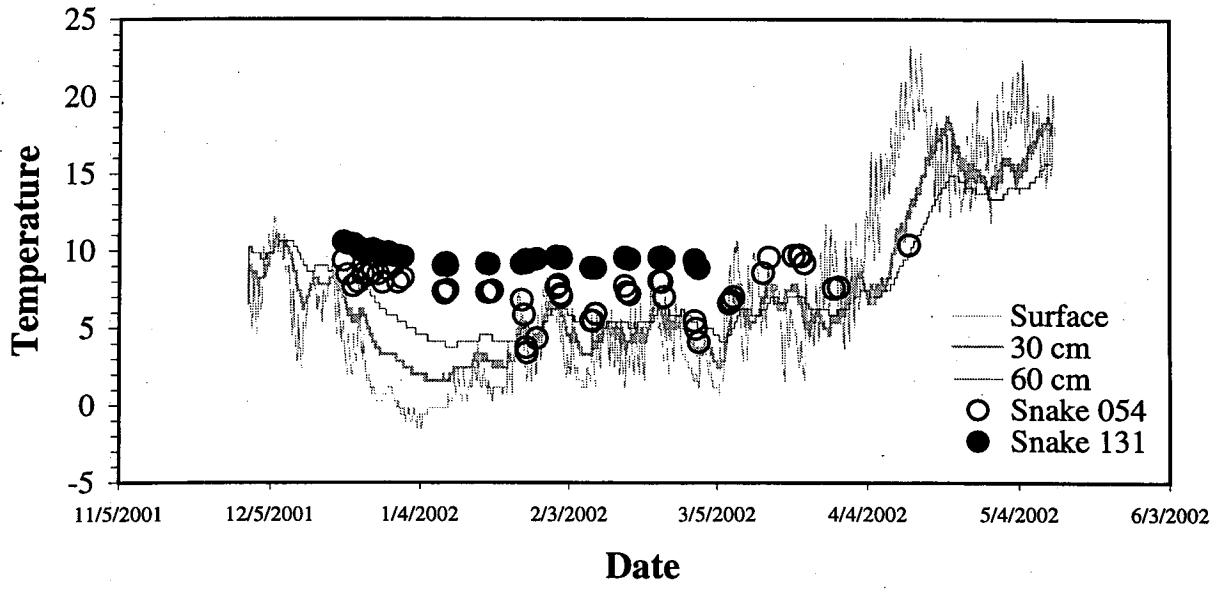


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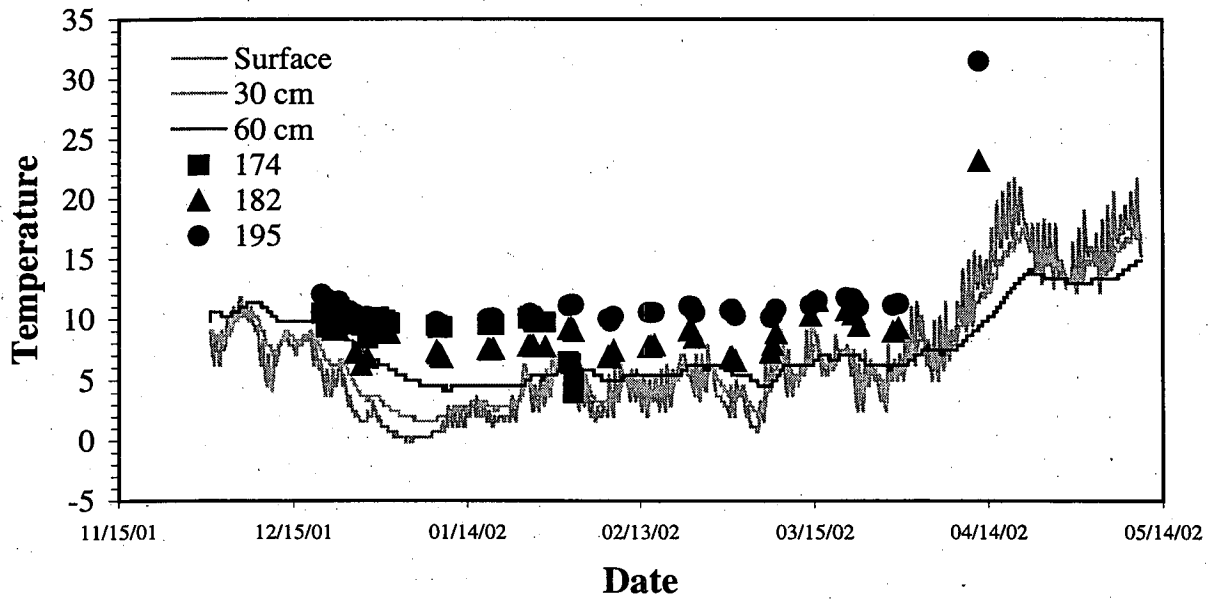
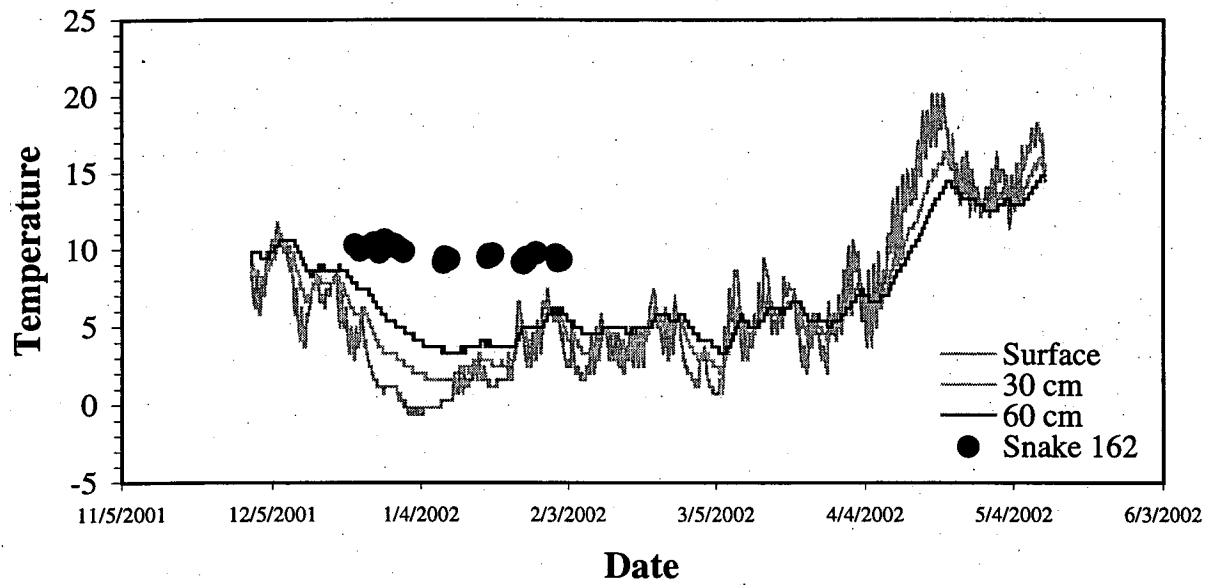


