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Thermal Aspects of Melanistic and Striped Morphs of the Snake *Elaphe quadrivirgata*

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ABSTRACT—Temperature is a critical factor limiting various aspects of the biology of ectotherms. In addition to environmental factors, coloration and body size are two physical properties that influence ectotherms' body temperature (T_b). I compared the influences of these properties on thermal aspects of the two morphs of the color-dimorphic snake (*E. quadrivirgata*) under experimental conditions. First, I fitted T_b data during heating to the von Bertalanffy equation, but considered parameter values of the equilibrium temperature obtained to be biologically meaningless. Alternatively, I limited the data for comparison of the morphs to $T_b \leq 35°C$, which was the T_b at which snakes began to move vigorously in the experiment. The rate of T_b increase was significantly greater in the melanistic morph than in the striped morph. Heating rate was negatively correlated with body size in both morphs. The interaction of body size and heating rate did not significantly differ between the two morphs. The possibility of linkage, due to thermal advantage, between small body size and the prevalence of melanism in the population studied is briefly discussed. Rapid increase of T_b is biologically advantageous because snakes with such ability would be released from various time and environmental constraints associated with thermoregulation under particular environmental conditions.

Key words: body temperature, body size, coloration, *Elaphe quadrivirgata*, Yakushima Island

INTRODUCTION

Ectotherms rely on external resources for heat gain, and thus temperature is a critical factor limiting their distribution, diversity, and activity (*e.g.*, Cowles and Bogert, 1944; Huey, 1982; Coxwell and Bock, 1995). Although the range of body temperature (T_b) available to them is constrained by environmental factors, they can adjust T_b by physical, physiological, and behavioral means (see Lillywhite [2001] for review). For many ectotherms, thermoregulation is of central importance in their daily life because T_b directly affects their physiological processes, performance, and behavior (*e.g.*, Dawson, 1975; Christian and Tracy, 1981; Hertz *et al.*, 1983; Stevenson *et al.*, 1985; Bennett, 1987; van Berkum, 1988; Huey and Kingsolver, 1989; Willmer, 1991; Bauwens *et al.*, 1995; Dorcas *et al.*, 1997; Forsman, 1999). Thus, selection should act to favor characteristics that enhance the thermoregulatory ability of ectotherms, because the latter is biologically important to them.

Coloration and body size are two physical properties that influence the T_b of ectotherms (*e.g.*, Watt, 1968; Gibson and Falls, 1979; Brakefield and Willmer, 1985; Stevenson, 1985; Stewart and Dixon, 1989; Forsman, 1995a, 1997; de Jong *et al.*, 1996; Bittner *et al.*, 2002; Forsman *et al.*, 2002; Gross *et al.*, 2004). These two properties are consequences of adaptive compromise among various conflicting demands, such as social, predatory, antipredatory, and thermoregulatory demands (Cooper and Greenberg, 1992). Thus, if a particular combination of coloration and size is advantageous to the thermoregulation of a certain species, and innocuous for other demands, it is possible that these two properties will be highly correlated with each other.

Snakes are a suitable experimental ectothermic animal for examining the influence of coloration and body size on T_b, because they exhibit a wide range of variation in these two physical properties, yet have a simple body form (Greene, 1997). Furthermore, the occurrence of intraspecific variation in both properties in some snakes (*e.g.*, Mitchell, 1977; Rossman *et al.*, 1996; Tanaka and Ota, 2002) enables us to examine the relationship between coloration and body size and their effects on thermal properties without the confounding factor of phylogenetic constraints.

