Heating rates and body temperature variation in melanistic and zigzag *Vipera berus*: does colour make a difference?

Anders Forsman

Forsman, A., Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

Reptiles rely upon external heat sources to increase body temperature, and it has been suggested that thermoregulatory capacity may vary among individuals of different colour morphs because colours differ in reflectance and may influence the rate at which solar radiation is converted into body heat. Individuals with superior thermoregulatory abilities may either maintain higher body temperatures, and thereby enjoy increased performance, or they may decrease time spent basking, and thereby reduce the potential costs, e.g. predation, associated with thermoregulation. In a comparison of thermoregulatory capacity, daily body temperature, and proportion of time exposed between melanistic and zigzag individuals in a population of *Vipera berus* polymorphic for colour pattern, melanistic individuals were found to heat faster and to reach slightly higher body temperatures than did zigzag individuals when experimentally exposed to identical environmental conditions. However, there was no consistent difference in daily body temperature variation or in exposure between radiotelemetered free ranging melanistic and zigzag individuals, despite the fact that snake body temperatures appeared to be constrained by the physical environment for most of the study period. Either colour exerts only a trivial effect on the body temperatures of adders or melanistic individuals use their thermoregulatory advantage differently depending on gender and reproductive condition.

1. Introduction

The dependence of performance on body temperature in reptiles is well documented. For example, rates of metabolism, digestion, growth, crawling speed, embryonic development, defense behaviour, and morphology and mobility of off-spring all show temperature dependence (Huey 1982, Lillywhite 1987, Peterson, Gibson & Dorcas 1993 and references therein). When plotted as a function of body temperature many traits show a performance optimum at relatively high body temperatures, though with some variation among traits in location of the optimum (e.g.

Stevenson, Peterson & Tsuji 1985, Huey & Kingsolver 1989). Snakes and other reptiles control body temperature by regulating heat exchange with the environment using a variety of behavioural and physiological modifications, such as basking and seeking cover below surface, moving in and out of shade, stretching and flattening the body to increase the surface area exposed to the sun or coiling up to decrease the surface exposed, and by changing the blood flow (e.g. Huey 1982). Although individuals may select different body temperatures depending on their sex, feeding status, shedding status, reproductive condition, and health (Huey 1982, Lillywhite 1987, Peterson et al. 1993), body temperature variation of free ranging individuals may be attributable also to constraints imposed by the thermal environment (e.g. Peterson 1987). Thus, individual differences in thermoregulatory capacity may be an important source of variation in performance and fitness.

Individuals may vary in thermoregulatory efficiency or capacity due to differences in colouration because colours differ in reflectance and thus influence the rate at which solar radiation is converted into body heat (Gibson & Falls 1979, Peterson et al. 1993). For example, Gibson and Falls (1979) showed experimentally that melanistic (black) garter snakes *Thamnophis sirtalis* heat faster and attain slightly higher body temperatures than do their lighter conspecifics. They suggested that this thermoregulatory advantage may enable melanistic individuals to maintain higher body temperatures and thereby achieve increased performance (e.g. faster growth) relative to lighter individuals in populations polymorphic for colour pattern. This hypothesis has been tested several times using different species of snakes exhibiting dorsal colour pattern polymorphism (e.g. Gibson & Falls 1979, 1988, Andrén & Nilson 1981, King 1987, 1988, Forsman & Ås 1987, Madsen & Stille 1988, Forsman 1991, 1993, 1995, Luiselli 1992, 1993, Capula & Luiselli 1994). Although the predicted difference in body temperature between different colour morphs of free ranging *T. sirtalis* was indeed confirmed by field data, no significant difference was established between the morphs in performance (Gibson & Falls 1979, 1988, King 1988). Similarly, when I tested for ecological

differences between melanistic and zigzag patterned individuals in island populations of the adder *Vipera berus* (L.), I was unable to demonstrate any difference between morphs in condition (body mass relative to length), growth rate or body size (Forsman & Ås 1987, Forsman 1991, 1993, 1995, but see Andrén & Nilson 1981, Madsen & Stille 1988, Luiselli 1992, 1993, Capula & Luiselli 1994 for contrasting results in other populations). There are two possible explanations for this lack of difference between colour morphs in the populations that I have studied: Either thermoregulatory capacity is about the same in melanistic and zigzag patterned individuals in this species, or melanistic individuals use their superior thermoregulatory capacity to decrease time spent basking and thereby reduce their vulnerability to predators, rather than to maintain higher body temperatures. Reducing time exposed to predators may be especially important to melanistic individuals because previous studies have suggested that melanistic snakes are less cryptic and, as a consequence, presumably more susceptible to visually guided predators than are patterned snakes (e.g. Andrén & Nilson 1981, King 1988, 1992, Forsman 1995).

In the study reported here I investigated: (1) whether melanistic and zigzag *Vipera berus* differed in heating rates and body temperatures when exposed to identical environmental conditions, (2) whether radiotelemetered free-ranging melanistic and zigzag individuals differed in patterns of daily body temperature, and (3) whether radiotelemetered free-ranging melanistic and zigzag individuals differed in proportion of time exposed.