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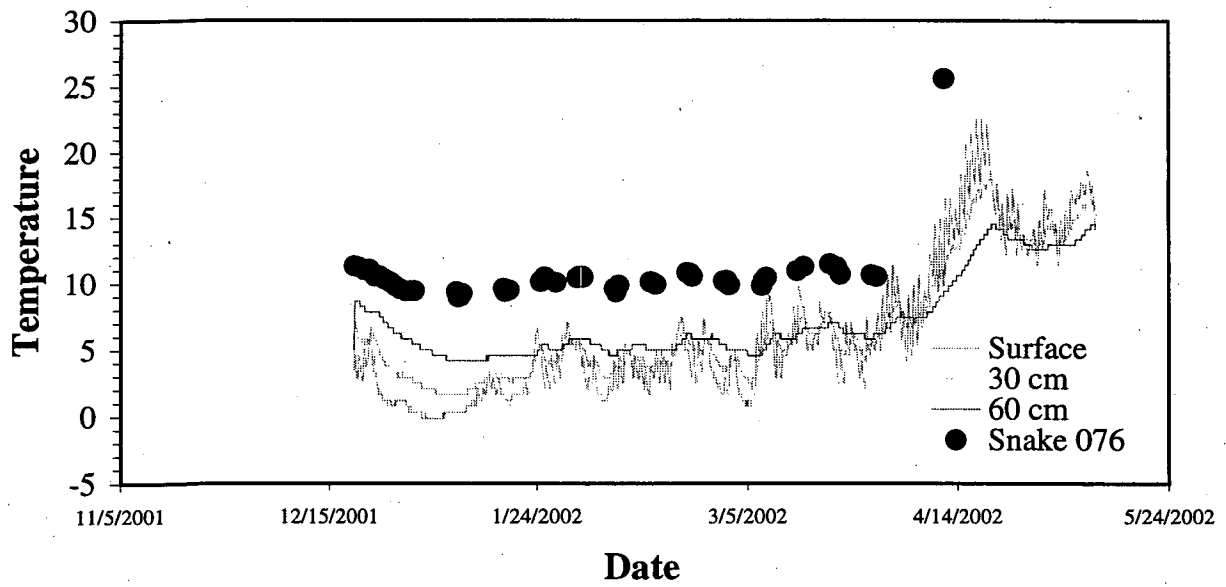
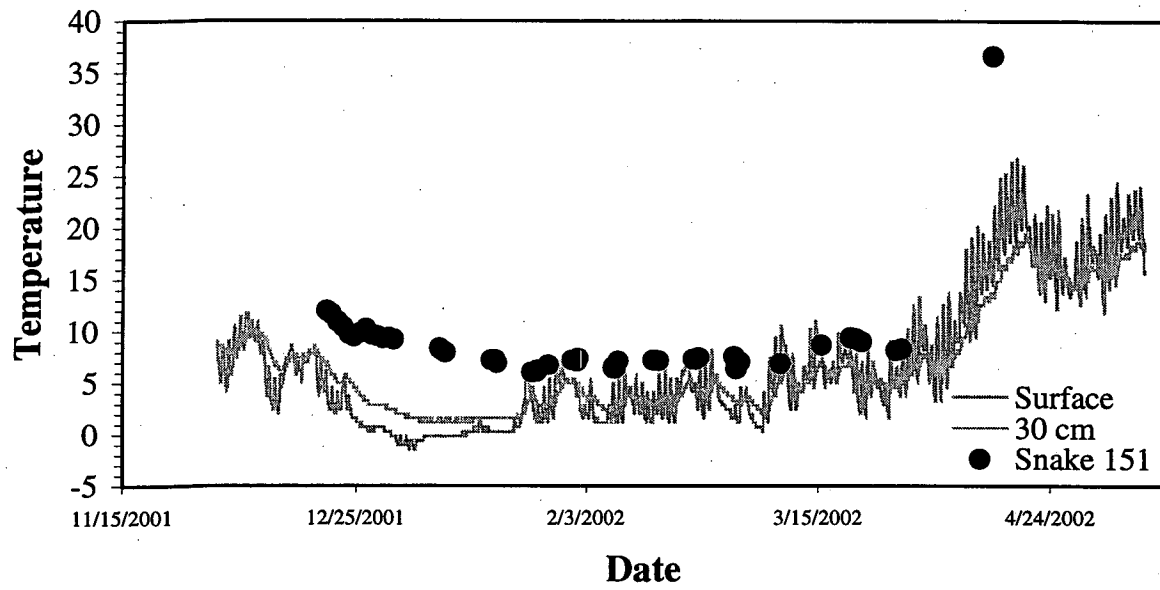