Among many color variants of snakes, the melanistic morph has been attractive for numerous studies that attempted to elucidate the biological significance of color mor-

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phs. Because the melanistic morph has been thought to have thermoregulatory advantages over normal-colored morphs (Gibson and Falls, 1979), studies of melanism in snakes have heavily focused on the thermal aspects. For example, Bittner *et al.* (2002) investigated the effects of color and body size on T_b of the garter snake, *Thamnophis sirtalis*, and found that the melanistic morph has a higher equilibrium temperature than the striped morph only in large size classes, whereas heating rate does not differ between the two color morphs in any size class. Based on their results and those of Shine and Kearney (2001), who investigated the effects of several attributes of a physical model (*e.g.*, color, size) on its temperature, Bittner *et al.* (2002) suggested that the thermal advantages of melanism would be restricted to larger individuals. Forsman (1995a) found that when exposed to natural insolation, the melanistic morph of the adder (*Vipera berus*) heated faster and reached slightly higher T_b than the normal-colored morph, whereas no consistent difference occurred in daily T_b variation between free-ranging melanistic and normal-colored individuals, monitored by radiotelemetry. He concluded that either color exerted only a trivial effect on T_b of the adders, or melanistic individuals used their thermoregulatory advantage differently, depending on gender and reproductive condition (Forsman, 1995a).

Snakes are a highly diversified group of reptiles (Greene, 1997), and thus they offer the valuable advantage of comparative study of biologically dissimilar species. The Japanese four-lined snake (*Elaphe quadrivirgata*) is a suitable candidate in this respect because not only does it exhibit color polymorphism, including melanism (Stejneger, 1907; Goris and Maeda, 2004; Mori *et al.*, 2005), but it also differs from the garter snake and the adder in several life-history traits. For example, *T. sirtalis* and *V. berus* are viviparous, whereas *E. quadrivirgata* is oviparous. In addition, the female is the larger sex in *T. sirtalis* and *V. berus*, whereas the male is the larger sex in *E. quadrivirgata*.

Temperatures during the developmental period affect the post-hatching behavior and morphometrics of hatchlings in several snakes (*e.g.*, Vinegar, 1974; Osgood, 1978; Burger, 1989, 1990; Blouin-Demers *et al.*, 2000; Lourdais *et al.*, 2004). Precise thermoregulation is particularly critical for viviparous snakes because they retain their embryos for relatively long periods. In contrast, appropriate nest-site selection may be more critical than precise thermoregulation for oviparous snakes to produce healthy hatchlings (Plummer and Snell, 1988; Shine *et al.*, 1997). If this dichotomy applies to *T. sirtalis* and *V. berus* compared to *E. quadrivirgata*, thermoregulatory ability is most important for the adult female garter snakes and adders (*i.e.*, the larger sex of viviparous snakes). These biological differences may affect the relative importance of body size and coloration to the thermal aspects of each species in different ways.

Here, I investigated the effects of color and body size on thermal aspects of *E. quadrivirgata* under experimental conditions. Specifically, I compared the relationship of body size to heating rate between melanistic and normal-colored (striped) morphs.

MATERIALS AND METHODS

Subject animals

Elaphe quadrivirgata is a diurnal snake widely distributed in Japan (Stejneger, 1907; Goris and Maeda, 2004; Mori *et al.*, 2005). The normal coloration of adult snakes is a brown ground color with four black longitudinal stripes. Color patterning is, however, variable both among and within populations (*e.g.*, variants include yellowish ground color with vivid stripes, or dark-brown ground color with pale stripes). Melanistic snakes are black from hatching, and thus melanism is not an ontogenetic darkening of the ground color, as is seen in the adders (Naulleau, 1973; Forsman, 1995a, b).

For the past seven years, I have been conducting an ecological study of the snakes on Yakushima Island (30°20'N, 130°32'E), Kagoshima Prefecture, Japan. Yakushima, a large island (503 km^2 in area) located southwest of the main-islands of Japan, has a warm-temperate climate (annual mean air temperature approximately 20°C in the lowlands) with extensive precipitation (>2500 mm/year) (Eguchi, 1985).

On Yakushima Island, *E. quadrivirgata* exhibits features of both coloration and body size that differ from those of main-island populations. There is a distinct striped/melanistic color dimorphism, with a high proportion of melanistic individuals (approximately 85%; Tanaka and Ota, 2002). Body size is smaller than that of the main-island populations (Fukada, 1992; Kadowaki, 1996; Tanaka and Ota, 2002). For example, mean snout-vent length (SVL) and body mass (BM) of adults on Yakushima Island are approximately 80% and 30%, respectively, of those in the Kyoto population studied by Fukada (1992) (mean male SVL=1078 mm and 828 mm for Kyoto and Yakushima, respectively, and mean BM=300 g and 114 g, respectively; see also Tanaka and Ota [2002]).

