

Effects of Body Size and Melanism on the Thermal Biology of Garter Snakes (*Thamnophis sirtalis*)

TONYA D. BITTNER, RICHARD B. KING, AND JAMES M. KERFIN

Both color (i.e., reflectance) and body size should influence body temperature in heliothermic ectotherms. We compared heating rates and equilibrium temperatures between the normal striped morph and the solid black melanistic morph of the garter snake, *Thamnophis sirtalis*, from polymorphic populations in the Lake Erie region. Snakes ranging in mass from 2.6–216.2 g were divided into three size classes (small, medium, and large). Using temperature-sensitive PIT tags, we tested pairs of snakes under artificial light in an environmental chamber, then used curvilinear regressions to estimate heating rate and equilibrium temperature. In small and medium-sized snakes, we found no difference in heating rate nor equilibrium temperature between morphs, suggesting that melanism does not provide a thermal advantage in young snakes. In large snakes, morph affected equilibrium temperature, but not heating rate. Melanistics averaged 1.3 C warmer than striped snakes. This difference may represent a thermal advantage for adults, of which gravid females are the largest and may have the most to gain from a thermal advantage.

THE common garter snake *Thamnophis sirtalis* exhibits a striking color polymorphism in populations on islands and adjacent mainland areas of the western basin of Lake Erie (Gibson and Falls, 1979, 1988; King, 1988); normal striped morphs are present along with almost uniformly black melanistic morphs (fig. 1 in Lawson and King, 1996). Reflectance of melanistic and striped garter snakes differs by about 11% over the human visual spectrum (400–700 nm; table 7.2 in Peterson et al., 1993; Bittner, 2000). Furthermore, heat-flow through excised skin is 6.3% greater, and adult equilibrium T_b is 0.86 C higher for melanistic compared to striped morphs (Gibson and Falls, 1979). Gibson and Falls (1979, 1988) concluded that these differences may allow melanistic snakes to be more efficient thermoregulators and, therefore, grow faster than their striped counterparts. However, there is no conclusive evidence for faster growth of melanistic garter snakes (King, 1988). An analogous color polymorphism in adders (*Vipera berus*) is also characterized by a difference in heating rate (Forsman, 1995) but not growth rate (Forsman and As, 1987).

The thermal benefit of melanism is thought to carry with it a cost in terms of reduced crypsis and increased risk of predation (Gibson and Falls, 1979, 1988; but see Bittner, 2000). Furthermore, costs and benefits of melanism are likely to differ between snakes differing in size. Differences in thermal inertia mean that melanism has a smaller effect on the body temperature of small versus large snakes (fig. 6 in Stevenson, 1985). Furthermore, because small snakes are susceptible to a wider array of pred-

ators (Mushinsky and Miller, 1993), any reduction in crypsis associated with melanism may be more costly for small versus large snakes.

We investigated the effect of melanism on heating rates and equilibrium T_b of *T. sirtalis* ranging in size from neonates to adults using temperature-sensitive PIT tags (Passive Integrated Transponder; BioMedic Data Systems, Inc.; model IPTT-100). The small size of these tags (0.13 g, 14.5 mm long, 2.4 mm in diameter) allows one to study the thermal biology of small ectotherms with a minimum of restraint or handling.

MATERIALS AND METHODS

Accuracy and precision of PIT tags.—PIT tags were factory calibrated to an accuracy of 0.5 C within the range 32–43 C. Because our experiment was performed below this range (12–32 C), we determined the accuracy and precision of tags at lower temperatures. Ten tags were selected at random from among those used in the experiments and placed in a walk-in environmental chamber set at 12, 24, and 32 C. Among-tag variation (precision) was assessed by calculating the Coefficient of Variation (CV) at each temperature. Accuracy was assessed by calculating the mean deviation from a laboratory thermometer.