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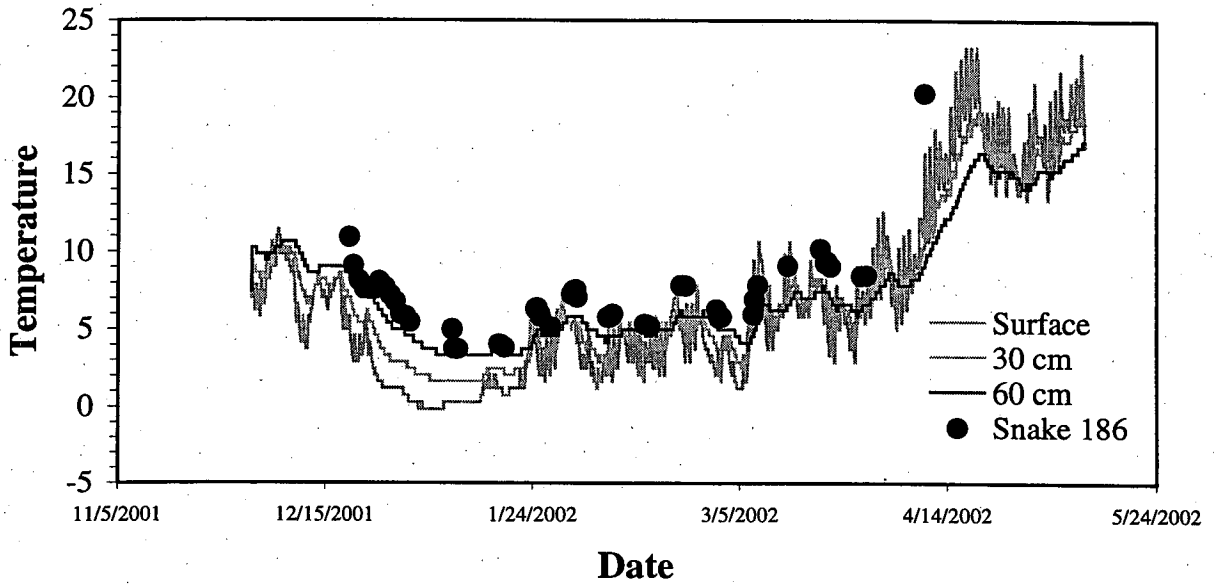
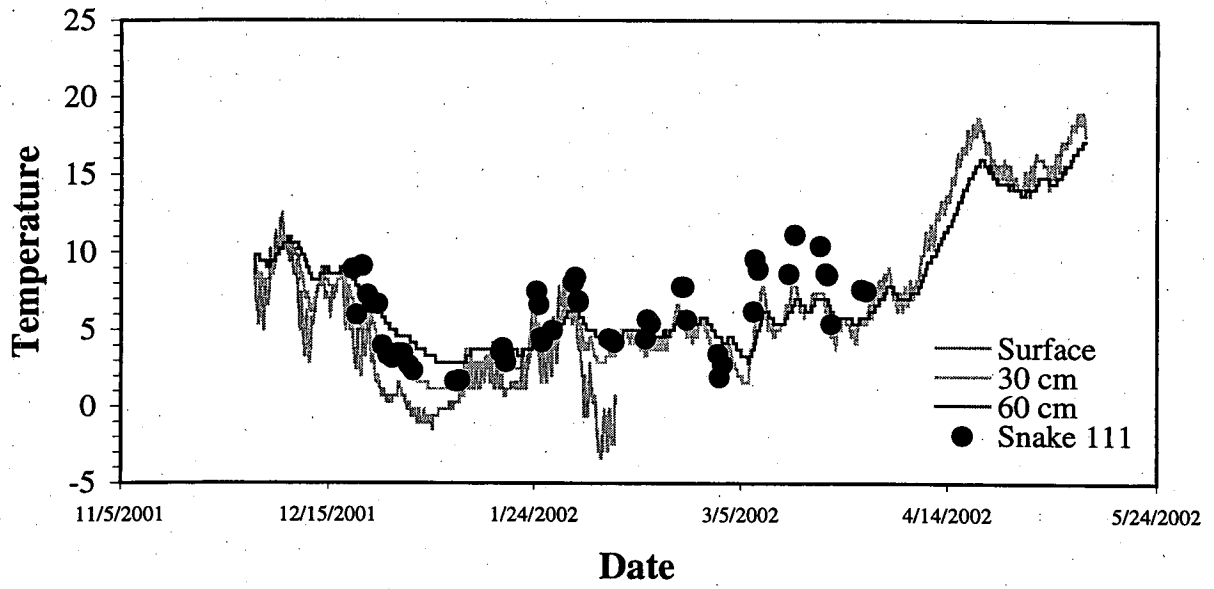


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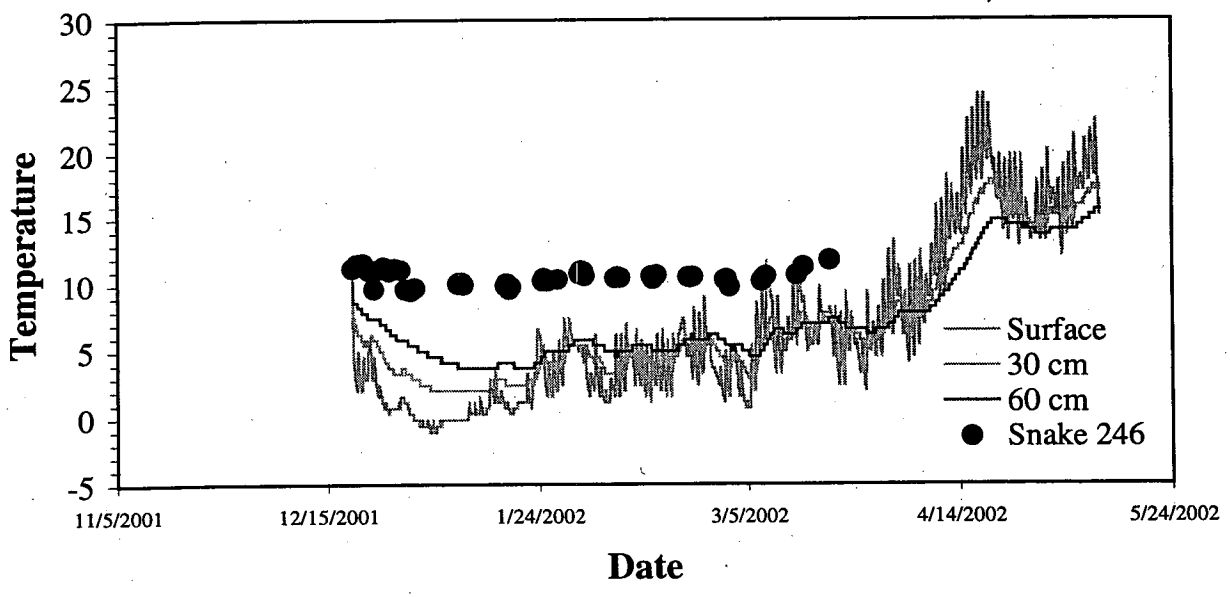
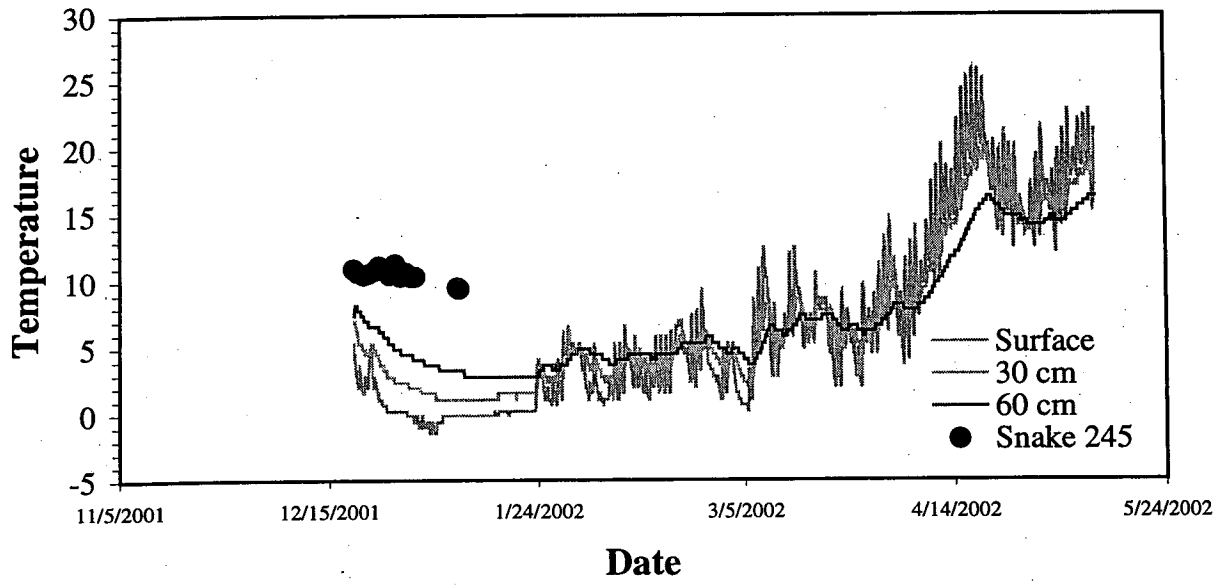