2. Materials and methods

2.1. Study species

Vipera berus is a viviparous, venomous snake species widely distributed in Europe. Sexes differ in coloration; females are usually light brown with a darker brown dorsal zigzag pattern, while males are grey with a black zigzag pattern. Some populations contain individuals of both sexes that are melanistic (black). On islands in the Baltic, where this study was conducted, melanistic individuals were either jet-black, or black with a zigzag pattern weakly discernible in bright light. Both categories

differed greatly from the zigzag morph. The genetic background of melanism in this species is not known. There are reports of adders being melanistic at birth (e.g. Biella 1977, Forsman 1995), but most individuals destined to become melanistic are born with a contrasting pattern, attain their black colour gradually as they grow, and are fully darkened by two to three years of age (Naulleau 1973, A. Forsman, pers. obs.).

In my study area adders enter hibernation in late September or October and emerge in late March or April. During the mating period, beginning about four weeks after emergence, males fight for access to females. Large males often win these combats and as a result obtain more matings than do small males (Andrén & Nilson 1981, Madsen 1988). Females reproduce at the most every second year and give birth in late August. Litter size varies between 5 and 20, and increases with increasing female body size (e.g. Madsen 1988). Newly born young average 150–200 mm snout-vent length. Reproduction commences at three or four years of age when snout-vent length is 400–500 mm (Madsen 1988). Females grow faster and to a larger size than males (Forsman 1991). In this area adders feed primarily on field voles *Microtus agrestis* (L.), and use frogs and bird nestlings as alternative prey species (Forsman 1991).

2.2. Study area

Adders used in the heating rate and body temperature experiments were gathered from a group of islands (Ängskär 59°32′N; 19°18′E, see Forsman 1991 or 1992 for a map and description of the study area) approximately 23 km off the Swedish east coast in the Baltic Sea. The telemetry study was conducted on one of the islands approximately 8 ha in size, and characterized by small stands of deciduous trees, dense juniper shrub (*Juniperus communis* L.), heather (*Calluna vulgaris* (L.)), small meadows and bare rocks. The only potential predators on adders seen regularly in the area were gulls (*Larus* spp.) and hooded crows (*Corvus corone*). Birds of prey occasionally prey on adders, but do not breed on the islands. However, they may pass through the area during spring and autumn migrations.

2.3. Heating rates

To assess a possible difference in heating rates between colour morphs I measured body temperatures of pairs of snakes (one melanistic, one zigzag) situated side by side, simultaneously exposed under natural solar radiation. Each snake was affixed to a Styrofoam stick using adhesive tape. Flexible thermocouples were inserted into the cloacas of both snakes and the two thermocouples were attached to a quick-reading digital thermometer (FLUKE model 52 K/J), allowing alternate recordings of the two snakes. This unit was placed in a refrigerator for approximately 2 h before the onset of the trial. At the start of each trial the experimental pair was moved out-of-doors and the affixed snakes were placed on the ground, about 0.5 m apart, fully exposed to the sun. I recorded body temperature at 30 s intervals, and calculated the difference between the melanistic and the zigzag individual for each measurement. Following the procedure outlined by Gibson & Falls (1979) I analyzed the sequence of differences for each trial using a paired *t*-test (Sokal & Rohlf 1981). In addition, I tested for a relationship between the between-morph difference in body temperature and elapsed time. Trials were terminated either when there was risk of overheating, or when body temperature of one of the snakes in a pair approached the environmental temperature (see below) and no longer increased with time. The duration of these trials ranged from 13 to 30 min.

I performed one trial each with 5 different melanistic–zigzag pairs of snakes that were matched with respect to sex and as closely as possible to snout-vent length (SVL) and body mass. The within-pair differences in the latter two characters was always less than 7%, did not differ significantly from 0 (Paired *t*-test: mean SVL-difference = 0.2 mm, $t = 0.34$, $df = 4$, $P = 0.75$; body mass-difference = – 0.4 g, $t = – 0.31$, $df = 4$, $P = 0.77$), and the signs of the differences varied among pairs.

2.4. Body temperature

To test for a difference in body temperature between colour morphs I performed three different experimental runs using two different sets of individuals, each set consisting of equal numbers of melanistic and zigzag individuals. The snakes were placed on a board of Styrofoam (1 200 by 600 by 60 mm) and covered with a nylon net to prevent them from moving away. I placed the experimental unit in an outdoor site that was not shaded by trees, so that the snakes were exposed to natural solar radiation. After one hour I measured snake body temperature using a digital quick reading thermometer with an attached thermocouple that was inserted into the cloaca, alternating between morphs for every measurement.