Tags were least accurate at the lowest temperature, averaging 2.5 C higher than the laboratory thermometer. At 24 C and 32 C, tags averaged 0.3 and 0.5 C lower than the laboratory thermometer. Precision increased with temperature ($CV_{12} = 3.4\%$, $CV_{24} = 1.2\%$, $CV_{32} =$

0.5%), that is, the tags' readings became more similar to each other as temperature increased. Because temperatures measured at the beginning of the experiment were about 2.5 C too high, our estimates of heating rate were somewhat lower than the true rate. Because the tags were consistent with each other (CV = 3.4%), this error should be similar across all experiments and, therefore, should not affect our conclusions regarding possible differences in heating rate between morphs, but we urge caution in comparing our heating rates with those observed in other studies. A mathematical correction would be needed for comparisons outside this study.

Experimental animals.—Study animals were captive-born offspring of wild-caught females from Ottawa County, Ohio. The small snakes were born in July 1997 and maintained on a diet of small earthworms twice weekly. They were housed in plastic "shoe boxes" (with water available ad libitum) in a colony room maintained at 25 C, ~50% humidity, and 12:12 L:D photoperiod. Snakes born in 1995 or 1996 were raised under the same conditions except they were fed three times per week and were larger than those born in 1997.

In all experiments, a pair consisted of one striped and one melanistic snake matched for sex and body mass. In experiment 1 (small snakes), 11 pairs (five male, six female) of neonates from the same litter were matched for sex and mass within 0.30 g (i.e., 10% of mean mass). The mean difference in mass between morphs was 0.019 g, which was not significantly different from zero (paired $t = 0.54$, $df = 10$, $P = 0.60$). The mean mass (SE) of this group was 3.17 g (± 0.08), and the range was 2.56–3.81 g.

In experiment 2 (medium-sized snakes), 12 pairs (five male, seven female) were matched within 2.81 g, that is, 5% of mean mass. The mean difference in mass between morphs was 0.39 g, which was not significantly different from zero (paired $t = 1.03$, $df = 11$, $P = 0.33$). The mean mass (SE) of this group was 53.75 (± 2.12) and the range was 38.37–73.89 g.

In experiment 3 (large snakes), seven pairs of females were matched within 19.5 g, that is, 14% of mean mass. The mean difference in mass between morphs was 2.76 g, which was not significantly different from zero (paired $t = 0.67$, $df = 6$, $P = 0.53$). The mean mass (SE) of this group was 141.96 (± 9.86) and the range was 84.3–216.2 g.

Testing environment.—Experiments were performed in a walk-in environmental chamber set

to 12 C and 50% relative humidity. The testing apparatus consisted of two 100-watt ESU Reptile BrightLights (experiment 1) or 120 watt GE Miser Indoor Floodlights (experiments 2 and 3) mounted 25.5 cm (experiment 1) or 31.5 cm (experiments 2 and 3) above the test subjects. Bulbs were wired in parallel 25.5 cm apart from each other. Power to the lights was supplied by a constant voltage transformer. Painted physical models (copper tubing) of appropriate size were tested to confirm that snakes should heat up under these conditions.

The day before each trial, a pair of snakes was placed in the chamber to adjust to the ambient temperature. The most recent feeding occurred more than 24 h before a trial (usually 48–72 h). At least 2 h before a trial, one PIT tag was placed into the gastrointestinal tract of each snake via oral gavage; PIT tags were passed after several days, causing no apparent harm.

During an experiment, each snake was placed in the bottom of a 9 cm (experiment 1) or 14 cm (experiment 2) diameter glass petri dish covered with one-eighth-inch mesh hardware cloth. In experiment 3, 6-cup square plastic Rubbermaid® containers with numerous ventilation holes were used to accommodate the larger snakes. These were also covered with one-eighth-inch mesh hardware cloth. Snakes could move about within the dishes, but vertical movement was restricted by the shallowness of the dishes.