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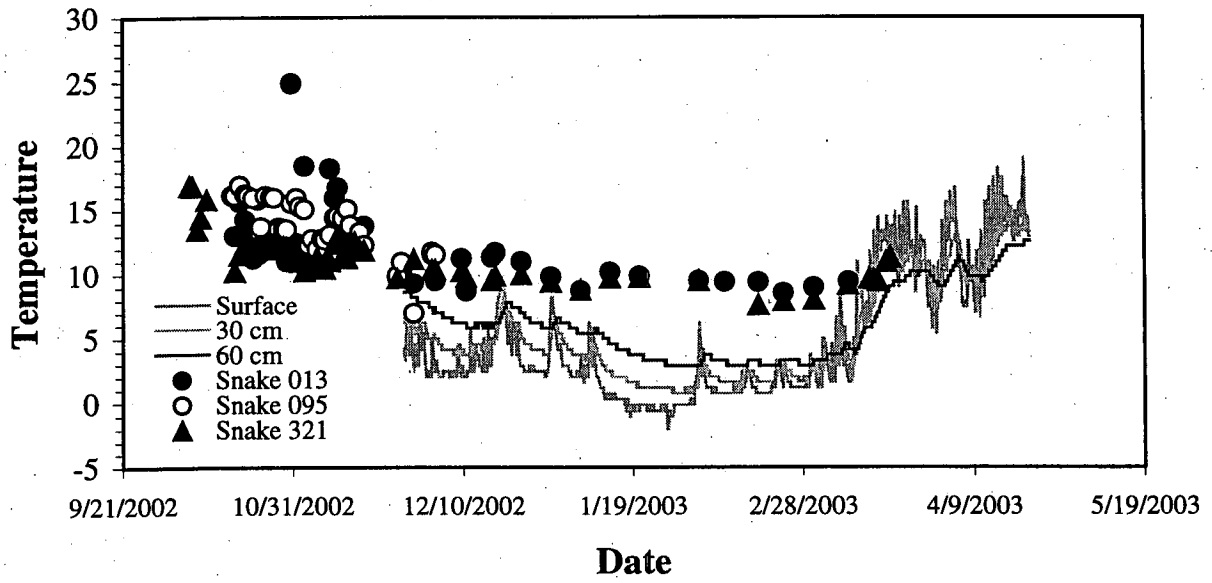
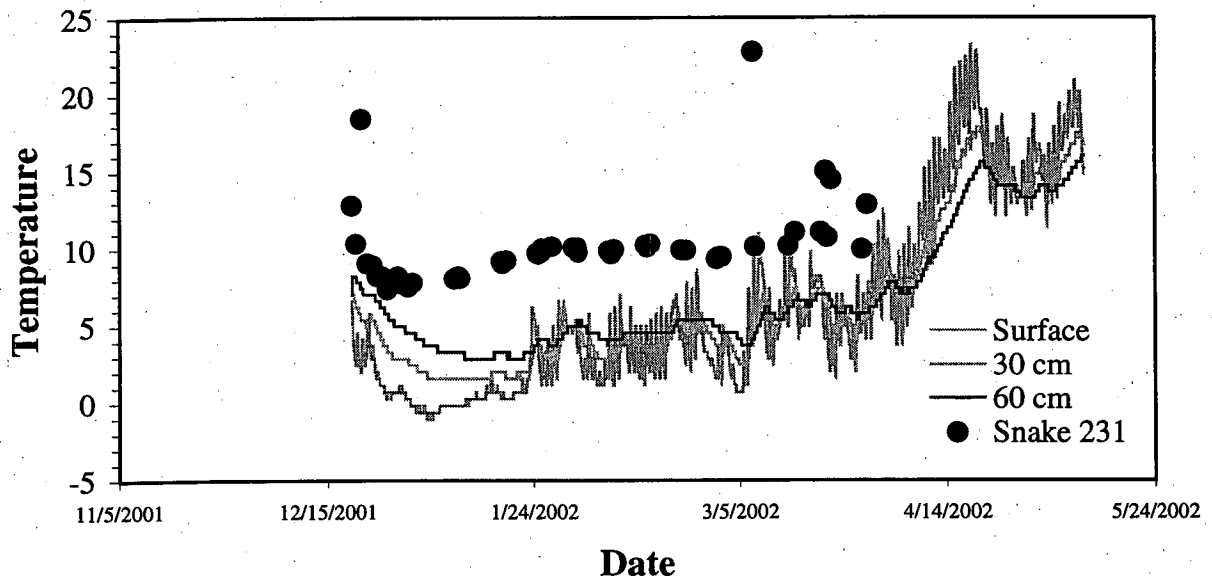