The first experimental group consisted of 14 (seven melanistic and seven zigzag) snakes that were matched with respect to sex and as closely as possible with respect to SVL and body mass so as to make up seven melanistic–zigzag pairs. The within pair differences in the latter two characters was less than 7%, and the mean difference did not differ significantly from 0 (Paired comparisons *t*-test for a difference between morphs; SVL: $t = 0.99$, $df = 6$, $P = 0.36$; body mass: $t = – 0.63$, $df = 6$, $P = 0.55$). Furthermore, the signs of the differences varied among the seven pairs. This group was tested once on a clear (cloud cover < 5%) and sunny morning, and I tested for a difference in body temperature between morphs using a paired comparisons *t*-test.

Another set of 14 (seven melanistic and seven zigzag) individuals was used in two different trials, one under

clear skies and one under overcast (cloud cover > 95%). Because I could not match the individuals in this set with respect to SVL and body mass, I tested for a difference in mean body temperature between melanistic and zigzag snakes using a *t*-test (Sokal and Rohlf 1981).

2.5. Body temperature variation of free-ranging snakes

Daily body temperature variation of individual free ranging snakes was investigated using radio telemetry. Model UL81T temperature monitoring radio transmitters (Austec Electronics, Alberta, Canada) fitted with a loop antenna and one 2.8-V 1/3N battery were contained in shrinkwrap and embedded in beeswax (approximately 30 by 15 by 11 mm and 6 g). Transmitters operated at 150 MHz with 10 kHz frequency separation and had a range of about 20–250 m depending upon orientation and degree of surface obstruction. I used a RX-810 receiver fitted with a LA88 IPP-processor (Televilt, Storå, Sweden) that recorded and showed transmitter pulse rate on a digital display and a 4-element Yagi antenna. Transmitters were calibrated in a temperature controlled water bath against a quick reading digital thermometer (Fluke 52K/J) both before and after use in the snakes. Temperature accounted for more than 99% of the variation in transmitter pulse rate in all calibration equations. Because there was a slight calibration shift, I calculated temperature from both calibration equations and used the mean of the two values in subsequent analyses.

Sex, colour morph, SVL, body mass, digestive state (via palpation), and reproductive condition (via palpation) of each telemetered snake were noted both before and after the study period. I force fed radio transmitters to the snakes and released them at the site of capture within 5 h. Body temperature, exposure (visible or non-visible), and activity (moving or non-moving) was recorded at 2-h intervals from 0800 to 2000 h in 1988, and from 0600 to 2000 h in

1989 and 1990, except during heavy rain. I only used data recorded 24 h or more after release of the snake. Transmitters were removed by forced regurgitation. Three individuals (two reproductive females and one male) fed when carrying the transmitters but they were not included in the analyses.

Seven, eight and nine snakes (SVL 430–660 mm, mass 65–262 g) were monitored from 29 June to 8 July 1988, from 10 to 16 July 1989, and from 14 to 20 July in 1990, respectively. Individuals may select different body temperatures depending on sex, feeding status, shedding status, and reproductive condition (Huey 1982, Lillywhite 1987, Peterson et al. 1993). In the analyses I therefore only used data from six pairs (each pair consisting of one melanistic and one zigzag individual) of snakes that were matched exactly with respect to sampling period, sex and reproductive condition, and as closely as possible with respect to digestive status, shedding status, SVL, and body mass.

To characterize the thermal environment of the snakes I measured operative temperatures (Te) using a physical model of a snake (Bakken, Santee & Erskine 1985). The model consisted of a straight, hollow copper pipe, 500 mm long, 20 mm in diameter, with a thermocouple suspended in its centre. The ends of the model were sealed with cork stoppers, and the model was painted black (model airplane paint) to resemble a melanistic adder. To measure maximum Te, I placed the model on the ground, in the open, oriented perpendicular to the path of the sun. Both mean model temperatures and relative frequency of model temperatures above 35°C varied among the three different sampling periods (see section 3.3).

To quantify daily body temperature variation I pooled data from all days and calculated mean body temperature at each monitored time of day for each individual snake. To test for a difference in body temperature between melanistic and zigzag snakes I analyzed data for the six different melanistic- zigzag pairs separately using paired comparisons *t*-tests, regarding the mean body temperature at each monitored time of day as one observation. To test

Table 1. Results from heating rate experiments with five melanistic-zigzag pairs of *Vipera berus*. Snout-vent length (SVL mm) and body mass (g) are given for both individuals in each pair. Mean Tb difference represents the mean of the differences in body temperature between the melanistic and the zigzag snake measured at 30 s intervals. *t* and *P* represent statistics from paired *t*-tests for a difference in Tb between morphs. *n* denotes number of measurements. Slope represent the least squares linear regression coefficient from the regression of the between-morph difference in Tb on elapsed time.

| | Melanistic | | Zigzag | | Mean Tb difference | | | | | | |
#	SVL	Mass	SVL	Mass	°C	*S.E.*	*t*	*P* <	*n*	Slope	*P* <
1	480	52	480	56	2.8	0.17	16.6	0.0001	32	0.06	0.0001
2	560	70	550	68	2.6	0.20	13.2	0.0001	26	0.05	0.05
3	520	49	510	50	0.5	0.09	6.1	0.0001	61	0.03	0.0001
4	550	53	570	55	0.6	0.09	6.2	0.0001	38	0.03	0.0001
5	510	50	500	47	1.0	0.12	8.6	0.0001	54	0.01	0.05

for a difference in degree of exposure between individuals of different colour morphs I used data from the six melanistic-zigzag pairs of snakes, calculated the proportion of telemetered observations on which the snake was visible, and tested for independence between colour morph and exposure (visible non-visible) using a *G*-test. Statistical tests were performed using SAS (SAS Inst. Inc. 1988), and all probability values given are two-tailed.