Each dish was placed on the shelf directly under one of the two light bulbs. Because handling during transfer may have affected body temperature, we allowed snakes to reequilibrate to the ambient temperature for 10 min before beginning the experiment. PIT tags were read using a DAS-5007 pocket scanner (BioMedic Data Systems) capable of storing PIT ID numbers and temperature readings in memory. First, we scanned the snakes before turning on the lights (time zero). Then, we turned on the lights and recorded the temperature of each snake at 1-min intervals for the first 30 min, then every 2 min up to 45 or 60 min. At 10-min intervals, we made notes summarizing the behavior of each snake during that interval (body position and activity level). Between trials, lights were allowed to cool completely and dishes were washed with soap and water. All trials were performed between 1100 and 1400 h.

In experiments 1 and 2, for each trial, we switched which morph was under the left light; the snake on the left was always scanned first. This procedure controlled for any difference in light output and air movement between the left and right bulbs. Continuous air circulation with-

TABLE 1. MEAN PARAMETER ESTIMATES CALCULATED FROM SNAKE BODY TEMPERATURES.

	Mean equilibrium temp (C) \pm SE	Mean heating rate (min ⁻¹) \pm SE
Exp. 1 ($n = 11$ pairs)		
Striped	19.86 \pm 0.219	0.1504 \pm 0.0127
Melanistic	19.87 \pm 0.089	0.1451 \pm 0.0083
Exp. 2 ($n = 12$ pairs)		
Striped	29.75 \pm 0.408	0.0538 \pm 0.0030
Melanistic	30.38 \pm 0.604	0.0501 \pm 0.0035
Exp. 3 ($n = 7$ pairs)		
Striped	35.21 \pm 0.561	0.0460 \pm 0.0039
Melanistic	36.53 \pm 0.692	0.0434 \pm 0.0047

in the environmental chamber resulted in air movement of 1.0–1.8 m/s as measured with a Turbometer (Davis Instruments, Inc.), with greater air movement under the right light than the left (maximum difference between sides = 0.8 m/s).

Because of the possibility of slight differences between the two light bulbs, we took a different approach in experiment 3. Each pair of snakes was tested twice, such that each morph was tested once under each light bulb.

Data analysis.—Temperature data from each snake were fitted to the following equation: $temp = A \{1 - B \exp[-C (time)]\}$, using nonlinear regression. We chose this curve (a form of the von Bertalanffy growth model; Lovich et al., 1990) because it provides an extremely good fit and has readily interpretable parameters. Parameter A is the asymptotic (or equilibrium) temperature, B is the proportion of A realized at time = 0, and C is the instantaneous (or intrinsic) heating rate (in 1/min) and is proportional to heat yet to be gained (Draper and Smith, 1981). The parameters of greatest interest for this study were the heating rate (C) and the asymptotic temperature (A). These parameters can be used to address the questions, “Do melanistic snakes heat up faster than striped snakes?” and “Do melanistic snakes reach higher body temperatures than striped snakes?”

The distributions of equilibrium temperature and of heating rate were plotted as histograms, which appeared qualitatively normal, so we did not transform data. For experiment 1, randomized block ANOVA was used to partition the variance in asymptotic temperature (hereafter, Temp or equilibrium temperature) and in instantaneous heating rate (hereafter, Rate or heating rate) resulting from three factors: Morph, Pair, and Light (left or right bulb). Pair

and Light were treated as randomized blocks, and interactions were not tested. Because mass and equilibrium temperature are positively correlated (Stevenson, 1985), the larger range of body sizes in experiment 2 was expected to introduce variation resulting from body size. For this reason, in experiment 2, we used $\ln(\text{Mass})$ as a covariate and tested the main effects of Morph and Light after confirming there was no factor-by-covariate interaction (i.e., no heterogeneity of slopes). For experiment 3, we first tested for a difference in Temp and Rate between the two lights using repeated measures ANOVA with light as a within-subjects factor, morph as a between-subjects factor, and $\ln(\text{Mass})$ as a covariate. Then we proceeded to test the mean Temp and Rate using ANCOVA with morph as a factor and $\ln(\text{Mass})$ as the covariate. SPSS version 10 and a significance level of 0.05 were used for all analyses.