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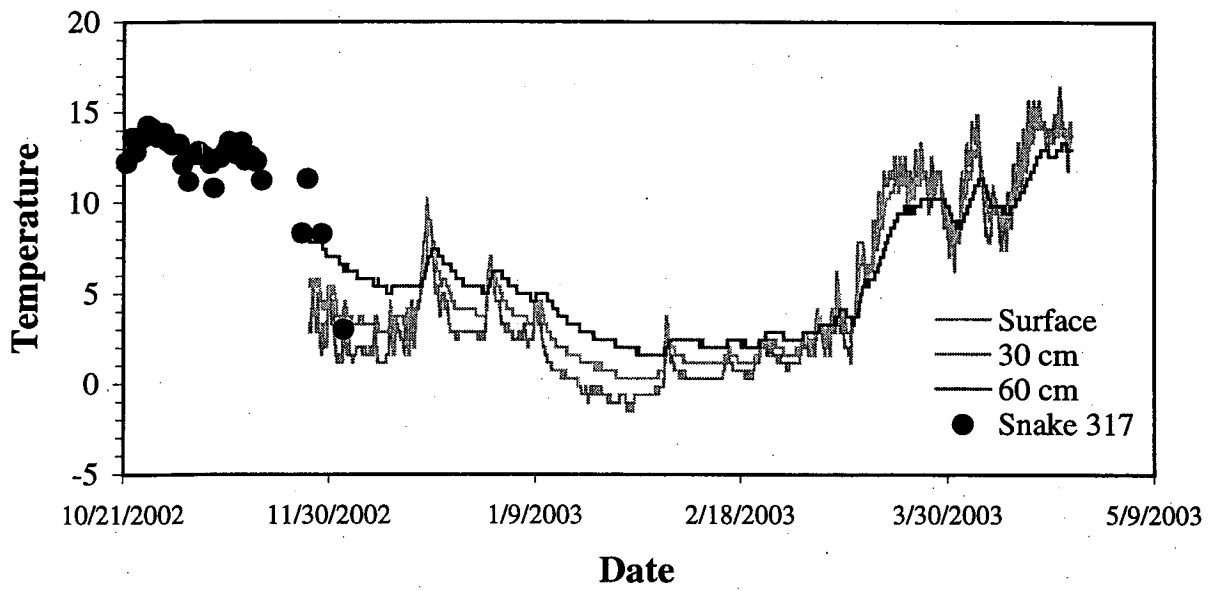
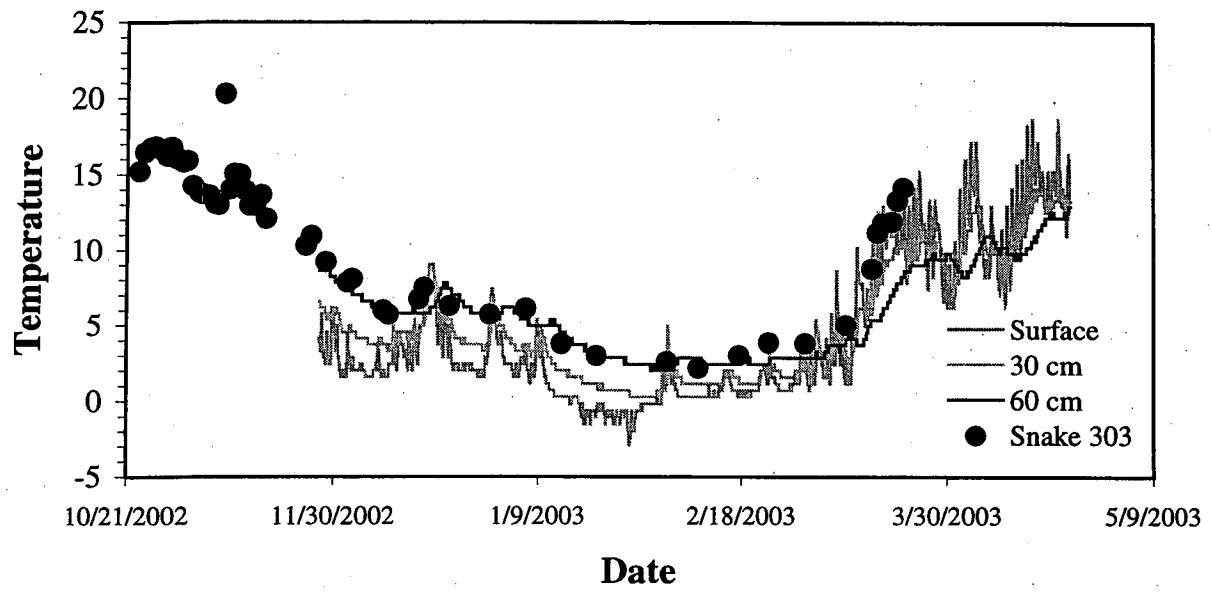


Figure 19 (Cont.)