3. Results

3.1. Heating rates

The heating rate experiment showed that melanistic snakes heated significantly faster than did zigzag snakes (Table 1, Fig. 1). Thus, the mean difference in body temperature between melanistic and zigzag individuals was positive and significantly different from 0 in all five trials (mean of 5 trials = 1.5°C, range 0.54–2.83, paired *t*-test within trials: $P < 0.0001$ in all five cases). The binomial probability of this outcome is 0.031. Furthermore, the between-morph difference in temperature increased significantly with time elapsed within all five trials (Table 1, Fig. 1).

3.2. Body temperatures

The body temperature experiment showed that melanistic snakes enjoyed a small thermal advantage over zigzag snakes under clear skies, but that this advantage disappeared when the sky was covered by clouds (see also Gibson & Falls 1979 and Kjaergaard 1981). Melanistic snakes attained a slightly higher body temperature (mean difference 0.5°C) than zigzag snakes in the matched pair comparison trial performed under clear skies (melanistic: mean = 16.2°C, *S.D.* = 0.66; zigzag: mean = 15.7°C, *S.D.* = 0.65, paired *t*-test, $t = 2.86$, $df = 6$, $P < 0.05$). Melanistic snakes attained a significantly higher (mean difference 0.8°C) mean body temperature than zigzag snakes also in the unmatched group when exposed to clear skies (melanistic: mean = 21.6°C, *S.D.* = 0.23; zigzag: mean = 20.8°C, *S.D.* = 0.29, $t = 5.55$, $df = 12$, $P < 0.0001$), but not under overcast skies (melanistic: mean = 23.8°C, *S.D.* = 0.34; zigzag: mean = 23.6°C, *S.D.* = 0.50, $t = 0.68$, $df = 12$, $P = 0.51$).
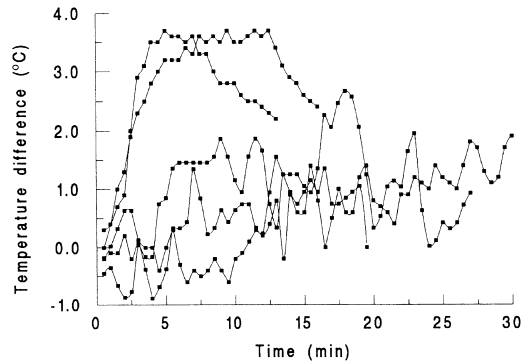

Fig. 1. Difference in body temperatures between melanistic and zigzag *Vipera berus* plotted against time. Data from five pairs (one melanistic, one zigzag) of snakes simultaneously moved from a refrigerator and exposed under natural insolation. See Table 1 for statistical results.

3.3. Body temperature variation of free-ranging snakes

Mean body temperatures of individual free ranging adders, calculated from all telemeter readings, ranged from 19 to 32°C (Table 2). On sixteen occasions the snake was moving at the time of monitoring. Mean body temperature of these active snakes was 28.9°C (*S.D.* = 6.35, range 16.1–36.9). The lowest and highest body temperatures recorded were 8 and 39°C, respectively, but most individuals never selected body temperatures above 35°C (Table 2).

With no exception, mean snake body temperature calculated only from telemeter readings taken when the black copper model snake exceeded 35°C were higher than the means calculated on all readings (Table 2), suggesting that in all years the physical environment prevented the snakes from always attaining preferred body temperatures. There was, however, a large difference in thermal environment among the three sampling periods. Mean temperature of the copper model snake was 32.5, 28.0, and 22.2°C, and the relative frequency of model snake temperatures > 35°C was 39, 24, and 14 % in 1988, 1989, and 1990, respectively. This variation was associated with a parallel variation in mean snake body temperatures which were highest in 1988

and lowest in 1990 (Table 2). Moreover, visual inspection revealed that body temperature frequency distributions of individual snakes tended to be negatively skewed in 1988 which was the warmest year, uniform in 1989, and positively skewed in 1990 which was the coldest year.