Experimental subjects were wild-caught adults comprising 13 melanistic (8 males and 5 females) and 14 striped snakes (8 males and 6 females). All melanistic snakes and two striped females were collected from Yakushima Island. Due to the difficulty of obtaining striped individuals from Yakushima (I captured only 33 striped individuals during a 7-year ecological survey), the remaining striped snakes were collected from Shiga Prefecture (34°55'N, 136°05'E), Honshu Island (the main-island of Japan). All striped snakes used in the experiment had a brown ground color with vivid stripes, and all melanistic snakes were jet-black. Although striped snakes came from two populations, the small sample size precluded the analysis of population effects on thermal properties. However, at least the appearance of the snakes did not differ between the two populations, and thus I assumed that population effects, if any, were negligible.

Prior to experimental trials, each snake was housed individually in a plastic cage (35×20×15 cm) with a water dish, in a building in which air temperature fluctuated with changes in ambient temperature throughout the experimental period (range 22–34°C).

Heating experiment

As has been done in other studies (*e.g.*, Forsman, 1997; Bittner *et al.*, 2002), I used an artificial heat source, in this case a 100-watt light bulb (Vivarium Basking Spot, Pogona Club Inc., Japan) hung 40 cm above the snake. This was done because experiments under natural conditions introduce many uncontrollable factors. To simulate the emergence of a snake from an overnight refugium, the heating experiment was performed in a walk-in environmental chamber at a temperature of 25°C, which is the approximate air temperature measured when *E. quadrivirgata* was captured between 0700 and 1000 hr on Yakushima Island (n=82, mean= 25.7°C, SE=0.30°C; Tanaka, unpubl. data). Snakes were not fed for at least 3 days prior to trials so that they could expel their gut contents.

On the day before an experimental trial, a snake was removed from its cage, put into a 5-mm mesh nylon bag, and kept in an incubator at 18°C until the trial began. Immediately before the trial, the snake was removed from the incubator. The small sensor bulb of a thermistor was inserted into the cloaca of the snake, and the wire of the thermistor probe was taped to its tail to prevent the sensor bulb from pulling out (Lutterschmidt and Lutterschmidt, 2002). The snake was then put into another 5-mm mesh nylon bag, which was sewn onto a 25×20×2.2-cm board of styrofoam to restrict the snake's movements and to minimize inter-trial differences in position of the snake relative to the heat source. Because these handling procedures affected T_b, I allowed the snake to re-equilibrate in the incubator to a T_b of approximately 20°C. The board with the snake was then transferred to the walk-in environmental chamber and placed under the heat source, within 30 sec after removal from the incubator.

I turned on the heating bulb when the T_b of the snake reached approximately 21.0°C (time zero of a trial), and began to record T_b at 1-min intervals. The mesh of the bag was large enough that most of the radiation reached to the snake. I simultaneously recorded the behavior of the snake. I terminated each trial either after 40 min had elapsed or when T_b reached 40°C, whichever came first. After the trial, I verified that the bulb sensor of the thermistor had remained in the cloaca, and I measured SVL and BM of the snake. Mean SVLs of the melanistic and striped morphs were 889 mm (range 780–1068 mm) and 869 mm (range 740–1010 mm), respectively, and mean BMs were 150 g (range 102–208 g) and 147 g (range 91–208 g), respectively. ANCOVA (with morph as factor, BM as dependent variable, and SVL as covariate) revealed that neither SVL-adjusted BM (t-test, df=1,24, F=1.03, p=0.21) nor SVL (t-test, df=25, t=0.53, p>0.6) differed between the two morphs. One to four snakes were tested in a day. After the experiment, all snakes were released at the site of capture.

Data analyses

Immediately after each day's experiments, T_b data for each snake were fitted to the following von Bertalanffy equation:

$$T_b = A\{1 - B \exp[-C\,(\text{time})]\},$$

where A is equilibrium temperature, B is proportion of A realized at time = 0, and C is a heating coefficient, which has units of time^{-1}. If data from a snake failed to converge on this equation due to a constant rise in T_b throughout a trial, the snake was re-tested another day.