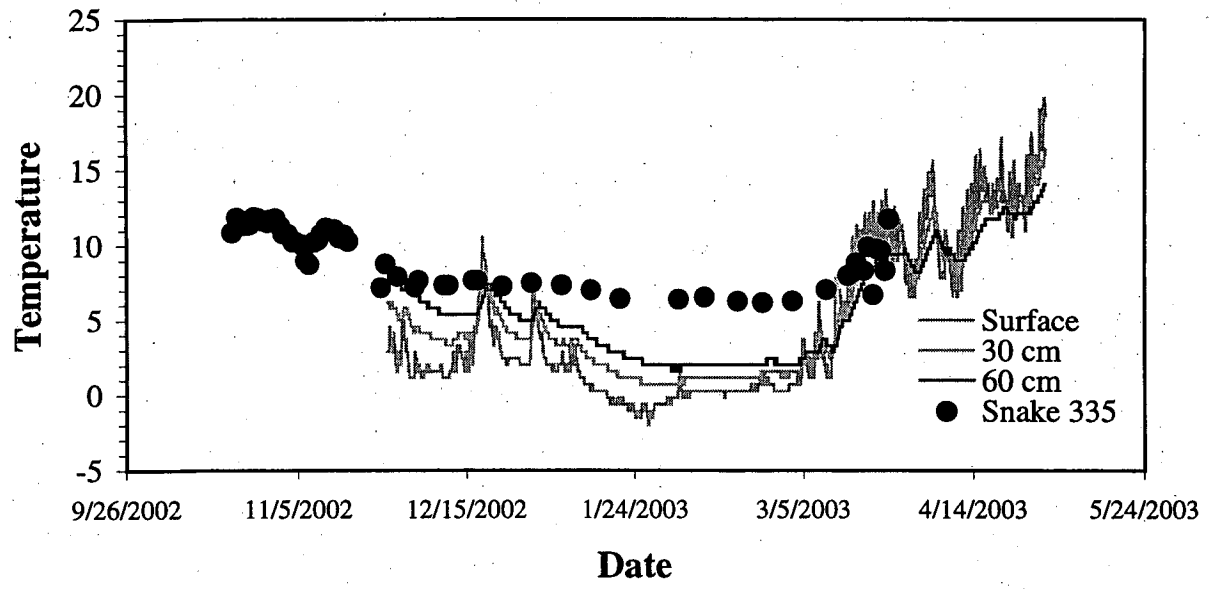
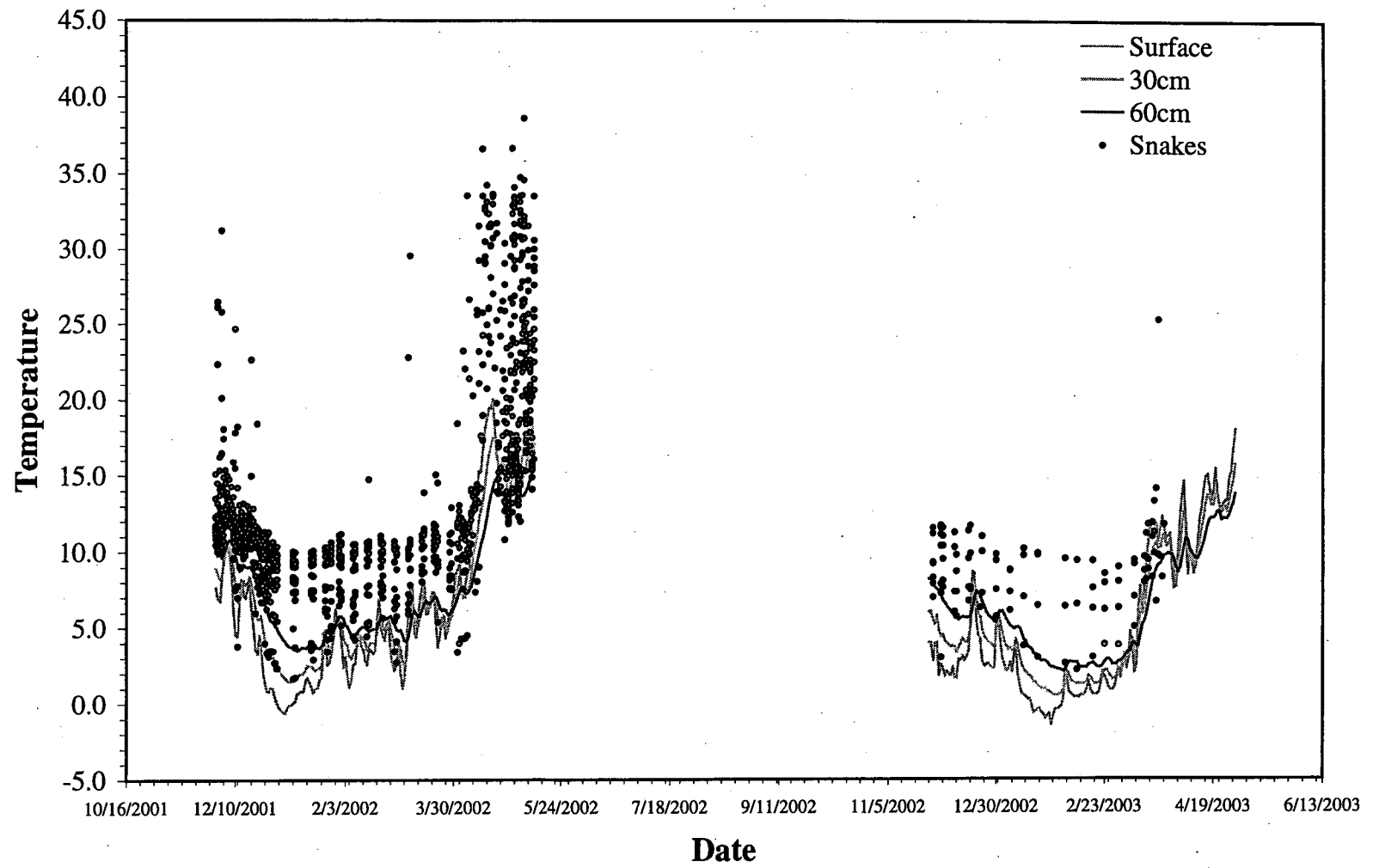
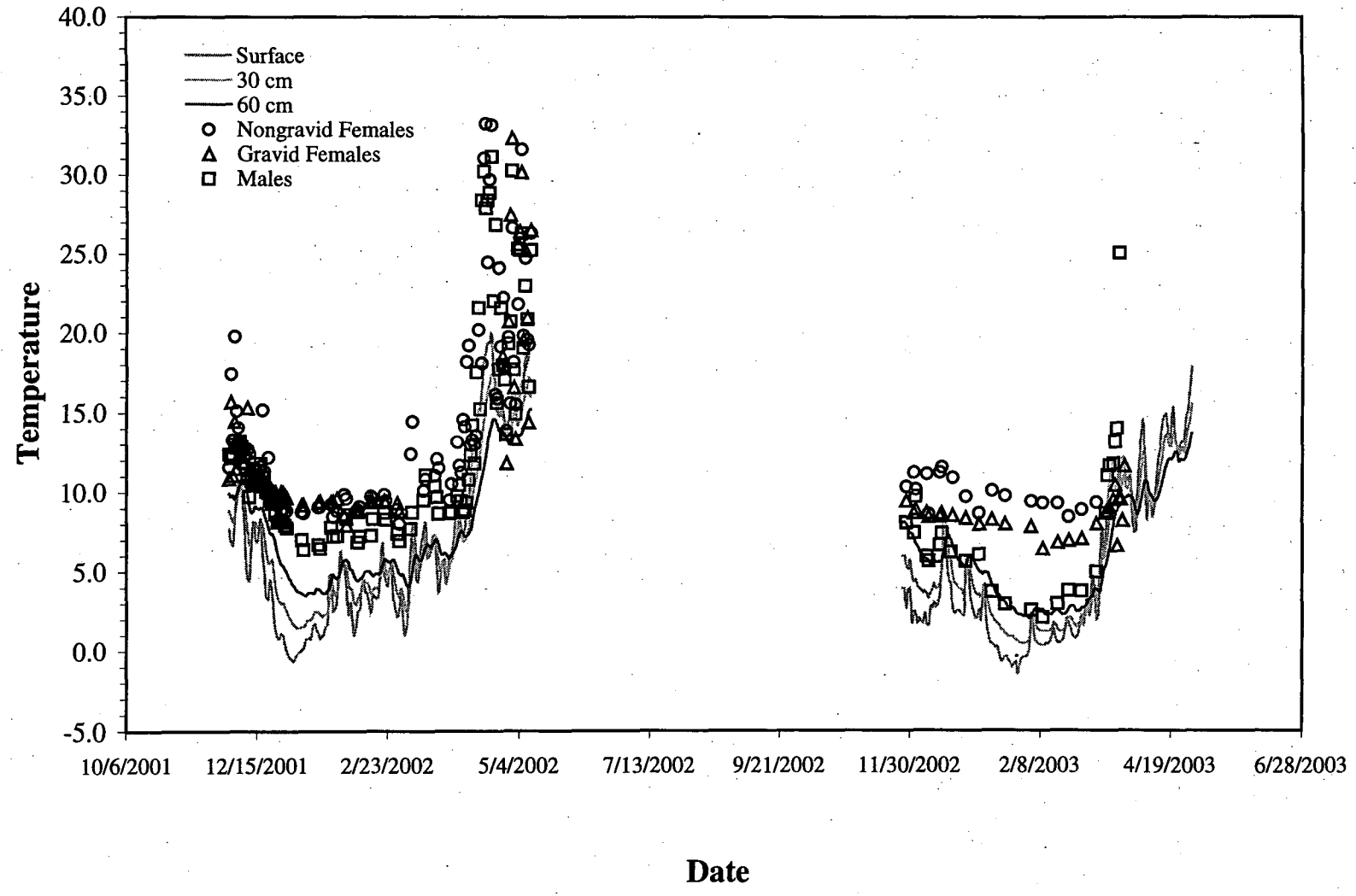