Daily body temperature variation typically showed a morning heating phase, a peak or plateau at midday, and an afternoon cooling phase, that is, a pattern rather similar to the temperature variation of the copper model snake (Fig. 2). There was no consistent difference in daily body temperature variation between melanistic and zigzag individuals in the six matched pairs that were monitored (Table 3, Fig. 2). The melanistic snake maintained significantly higher daily temperatures than the zigzag snake in one of the two male pairs (mean difference = 5.5°C, $S.E.$ = 1.22, t = 4.45, df = 6, $P < 0.01$), and in one of the two non-reproductive female pairs, mean difference = 4.1°C, $S.E.$ = 0.44, t = 4.64, df = 7, $P < 0.01$. In both of these comparisons (A and C in Fig. 2) the melanistic snake main-

tained higher temperature at all monitored times of day. But the melanistic snake was warmer also when temperatures were not constrained by the physical environment (Table 2), suggesting that the difference between morphs in these two pairs was partly due to a difference in preferred temperature. In contrast, the zigzag snake maintained significantly higher daily temperatures than the melanistic snake in one of the reproductive female pairs (E in Fig. 2; mean difference = 2.4°C, $S.E.$ = 0.94, t = – 2.51, df = 7, $P < 0.05$). The three remaining pairs showed no significant between-morph difference in body temperatures ($P > 0.15$).

Telemetered melanistic and zigzag snakes showed no consistent difference in degree of exposure (Table 3, Fig. 3). The melanistic snake was visible twice as often as the zigzag snake in one of the pairs consisting of non-reproductive females (45 viz. 17%, G = 7.88, df = 1, $P < 0.005$), but only half as often as the zigzag snake in one of the pairs consisting of reproductive females, 31 viz. 64%, G = 6.44, df = 1, $P < 0.05$. The other four comparisons were far from significant (Table 3).

4. Discussion

This study shows that melanistic adders heated faster and reached slightly (< 1°C) higher body temperatures than did zigzag conspecifics when experimentally exposed to identical environmental conditions. Despite this thermoregulatory advantage of melanism there was no consistent difference in the body temperatures maintained by free ranging radiotelemetered melanistic and zigzag individuals. Operative temperatures suggest that the physical environment was a potential constraint on snake body temperature during at least 60% of the time, even in the warmest year (Table 2). Thus, it cannot be argued that the difference in thermoregulatory capacity was unimportant simply because the snakes at all times could easily attain preferred body temperatures.

Circumstantial evidence suggests that melanistic and uniformly coloured snakes are less cryptic and, hence, presumably more susceptible to visually guided predators than are patterned snakes (e.g. Andrén & Nilson 1981, Gibson & Falls 1988, King 1988, 1992, Forsman 1995).

Table 2. Body temperature of free ranging radio telemetered melanistic and zigzag *Vipera berus.* Mean body tempeature and range is shown both when calculated on all readings and when calculated only from measurements that were taken when temperature of a copper model snake (Te) exceeded 35°C.

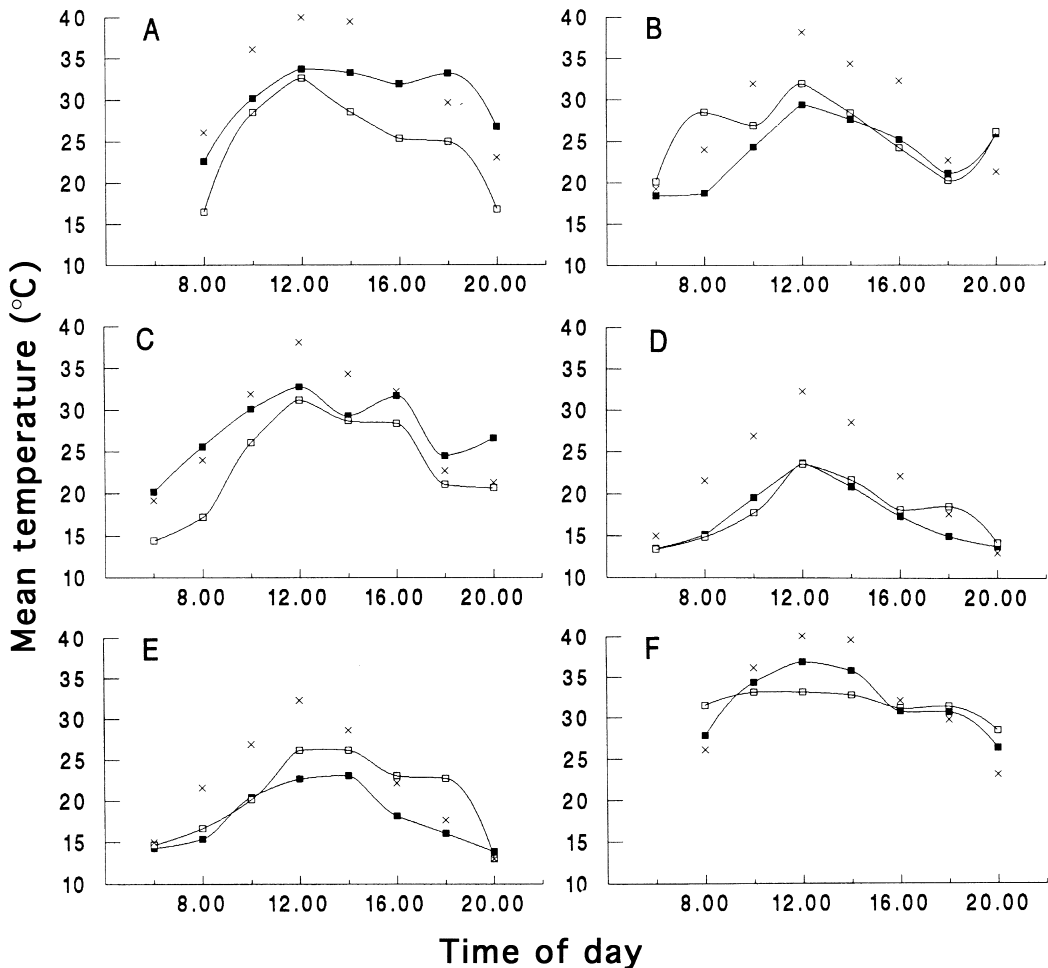|		Mean Body Tempearture (°C) (range)			
		All readings		Te > 35°C	
Pair	Year	Melanistic	Zigzag	Melanistic	Zigzag
Males					
A	1988:	30.3	25.1	32.5	29.4
		(17–36)	(8–35)	(18–36)	(22–35)
B	1989:	24.2	26.4	32.5	32.7
		(11–35)	(11–35)	(28–35)	(26–35)
Females non-reproductive					
C	1989:	28.2	24.6	33.2	33.1
		(17–35)	(13–35)	(30–34)	(32–36)
D	1990:	18.6	18.7	30.0	27.6
		(12–35)	(12–35)	(20–35)	(15–35)
Females reproductive					
E	1990:	19.1	21.7	27.8	29.6
		(13–34)	(13–34)	(17–34)	(16–34)
F	1988:	31.9	31.9	34.6	32.9
		(22–39)	(25–34)	(27–39)	(32–34)