Our analyses differ from those of Gibson and Falls (1979) and Forsman (1995) in that we compare equilibrium temperature and instantaneous heating rate between morphs, rather than successive measures of body temperature. Because successive measures of body temperature are not independent, statistical tests of these measures are problematical.

RESULTS

Experiment 1.—The curvilinear equations fit heating data of individual snakes extremely well ($R^2 > 0.93$). Mean heating rates and equilibrium temperatures were similar between morphs (Table 1). ANOVA revealed no significant effects of Morph, Pair, or Light (i.e., left or right side, Tables 2–3). Power to detect the Morph effect was low; however, calculation of minimum detectable difference (Zar, 1984:175) revealed that we would have been able to detect a differ-

TABLE 2. ANOVA OR ANCOVA RESULTS FOR EQUILIBRIUM TEMPERATURE (TEMP). Power = observed power, MDD = minimum detectable difference at 80% power.

Source	MS	df	F	P	Power	MDD
Exp. 1 ($n = 22$)						
Morph	1.349×10^{-3}	1	0.007	0.936	0.051	0.60 C
Light	1.493×10^{-2}	1	0.074	0.791	0.057	
Pair	0.432	10	2.151	0.132	0.531	
Error	0.201	9				
Exp. 2 ($n = 24$)						
Morph	2.580	1	0.906	0.353	0.148	1.43 C
Light	0.662	1	0.232	0.635	0.074	
ln (Mass)	12.420	1	4.361	0.050	0.511	
Error	2.848	20				
Exp. 3 ($n = 14$)						
Morph	4.892	1	4.955	0.048	0.528	1.17 C
ln (Mass)	22.483	1	22.774	0.001	0.991	
Error	0.987	11				

ence between morphs of only 0.60 C in Temp and 0.05 min^{-1} in Rate with power of 80% (Tables 2–3).

Experiment 2.—As in experiment 1, the curvilinear equations fit heating data of snakes extremely well ($R^2 > 0.96$). Mean heating rates and equilibrium temperatures were similar between morphs (Table 1). There were no effects of Morph, Light, or ln(Mass) on equilibrium temperature or heating rate (Tables 2–3). The minimum detectable difference in equilibrium temperature between morphs was 1.43 C at 80% power.

Experiment 3.—Again, the curvilinear equations fit the data well ($R^2 > 0.98$). There was no difference between the right and left light bulbs (Temp: $P = 0.49$; Rate: $P = 0.53$), and there were no interactions. Therefore, we calculated the average for each snake under both light bulbs and tested for morph differences. The covariate ln(Mass) was significant for both Temp (positive correlation) and Rate (negative correlation). Morph had a significant effect on Temp but not on Rate (Tables 2–3, Fig. 1). Melanistics were warmer on average by 1.32 C (Table 1).

Body position influences cooling rates of

TABLE 3. ANOVA OR ANCOVA RESULTS FOR HEATING RATE (RATE). Power = observed power, MDD = minimum detectable difference at 80% power.

Source	MS	df	F	P	Power	MDD
Exp. 1 ($n = 22$)						
Morph	1.263×10^{-4}	1	0.079	0.785	0.057	0.05 min^{-1}
Light	1.987×10^{-4}	1	0.124	0.733	0.062	
Pair	1.086×10^{-3}	10	0.678	0.724	0.177	
Error	1.603×10^{-3}	9				
Exp. 2 ($n = 24$)						
Morph	8.718×10^{-5}	1	0.793	0.384	0.136	0.009 min^{-1}
Light	2.278×10^{-4}	1	2.073	0.165	0.278	
ln (Mass)	3.509×10^{-4}	1	3.194	0.089	0.398	
Error	1.099×10^{-4}	20				
Exp. 3 ($n = 14$)						
Morph	8.190×10^{-6}	1	0.376	0.552	0.087	0.005 min^{-1}
ln (Mass)	1.327×10^{-3}	1	61.004	<0.001	1.000	
Error	2.176×10^{-5}	11				