Figure 20



200

Figure 21



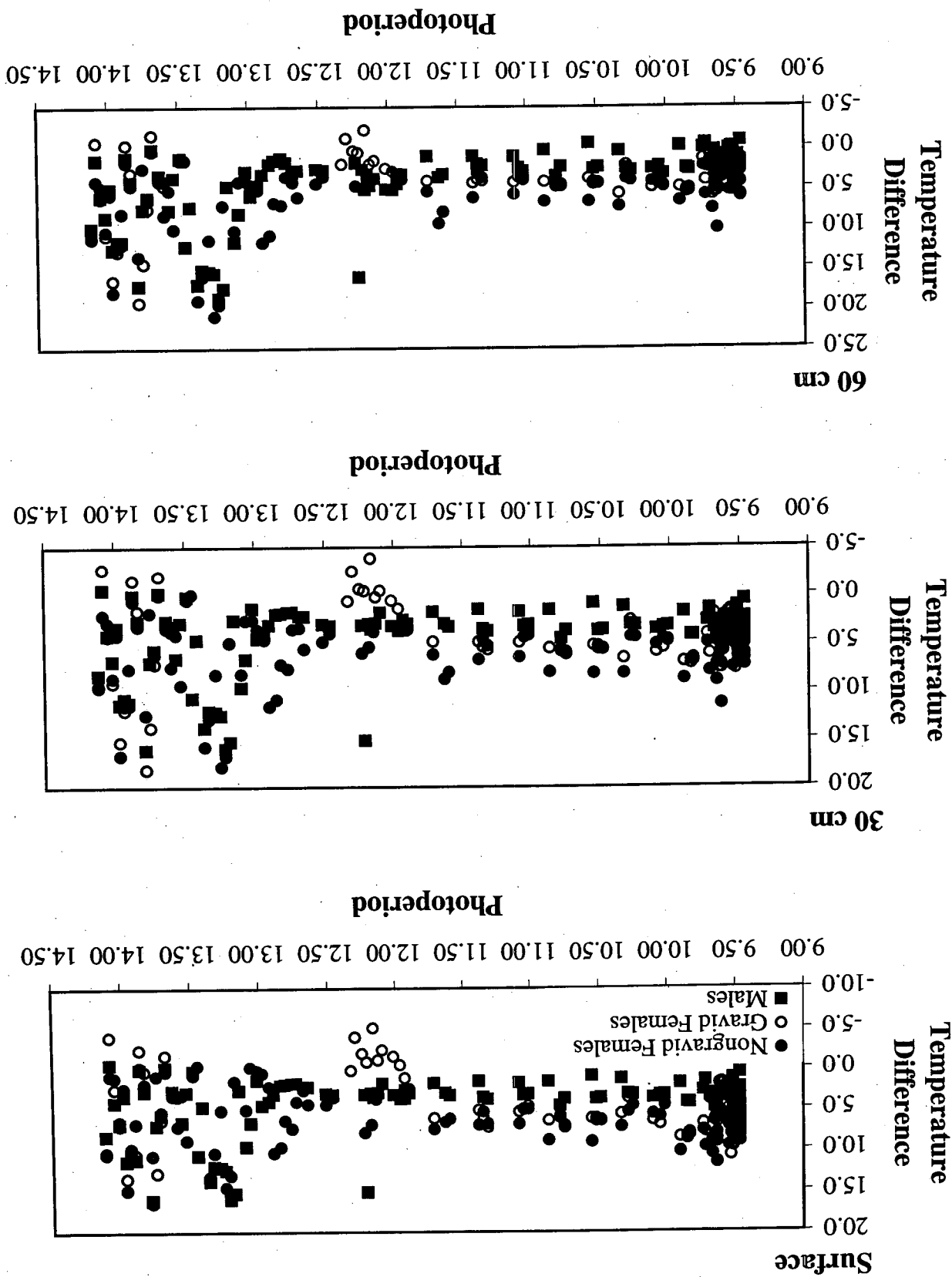


Figure 22

1000

PLATE LEGENDS

Plate 1: Map of the study areas at the southern end of Carlyle Lake, Clinton County, Illinois.

Plate 2: Comparison of snake body postures with A) coiled tight, B) coiled loose, C) looped and D) straightened out.

Plate 3: Construction and comparison of the biophysical thermal models, A) entire model and B) close up comparison.

Plate 4: Calibration of biophysical thermal models.

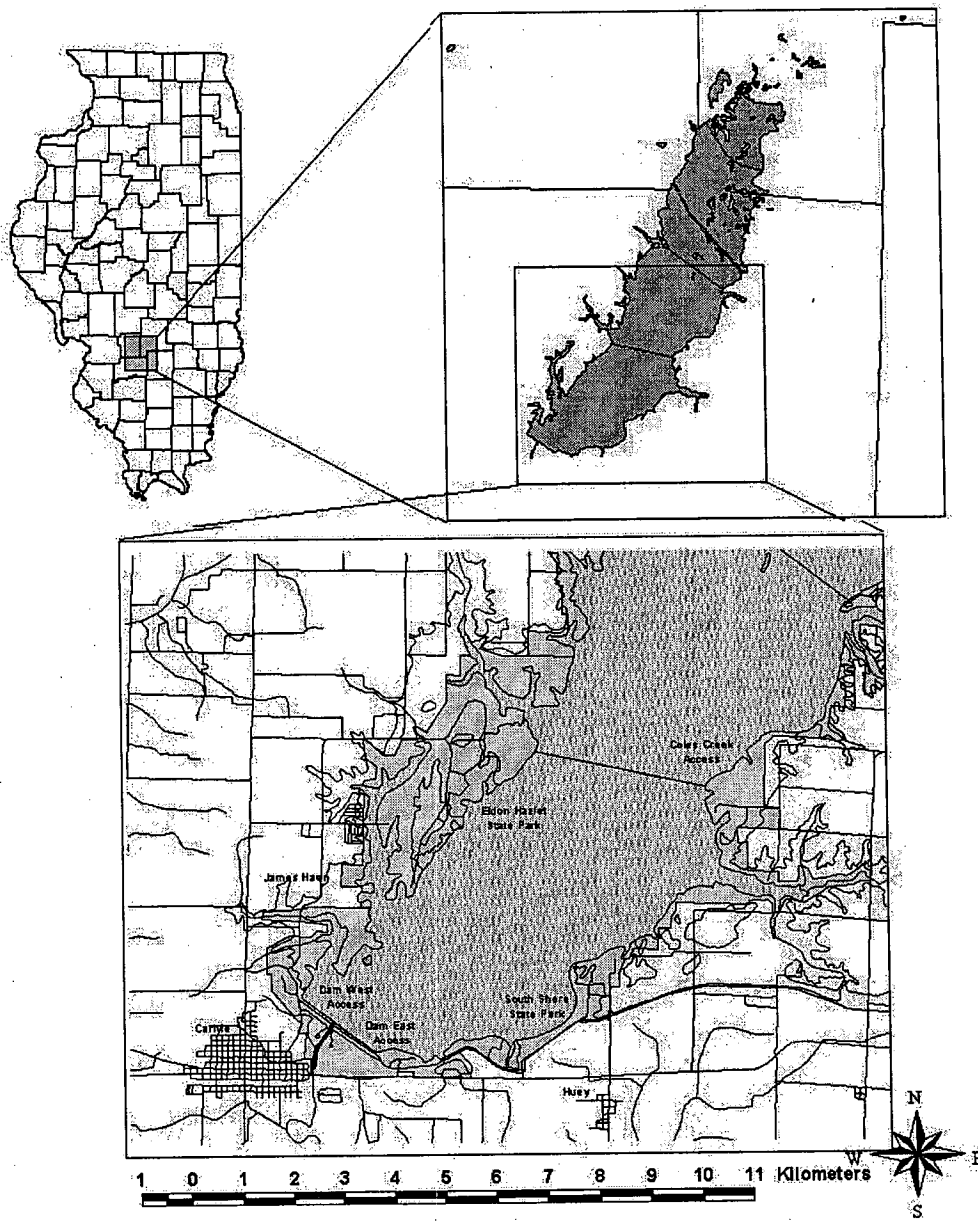
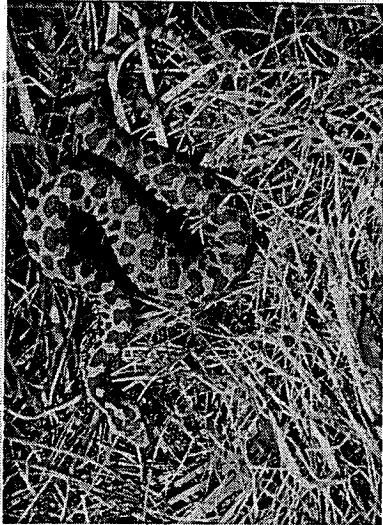