Fig. 2. Comparisons of daily body temperature variation of individual free-ranging melanistic (filled squares) and zigzag (open) *Vipera berus*. Mean snake model temperatures (x) and mean telemetered body temperatures of individual snakes monitored at 2 h intervals during the day for several days are plotted against time of day (local solar time) for six melanistic-zigzag pairs of snakes. — A, B: males. — C, D: non-reproductive females. — E, F: reproductive females. Significant differences in daily body temperatures between morphs were found in pairs A, C and E (See Table 2 for details). x represents mean temperature of a black copper model snake positioned on the ground in the open.

For instance, in my study area, the relative frequency of individuals with scars, presumably resulting from unsuccessful predation attempts, is twice as high in melanistic (7.8 %, n = 128) as in zigzag individuals (3.7%, n = 295, Forsman 1995). From recaptures of marked individuals I know that melanistic adders are easier to capture by hand than zigzag, the difference in capture rate being approximately 20% (Forsman 1995). Thus, selection may favour melanistic individuals that use their thermoregulatory advantage to reduce the time they expose themselves to predators, rather than to maintain higher body temperatures. However, I found no consistent difference in the proportion of observations on which radiotelemetered melanistic and zigzag individuals were visible.

One interpretation of these results is that colour exerts only a trivial effect on the thermoregulatory capabilities of snakes (see also Crisp et al. 1979), and that the slight thermoregulatory advantage of melanistic over lighter colored in-
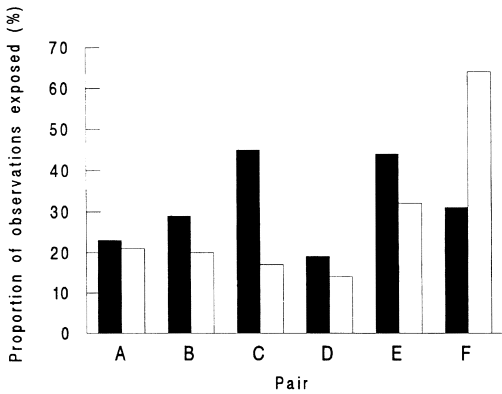
Fig. 3. Exposure of melanistic (filled) and zigzag (open) *Vipera berus*. The proportion of observations on which the snake was visible is shown for five pairs of radiotelemetered free ranging individuals. Males (A and B), non-reproductive females (C and D), reproductive females (E and F). Significant differences in exposure between colour morphs were found in pairs C and F (see Table 3 for details).

dividuals is of no ecological relevance. In fact, the similarity in body temperature in the two morphs may explain why melanistic and zigzag individuals do not differ in performance measures such as condition (body mass relative to

length), growth rate and body size in the island populations I have studied (Forsman & Ås 1987, Forsman 1991, 1993, 1995). Island populations of garter snakes *Thamnophis sirtalis* provide a parallel example with a similar slight thermoregulatory advantage of melanistic over lighter coloured individuals (Gibson & Falls 1979), and no apparent difference between morphs in growth rate, body size, frequency of reproduction, and morphology of offspring (Gibson & Falls 1988, King 1988). However, there is an alternative explanation why no consistent difference in body temperature or in exposure between radiotelemetered melanistic and zigzag individuals was demonstrable in this study.