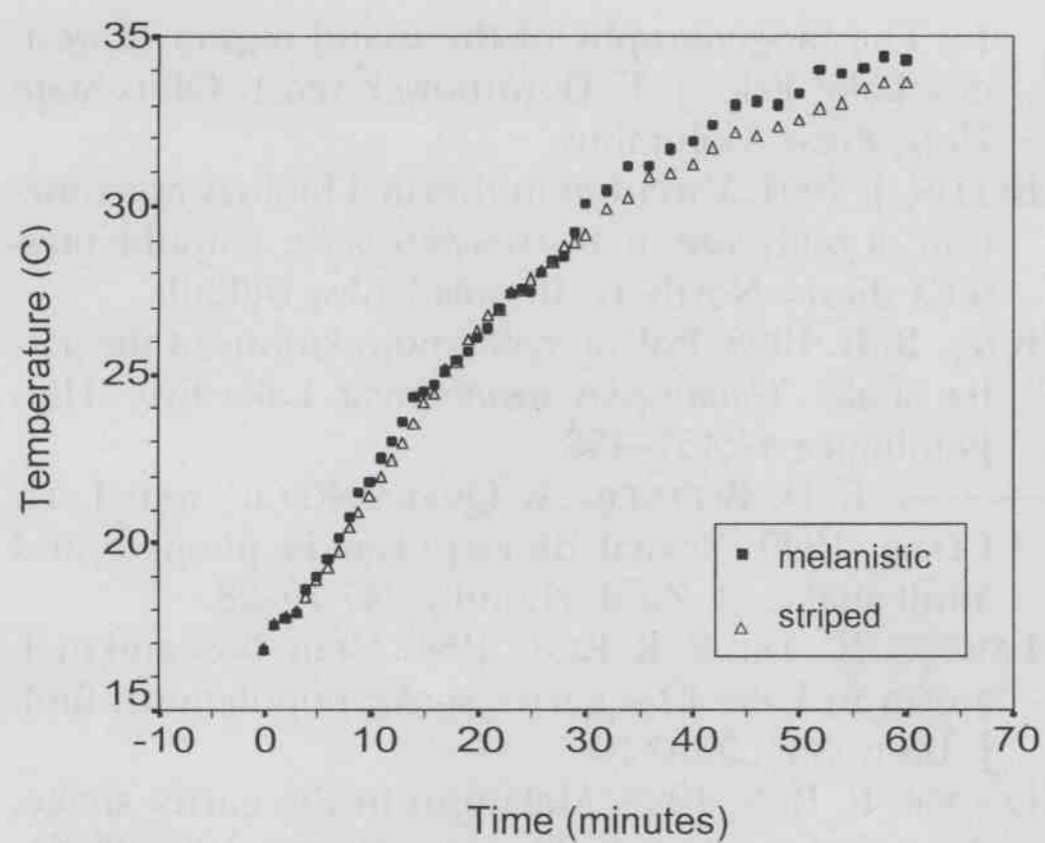


Fig. 1. Representative heating curves for one pair of large garter snakes in experiment 3. Each point represents the mean of two trials. The regression lines were omitted for clarity; $R^2 > 0.99$ for both regressions. Regression equation for the striped snake: $temp = 36.65 \text{ C} \{1 - 0.56 \exp[-0.03 \text{ min}^{-1} (\text{time})]\}$. For the melanistic snake: $temp = 38.45 \text{ C} \{1 - 0.58 \exp[-0.03 \text{ min}^{-1} (\text{time})]\}$.

snakes (Ayers and Shine, 1997); coiled snakes cool more slowly than outstretched snakes. Body position of our snakes varied over time within trials but without consistent difference between morphs. We compared behavior with plots of temperature versus time, looking for instances where a change in activity or body position produced a change in body temperature; we found no evidence that changes in position influenced the regressions of heating rate and equilibrium temperature.