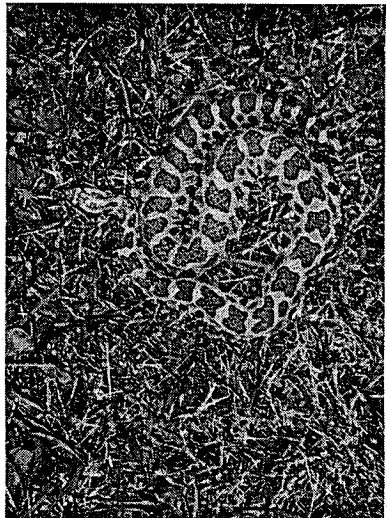
Plate 2



A)



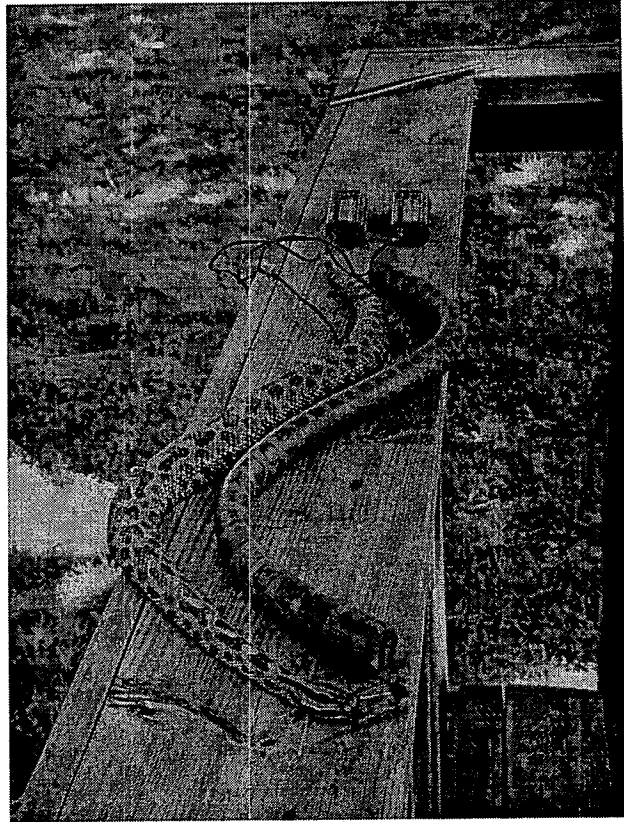
C)



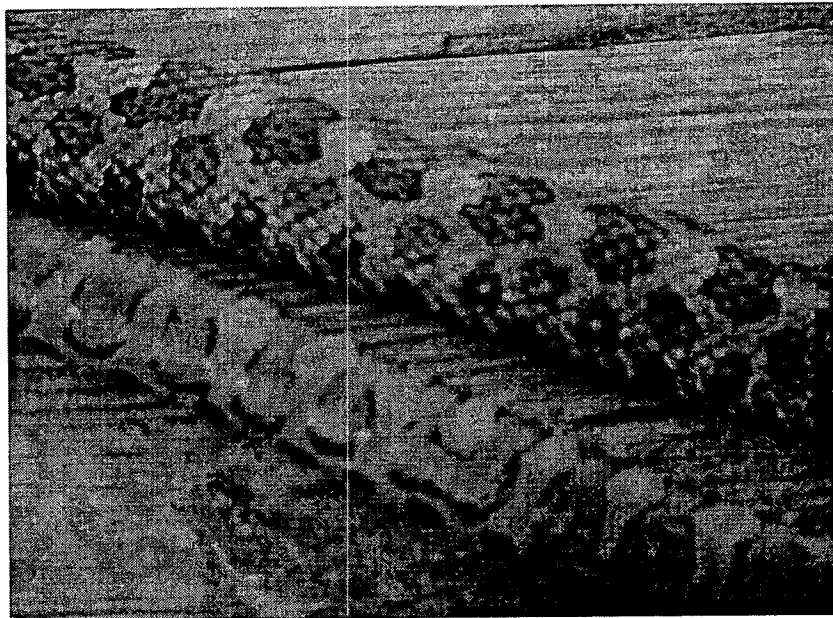
B)



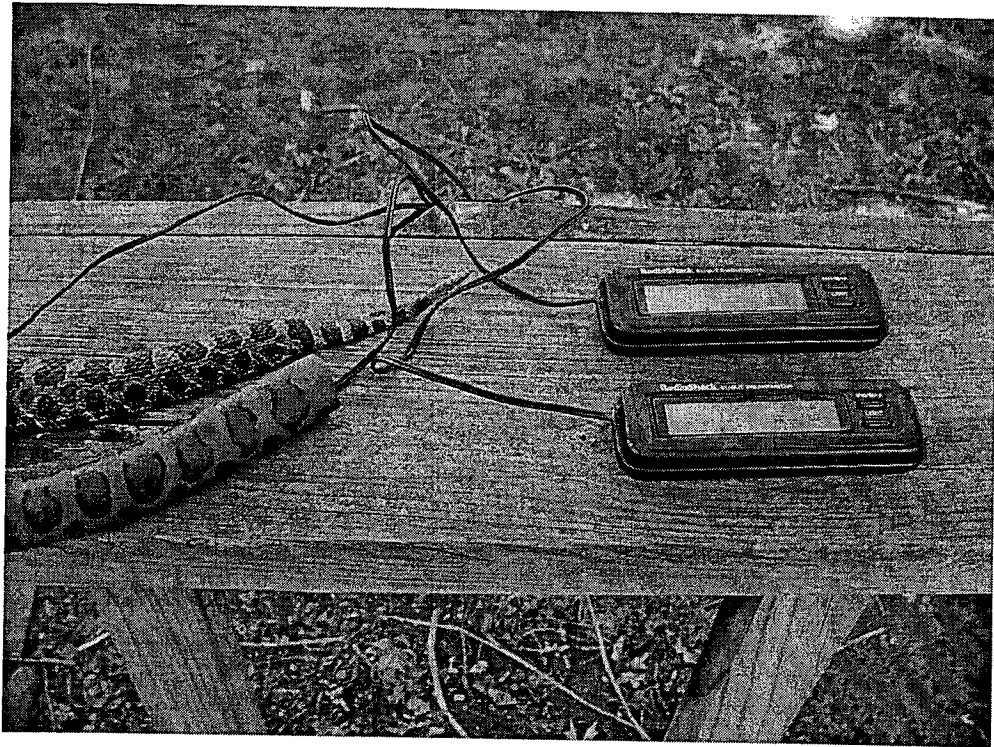
D)



A)



B)



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