Homogeneity of variance was checked with Bartlett's test before parametric tests were adopted. All statistical analyses were conducted with JMP (version 3) statistical software (SAS Institute, Inc., 1995) with α=0.05. Data are presented as mean±1SE.

RESULTS

Equilibrium temperatures obtained by the von Bertalanffy equation exceeded 50°C (Table 1). On Yakushima, operative environmental temperatures (Bakken and Gates, 1975; Bakken, 1992) under full sun during the active seasons of the snake frequently exceed 50°C (Tanaka, unpubl. data), and thus the heating curve may well represent changes in T_b of a basking snake in full sun. However, T_b of free-ranging snakes on Yakushima never exceeds 35°C (Tanaka, unpubl. data), and the equilibrium temperatures obtained were obviously much higher than a lethal temperature. Thus, detailed analyses of equilibrium temperatures exceeding 50°C are biologically meaningless. Nonetheless, this does not necessary mean that the heating curve obtained is irrelevant. Topology of the heating curve may differ between free-ranging and experimental conditions only above a particular T_b at which a basking snake in the wild would begin to move to another place. I assumed this point to be 35°C, for the following reasons. First, in the experiment, most snakes of both morphs began to move vigorously, with tongue flicking, when their T_b reached approximately 35°C. Second, the maximum T_b of *E. quadrivirgata* measured in the field on Yakushima Island was 34.6°C (Tanaka, unpubl. data). Third, the maximum voluntary T_b of *E. quadrivirgata* recorded under a laboratory thermal gradient was 34.9°C (Tanaka, unpubl. data). Thus, in the following analyses, I limited T_b data to no higher than 35°C in order to examine heating during basking (*i.e.*, from the beginning of basking until moving to another place). Use of linear regression equation was justified in because the exponential curves represented by the von Bertalanffy equation approximate a straight line (all, r>0.96, p<0.001; Fig. 1) during the presumed basking stage (*i.e.*, $T_b \leq 35$°C).

Heating rate (slope of T_b against time) during the presumed basking stage did not significantly differ between males and females in both morphs (melanistics: df=11, t=1.00, p=0.34; striped: df=12, t=1.38, p=0.19). Thus, I pooled the data from both sexes in the following analyses. Heating rate was negatively correlated with SVL (melanistics: r=–0.592, p=0.03; striped: r=–0.58, p=0.03) and BM (melanistics: r=–0.65, p=0.02; striped: r=–0.55, p=0.04; Fig. 2) in both morphs. ANCOVA (with morph as factor, BM as covariate, and heating rate as dependent variable) showed a significant difference in intercept between the two morphs, but no significant difference in slope (intercept: df=1,24, F=7.43, p=0.01; slope: df=1,23, F=2.24, p=0.15), although the slope was steeper in the melanistic morph (–0.00272) than in the striped morph (–0.00113) (use of SVL as covariate yielded the same conclusions). This means that the melanistic morph heats faster than the striped morph, but that the effect of BM (or SVL) on heating rate does not differ between the two morphs. These results did not change even when I used

Table 1. Mean±1SE of parameter values of the von Bertalanffy equation fitted to body temperature data during heating for melanistic and striped morphs of *Elaphe quadrivirgata*. Ranges are given in parentheses. N=sample sizes.

Morph	N	Equilibrium temperature (°C)	Heating coefficient (min^{-1})
Melanistic	13	50.3±3.4 (40.3–86.5)	0.0304±0.0038 (0.0085–0.0656)
Striped	14	53.4±3.3 (38.9–79.8)	0.0238±0.0035 (0.0071–0.0470)