Closer inspection of the results presented in Table 3 suggests that whether melanistic individuals use their thermoregulatory advantage to maintain higher body temperatures or to reduce time spent basking may be dependent upon gender and reproductive condition. Thus, in pair F (reproductive females) there was no difference in mean body temperatures between the melanistic and zigzag female despite the fact that the former was exposed only half as often as the latter. Conversely, the melanistic male in pair A maintained much higher body temperatures than the

Table 3. Results from six paired comparisons of body temperature (Tb) and exposure of radio telemetered free-ranging melanistic and zigzag *Vipera berus*. Mean Tb difference represent the mean of the within-pair differences in body temperature between melanistic and zigzag snakes monitored at 2 h intervals during the day for several days (see Fig. 1). Negative and positive values indicate a thermal advantage of the melanistic and zigzag snake, respectively. t and P represent results from paired t-tests for a difference in Tb betwen colour morphs. "% of obs. exposed" denotes the percentage of telemetered observations on which the snake was visible. G and P represent results from G-tests ($df = 1$) of independence of exposure and colour morph.

Pair Year	Mean Tb difference					% of obs. exposed			
	°C	S.E.	t	df	P	Melanistic	Zigzag	G	P
Males									
A 1988:	5.5	1.22	4.45	6	0.004	23	21	0.04	0.84
B 1989:	– 2.0	1.22	– 1.61	6	0.15	29	20	0.94	0.33
Females non-reproductive									
C 1989:	4.1	0.89	4.64	7	0.002	45	17	7.88	0.005
D 1990:	– 0.4	0.54	– 0.76	7	0.47	19	14	0.40	0.53
Females reproductive									
E 1990:	– 2.4	0.94	– 2.51	7	0.04	44	32	1.12	0.29
F 1988:	– 0.14	1.07	– 0.13	7	0.89	31	64	6.44	0.012

zigzag male even though the two males were exposed equally often. Again in pair C (non-reproductive females), the melanistic individual attained a higher mean body temperature, although this may have been due simply to the higher level of exposure. Note, however, that there were exceptions to this apparent advantage of melanistic snakes. For instance, the zigzag individual in pair E (reproductive females) maintained a higher body temperature than the melanistic individual without being exposed more often. This argues against any straight forward thermal advantage of melanism.

A higher body temperature of melanistic snakes was evident under clear but not under overcast skies. This suggests that the thermoregulatory advantage of melansim varies with weather conditions (see also Gibson & Falls 1979, 1988), and may explain why melanistic and lighter colored individuals have been found to differ in various performance measures in some populations (e.g. Andrén & Nilson 1981, Madsen & Stille 1988, Luiselli 1992, 1993, Capula & Luiselli 1994), but not in others (e.g. Forsman & Ås 1987, Gibson & Falls 1988, King 1988, Forsman 1991, 1993, 1995). The variation in morph frequency among populations (e.g. Kjaergaard 1981, Gibson & Falls 1988, Terhivuo 1990, Forsman 1995), with the black morph being particularly common in high altitude, coastal, and island populations further suggests that the difference in heating rates and body temperature is most important in areas with low ambient temperatures and high solar radiation (Gibson & Falls 1988). However, no formal test of this hypothesis has been carried out and care must be taken to consider intersite differences other than thermal constraints, such as predation intensity, that may influence the relative fitness of colour morphs. For instance, several studies have demonstrated differences in crypsis and survival among colour morphs in snakes (e.g. Andrén & Nilson 1981, Brodie 1992, King 1992, 1993, Forsman 1995). In the population I have studied zigzag males survive significantly better than melanistic males, whereas melanistic females survive better than zigzag females (Forsman 1995). This interaction between survival, sex and colour morph is probably due to behavioural differences between sexes, with melanism increasing susceptibility to predators when in combination with male but not with female behaviour. The opposing fitness consequences of colour pattern in the two sexes may help maintain colour polymorphism within populations of *Vipera berus* (Forsman 1995). The spatial distribution of the melanistic morph probably reflects an interactive effect of climate and predation.

References

Andrén, C. & Nilson, G. 1981: Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, Vipera berus. — Biol. J. Linn. Soc. 15: 235–246.

Bakken, G. S., Santee, W. R. & Erskine, D. S. 1985: Operative and standard operative temperatures: Tools for thermal energetics studies. — Amer. Zool. 25: 933–943.

Biella, H. J. 1977: Studien zur Verbreitung und Ökologie der Kreuzotter (Vipera b. berus L.) in der Oberlausitz. — Abhandlung und Berichte des Naturkunde Museums Görlitz 51: 1–9.