DISCUSSION

This study demonstrates that garter snakes differing markedly in coloration show significant differences in equilibrium body temperature only at larger body sizes. Small and medium-sized striped and melanistic morphs did not differ in equilibrium body temperature. According to Stevenson's (1985) body temperature model, we expected to see differences in equilibrium temperature in all three size classes. Given the approximately 10% difference in absorptance between striped and melanistic garter snakes, we expected a 1.5–2.5 C difference in equilibrium temperature for small to large sized garter snakes (interpolating from fig. 6 in Stevenson, 1985). The lack of a morph effect on equilibrium body temperature among small and medium-sized snakes does not appear to be simply the result of test conditions—small, medium, and large snakes reached equilibrium temperatures about 8, 18, and 23 C above ambient

temperature, respectively. Possibly, physiological differences between the morphs may influence body temperature by allowing melanistics to have greater control of heat gain under some circumstances (Gibson and Falls, 1979).

We found no difference in instantaneous heating rate between striped and melanistic morphs regardless of body size (Tables 1, 3). This result was unexpected given greater heat flow through melanistic excised skin segments (Gibson and Falls, 1979) and that we found greater equilibrium body temperatures in large melanistic snakes. Consistent with the greater thermal inertia of large versus small snakes, heating rate decreased in going from small to medium-sized to large snakes (Table 1) and was significantly negatively correlated with $\ln(\text{Mass})$ in experiment 3 (Slope = -0.04).

Artificial lighting provides fewer of the infrared and ultraviolet wavelengths found in natural sunlight. Nevertheless, body temperatures did rise markedly under artificial light in all experiments. Repeating the experiment outdoors in cool, sunny weather may be useful but would also introduce more noise into the data from solar fluctuations, passing clouds, and wind. In a study of small lizards (5 g) under natural sunlight, Crisp et al. (1979) found no effect of color (black and brown) on the thermal time constant of the lizards, consistent with our results for small snakes.

The discontinuous polymorphism in garter snake color pattern has intrigued investigators for 80 years (Patch, 1919; Logier, 1929) and inspired selective scenarios to explain variance in morph frequency (e.g., Gibson and Falls, 1979, 1988; Lawson and King, 1996). Although previous research has suggested a thermal advantage for melanism, such an advantage has not been demonstrated in the field. Gibson and Falls (1979) compared the body temperatures of 414 snakes upon capture in the field and found no significant difference in temperature between striped and melanistic snakes, although they did find a trend toward warmer melanistic snakes in the spring and fall. Similarly, body temperatures of free-ranging *Vipera berus* showed a significant thermal advantage for melanistics in only two of six comparisons (Forsman, 1995).

The results presented here and recent studies using model snakes (Kerfin, 2001; Shine and Kearney, 2001) suggest that, if melanism does confer a selective thermal advantage, this advantage is restricted to large individuals. Furthermore, because female garter snakes exceed males in size (in the Lake Erie area, adult males and females average 46 and 100 g, respectively,

King et al., 1999), this advantage is likely to be restricted to adult females. Female garter snakes give birth to live young, and large females are more fecund than small ones (Seigel and Ford, 1987). The ability to thermoregulate precisely around the best temperature for development of young may allow melanistic females to produce larger, healthier offspring or give birth earlier relative to striped females. In contrast, thermoregulatory ability may be relatively unimportant in adult male garter snakes; male body temperature was uncorrelated with predator detection or mating success in *T. sirtalis* in Manitoba (Shine et al., 2000). In continuing to look for selective advantages of melanism in garter snakes, research might profitably shift to the relative fitness of melanistic mothers.

ACKNOWLEDGMENTS

This material is based upon work supported by the National Science Foundation under Grant 9409464 (RBK). Captive-born animals came from females collected under permits obtained from the Ohio Department of Natural Resources. Research protocols were approved by the NIU Institutional Animal Care and Use Committee (IACUC) under ORC 143.