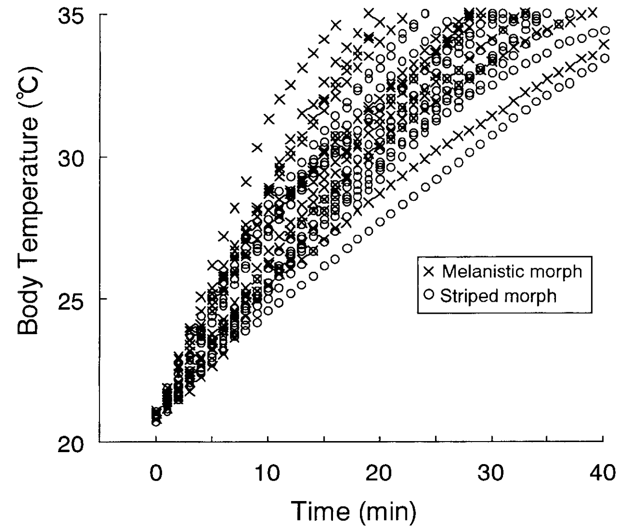

Fig. 1. Plots of body temperature (T_b) against time during the presumed basking stage (from the beginning of a trial until T_b reached 35°C) for 27 individuals of *Elaphe quadrivirgata* (13 melanistic and 14 striped morphs). The regression line for each individual is not shown (all, $r>0.96$, $p<0.001$).

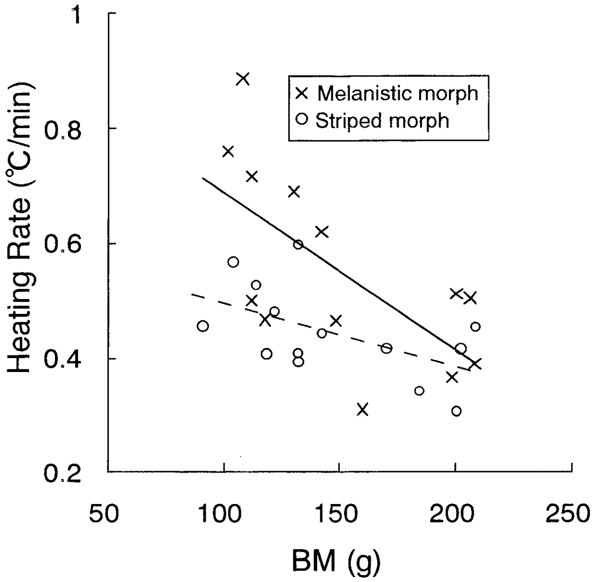

Fig. 2. Relationships between body mass (BM) and heating rate during the presumed basking stage (from the beginning of a trial until T_b reached 35°C) for melanistic and striped morphs of *Elaphe quadrivirgata*. Solid and dashed lines show least-squares regression lines fitted to the melanistic and striped morphs, respectively. Regression equation for melanistic morph: Heating rate=0.95962–0.00272 BM ($r^2=0.425$). For striped morph: Heating rate=0.60976–0.00113 BM ($r^2=0.300$).

another T_b value, such as the upper set-point (75% quartile; Hertz *et al.*, 1993) or median selected T_b under the thermal gradient, as the end point (31.6°C and 30.2°C, respectively; Tanaka, unpubl. data). The melanistic morph attained a T_b of 35°C significantly faster than the striped morph (melanistic: 27.0±2.1 min, range 16–40 min; striped: 32.4±1.4 min, range 24–40 min; df=25, t=−2.18, p=0.04).

DISCUSSION

The heating rate during the presumed basking stage was negatively correlated with body size in both morphs. This result corresponds with those of previous empirical and theoretical studies (*e.g.*, McNab and Auffenberg, 1976; Stevenson, 1985; Turner and Tracy, 1985; Seebacher *et al.*, 1999). An interesting trend in relation to heating rate and body size shown by the present study is that the slope of the regression equation for heating rate against BM is steeper in the melanistic morph than in the striped morph, although the difference is not statistically significant. This statistical non-significance may be due to the narrow range of body size used in the experiment or to small sample sizes. A larger inter-morph difference in heating rate in small snakes than in large snakes may be key to explaining the small body size and high frequency of melanism on Yakushima Island. Considering the superior heat absorption by black color, it may be possible that small body size helps maintain this prevalence of melanism.