Brodie, E. D. 1982: Correlational selection for colour pattern and antipredator behaviour in the garter snake Thamnophis ordinoides. — Evolution 46: 1284–1298.

Capula, M. & Luiselli, L. 1994: Reproductive strategies in alpine adders, Vipera berus. The black females bear more often. — Acta Oecologica 15: 207–214.

Crisp, M., Cook, L. M. & Hereward, F. V. 1979: Color and heat balance in the lizard Lacerta dugesii. — Copeia 1979: 250–258.

Forsman, A. 1991: Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. — J. Anim. Ecol. 60: 253–267.

— 1992: Adaptive body and head size variation in populations of the adder Vipera berus. — Acta Universitatis Upsaliensis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science 401.

— 1993: Growth rate in different colour morphs of the adder, Vipera berus, in relation to yearly weather variation. — Oikos 66: 279–285.

— 1995: Opposing fitness consequences of colour pattern in male and female snakes. — J. Evol. Biol. 8: 53–70.

Forsman, A. & Ås, S. 1987: Maintenance of colour

polymorphism in adder, Vipera berus, populations: a test of a popular hypothesis. — Oikos 50: 13–16.

Gibson, A. R. & Falls, B. 1979: Thermal biology of the common garter snake Thamnophis sirtalis L. II. The effects of melanism. — Oecologia, Berl. 43: 99–109.

— 1988: Melanism in the common garter snake: a Lake Eire phenomenon. — In: Downhower, J. F. (ed.), The biogeography of the island region of western Lake Eire: 233–245. Ohio State University Press, Columbus.

Huey, R. B. 1982: Temperature, physiology, and the ecology of reptiles. — In: Gans, C. & Pough, F. H. (eds.), Biology of the Reptilia, Vol. 12: 25–91. Academic Press.

Huey, R. B. & Kingsolver, J. G. 1989: Evolution of thermal sensitivity of ectotherm performance. — Trends Ecol. Evol. 4: 131–135.

King, R. B. 1987: Colour pattern polymorphism in the Lake Erie water snake, Nerodia sipedon insularum. — Evolution 41: 241–255.

— 1988: Polymorphic populations of the garter snake, Thamnophis sirtalis, near Lake Erie. — Herpetologica 44: 451–458.

— 1992: Lake Erie water snakes revisited: morph- and age-specific variation in relative crypsis. — Evol. Ecol. 6: 115–124.

— 1993: Colour-pattern variation in Lake Erie water snakes: prediction and measurement of natural selection. — Evolution 47: 1819–1833.

Kjærgaard, J. 1981: Udbredelsen af sort hugorm i Danmark. — Flora og Fauna 87: 27–29. (In Danish with English summary).

Lillywhite, H. B. 1987: Temperature, energetics, and physiological ecology. — In: R. A. Seigel, R. A., Collins, J. T. & Novak, S. S. (eds.), Snakes — ecology and evolutionary biology: 422–477. Macmillan Publishing Co, NewYork.

Luiselli, L. 1992: Reproductive success in melanistic adders: a new hypothesis and some considerations on Andrén and Nilson´s (1981) suggestions. — Oikos 64: 601–604.

— 1993: The ecological role of colour polymorphism in male adders, Vipera berus: testing the hypotheses. — Rev. Ecol. (Terre Vie) 48: 49–56.

Madsen, T. 1988: Reproductive success, mortality and sexual size dimorphism in the adder, Vipera berus. — Holarct. Ecol. 11: 77–80.

Madsen, T. & Stille, B. 1988: The effect of size dependent mortality on colour morphs in male adders, Vipera berus. — Oikos 52: 73–78.

Naulleau, G. 1973: Le mélanism chez Vipera aspis et chez Vipera berus. — Bulletin de la Societé Zoologique de France 98: 595–596.

Peterson, C. R. 1987: Daily body temperature variation in free-ranging garter snakes. — Ecology 68: 160–169.

Peterson, C. R., Gibson, A. R. & Dorcas, M. E. 1993: Snake thermal ecology: the causes and consequences of body-temperature variation. — In: Seigel, R. A. & Collins, J. T. (eds.), Snakes – Ecology and Behavior: 241–314. McGraw-Hill, New York.

SAS Institute Inc. 1988: SAS/STAT User´s guide, Release 6.03 ed. — SAS Institute Inc., Cary, NC.

Sokal, R. S. & Rohlf, F. J. 1981: Biometry, 2 ed. — W. H. Freeman and Company, New York.

Stevenson, R. D., Peterson, C. R. & Tsuji, J. S. 1985: The thermal dependence of locomotion, tounge flicking, digestion, and oxygen consumption in the wandering garter snake. — Physiol. Zool. 58: 46–57.

Terhivuo, J. 1990: Relative regional abundance and colour morphs of the adder (Vipera berus L.), grass snake (Natrix natrix L.), slow worm (Anguis fragilis L.) and common toad (Bufo bufo L.) in Finland. — Ann. Zool. Fennici 27: 11–20.