LITERATURE CITED

- AYERS, D. Y., AND R. SHINE. 1997. Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Func. Ecol.* 11:342–347.
- BITTNER, T. D. 2000. The evolutionary significance of melanism in the common garter snake, *Thamnophis sirtalis*. Unpubl. Ph.D. diss. Northern Illinois Univ., DeKalb.
- CRISP, M., L. M. COOK, AND F. V. HERWARD. 1979. Color and heat balance in the lizard *Lacerta dugesii*. *Copeia* 1979:250–258.
- DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis. 2d ed. John Wiley and Sons, Inc., New York.
- FORSMAN, A. 1995. Heating rates and body temperature variation in melanistic and zigzag *Vipera berus*: does colour make a difference? *Ann. Zool. Fennici* 32:365–374.
- , AND S. AS. 1987. Maintenance of colour polymorphism in adder, *Vipera berus*, populations: a test of a popular hypothesis. *Oikos* 50:13–16.
- GIBSON, A. R., AND J. B. FALLS. 1979. Thermal biology of the common garter snake *Thamnophis sirtalis* (L.): II. The effects of melanism. *Oecologia (Berl.)* 43:99–109.
- , AND ———. 1988. Melanism in the common garter snake: a Lake Erie phenomenon, p. 231–245. *In: The biogeography of the island region of western Lake Erie.* J. F. Downhower (ed.). Ohio State Univ. Press, Columbus.
- KERFIN, J. 2001. Variation in thermal biology as a function of body size in *Thamnophis radix*. Unpubl. master's thesis. Northern Illinois Univ., DeKalb.
- KING, R. B. 1988. Polymorphic populations of the garter snake *Thamnophis sirtalis* near Lake Erie. *Herpetologica* 44:451–458.
- , T. D. BITTNER, A. QUERAL-REGIL, AND J. H. CLINE. 1999. Sexual dimorphism in neonate and adult snakes. *J. Zool. (Lond.)* 247:19–28.
- LAWSON, R., AND R. B. KING. 1996. Gene flow and melanism in Lake Erie garter snake populations. *Biol. J. Linn. Soc.* 59:1–19.
- LOGIER, E. B. S. 1929. Melanism in the garter snake, *Thamnophis sirtalis*, in Ontario. *Copeia* 1929:83–84.
- LOVICH, J. E., C. H. ERNST, AND J. F. MCBREEN. 1990. Growth, maturity, and sexual dimorphism in the wood turtle, *Clemmys insculpta*. *Can. J. Zool.* 68:672–677.
- MUSHINSKY, H. R., AND D. E. MILLER. 1993. Predation on water snakes: ontogenetic and interspecific considerations. *Copeia* 1993:660–665.
- PATCH, C. L. 1919. A rattlesnake, melano garter snakes, and other reptiles from Point Pelee, Ontario. *Can. Field-Nat.* 33:60–61.
- PETERSON, C. R., A. R. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body temperature variation, p. 241–314. *In: Snakes: ecology and behavior.* R. A. Seigel and J. T. Collins (eds.). McGraw-Hill, Inc., New York.
- SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology, p. 210–253. *In: Snakes: ecology and evolutionary biology.* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). McGraw-Hill, Inc. New York.
- SHINE, R., AND M. KEARNEY. 2001. Field studies of reptile thermoregulation: how well do physical models predict operative temperatures? *Func. Ecol.* 15:282–288.
- , P. S. HARLOW, M. J. ELPHICK, M. M. OLSSON, AND R. T. MASON. 2000. Conflicts between courtship and thermoregulation: the thermal ecology of amorous male garter snakes (*Thamnophis sirtalis parietalis*, Colubridae). *Physiol. Biochem. Zool.* 73:508–516.
- STEVENSON, R. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* 126:362–386.
- ZAR, J. H. 1984. Biostatistical analysis. 2d ed. Prentice-Hall, Inc., Englewood Cliffs, NJ.

DEPARTMENT OF BIOLOGICAL SCIENCES, NORTHERN ILLINOIS UNIVERSITY, DEKALB, ILLINOIS 60115. E-mail: (TDB) tbittner@theramp.net. Send reprint requests to RBK. Submitted: 20 June 2001. Accepted: 10 Sept. 2001. Section editor: R. E. Gatten Jr.