A high proportion of melanistic morphs in dwarf populations of *E. quadrivirgata* also occurs on Oh-shima Island, located off the south coast of central Honshu Island (Hasegawa and Moriguchi, 1989; Goris and Maeda, 2004). The body size of snakes is geographically highly plastic, and has primarily been considered to be a direct phenotypic response to local prey type and size (Schwaner, 1985; Hasegawa and Moriguchi, 1989; Forsman, 1991; Kohno and Ota, 1991; Mori, 1994; Tanaka and Ota, 2002). Thus, the body size trend and the origin and maintenance of color dimorphism within a population must be maintained by independent mechanisms, but a secondary linkage between small size and a high frequency of melanism may exist on the basis of thermal advantage. Similarly to *E. quadrivirgata* in the present study, melanism usually prevails in species of ladybird beetles small in body size (Stewart and Dixon, 1989), although interpretation of this observation contrasts with that presented here (*i.e.*, advantage of rapid heating in small snakes vs. disadvantage of overheating in large ladybird beetles). From the perspective of evolutionary biology, direct and indirect links between morphology, physiology, behavior, and fitness are a fruitful area for future study (Willmer, 1991; Garland and Losos, 1992).

Under natural insolation, the melanistic morph of the garter snake maintains higher T_b than the striped morph (Gibson and Falls, 1979), and the melanistic morph of the adder heats faster and reaches slightly higher T_b than the normal-colored morph (Forsman, 1995a). The melanistic morph of *E. quadrivirgata* also heats faster than the striped morph. Rapid attainment of the preferred range of T_b is advantageous for ectotherms. This ability releases snakes from various time and environmental constraints associated with thermoregulation. For example, rapid heating enables a snake to utilize intermittently available, short-duration sun as a heat resource. Additionally, if thermally suitable sunlit sites are rare and appear patchily, and thus active movement is required for every basking effort, slow heaters must waste more time in thermoregulation than rapid heaters. This is because slow heaters may be unable to reach a T_b within their preferred range during a patch of clear sky. Furthermore, slow heaters may be restricted in their activities to the vicinity of thermally suitable microhabitats. The snake population on which I focused inhabits secondary forests, and the snakes may not be able to attain their preferred T_b by random use of microhabitats, except during summer (Tanaka, in prep.). In addition, unsettled weather conditions and high rainfall are well known climatic features of Yakushima Island (Eguchi, 1985). Thus, the hypothetical situations presented above are feasible ones.

In the wild, there are four possible ways in which slow heaters could manage their thermal inferiority. First, they could maintain a level of thermoregulation similar to that of melanistic morphs and accept a suboptimal T_b for activities. Second, they could turn into thermoconformers. Third, they could devote the time required and restrict other activities to the vicinity of a specific habitat to attain a T_b comparable to fast heaters. Fourth, they could lower their preferred T_b. To verify the ecological relevance of a rapid increase in T_b and its consequences, field studies of the thermal biology of *E. quadrivirgata* on Yakushima Island using temperature-sensitive radio transmitters will be necessary.

While some studies were consistent with the present study (see above), Bittner *et al.* (2002) reported inconsistent results. They revealed that when exposed to a light-bulb heat source, large melanistic garter snakes exhibited a higher equilibrium temperature than large striped ones, but heating rate did not differ between the two morphs. Interspecific differences in some characteristics (*e.g.*, physiological differences, differences in skin properties; also see Introduction) are possible causes of the inconsistency, however, a detailed discussion is impossible due to the lack of direct comparative data.

Lastly, I should mention the remarkable variance of T_b among individuals at a given time (see Fig. 1). It is obviously due, in part, to variation in body size (BM explained 42.5% and 30.0% of the total variation in heating rate for melanistic and striped morphs, respectively). In addition, either undetermined factor(s) or subtle differences in behavioral and physiological responses (see Bartholomew [1982]; Lillywhite [2001] for reviews) among individual snakes might have influenced their T_b change in complicated ways.

The present study revealed that physical properties play an important role in the heating of *E. quadrivirgata.* To validate the thermal superiority of the melanistic morph in an ecological context, it would be useful to study the differences between the two morphs in when, where, and how they behaviorally regulate their T_b in response to thermal environments.

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