

Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*

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In a population of adders (*Vipera berus*) in Southwest Sweden, melanistic males were heavier than normal coloured males of the same length. Victory in male–male sexual combats was positively related to size. Higher risk of predation in the black morph was inferred from experiments showing a high predator attack rate on models of the black morph. Even the bright colour in newly moulted basking males of the normal morph gives cryptic protection. In females, melanism probably also affects body size and risk of predation by visually searching predators. The thermoregulatory influence of black colour, the reproductive success and the maintenance of two colour morphs in the population are discussed.

KEY WORDS:—*Vipera berus* – melanism – thermoregulation – size – combat – predation – reproductive success.

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INTRODUCTION

Coloration of animals generally tends to be adapted to biotic and abiotic environmental factors. Coloration in reptiles has several important functions: it

may protect the animal from predation through background matching or aposematism; it may influence thermoregulation; it may protect critical structures from radiation and it is often important in intra and interspecific interactions and in reproductive communication (Porter, 1972).

Occasional melanistic specimens have been observed in many reptiles. Although generally rare, snake melanism may be locally very frequent (Logier, 1930; Catling & Freedman, 1977; Andrén & Nilson, 1979; Gibson & Falls, 1979). What is the advantage which maintains the dark morph in the population? By what mechanism is either morph prevented from totally replacing the other one?

The adaptive value of black coloration in reptiles and other poikilotherms has been subjected to much speculation. Gibson & Falls (1979) showed a thermoregulatory effect of black colour in garter snakes (*Thamnophis sirtalis* (L.)), which is also recognized in other reptiles (e.g. Parker, 1935; Lawrence & Wilhoft, 1958; Hutchinson & Larimer, 1960). In this paper we focus on the influence of black coloration and size on reproductive success and concealment.

STUDY AREA

Fieldwork was carried out in two free-living populations on the islands of Hallands Väderö (56° 27'N) and Stora Håstholmen (57° 46'N) Southwest Sweden, complemented with studies in an outdoor field terrarium at the Department of Zoology, University of Göteborg.

Hallands Väderö, a western outpost of the ridge Hallandsåsen in the Kattegat Sea, is a nature reserve of 310 ha, its highest point being 24 m. The climate is maritime with a high mean annual temperature of 7.7°C (Vallin, 1949). The central part of the island has low stone ridges important for reptile hibernation. One-quarter of the island is forested, mainly by alder (*Alnus glutinosa*), beech (*Fagus sylvatica*), oak (*Quercus ruber* and *Q. petraea*), hazel (*Corylus avellana*) and birch (*Betula verrucosa*). The remaining parts are bare rock and stony areas with juniper (*Juniperus communis*). The island was visited during two periods, 17–20 April 1978 and 27 May–1 June 1979.

Stora Håstholmen has an area of 54 ha of which one-third is bare rock and the remainder is covered with grass and heather (mainly *Calluna vulgaris*). There are at least 20 natural stone piles overgrown by bushy vegetation which are used by adders for night shelter and hibernation. Reproductive interactions mainly took place close to these hibernation places. The population of adult adders was estimated, by capture-mark-recaptures and counts, to be about 200 specimens in 1974 (Andrén, in prep.).

The outdoor 60 m² field terrarium is surrounded by a one m high concrete wall. It is constructed to resemble natural adder habitat, with grass, heather and a small pond in the lower part, and also including a mound with an overgrown, south facing stone pile. All adders were collected in SW Sweden and introduced in the terrarium in spring 1978.

MATERIAL AND METHODS

In April 1978 and May 1979 field investigations were made on the island Hallands Väderö, at the Swedish west coast, in an adder population with a high amount of melanism. By experiments and field observations we tested if coloration

was related to success in rivalry combats among males and if the colour morph had any influence on the attack rate of visually searching predators. In males we found significant differences between two colour morphs, black males being heavier than normally coloured males of the same length.

Adders used for tests of success in male-male sexual combats were caught by hand and individually marked by ventral scale clipping complemented with dorsal dots on the tail. Date of observation, sex, length, body mass and colouring were noted.

Experiment I: Size and male combats

The importance of size in male combats was tested in the outdoor field terrarium in 1978. Fourteen male and eight female adult adders were present in the terrarium. Thirteen males took part in combats. Social behaviour was documented daily to verify that its development was normal as compared to a free-living population (Andrén, in prep.). Between 29 April and 3 May the air temperature was high enough (about 15°C) for normal social interactions to occur for at least 6 h daily. Male adders defend females and small areas around them during the reproductive period through fightings. During this period a hierarchy is developed among males.

The outcome of all interactions between males, including combats and pursuing rivals, was recorded during five days. Similar observations of combats in male adders were recorded daily 21 April – 10 May in the free-living population on Stora Hästhölm in 1974. The relation between size and colour morph was measured on adders caught on Hallands Väderö in 1978 and 1979.

Experiment II: Colour morph and predation

The importance of colour pattern in relation to predation was experimentally tested on Hallands Väderö in 1979. Fifty plastic attraps, 65 cm long and shaped as adult adders, were put out at intervals of 30–50 m along a 2 km long track on the west side of the island. Sixty per cent of the snake models were painted in the colour pattern of moulted males: greyish white with a black dorsal zig-zag pattern along the back. The remaining 40% were painted all black. The ratio between normal and melanistic attraps was similar to the true ratio in the free-living population on the island. Black and normal morphs were allocated randomly to the predetermined experimental sites.

The attraps were put out in the middle of the day and checked at the same time 24 h later to avoid disturbance during the normal activity periods in the morning and late afternoon. The models were placed on suitable basking spots and were somewhat hidden by natural vegetation. We marked head and tail tip positions with two small sticks and under the snake, invisible from above, we placed a small piece of meat as a reward for predators attacking the model. The approximate position of each model was indicated by colour dots and numbers on already available rods along the tracks.

Attraps which had been moved several centimetres in relation to the small sticks and with the piece of meat removed were classified as subjected to predatory attack. Attraps were also vulnerable to predators using olfactory guidance rather than visual (e.g. nocturnal species), but such predators should not bias the result. A

possible non-visually searching predator is the hedgehog (*Erinaceus europaeus*), which was common in the study area.

Five experiments were run and during each experiment the order of normal and black models were randomly altered. The position of the snakes was also changed each day in an east-west direction, to avoid learning of their positions by predators from one day to the other. The arrangement and control of the models took 4–5 h (between 10.00–15.00 hours) for two persons.

RESULTS

Colour morph and body mass in relation to length

Forty per cent of male and 75% of female adult adders collected on Hallands Väderö in 1978 and 1979 were melanistic. Their sex, length, body mass and colour are shown in Table 1.

Table 1. Sex, length, body mass and colour morph of adders, *Vipera berus*, from Hallands Väderö 17–20 April 1978 and 27 May–1 June 1979.

	N	Length (cm)			Body mass (g)		
		Mean	Range	S.E.	Mean	Range	S.E.
♂ Normal	18	55.9	50–67	1.004	75.8	46–118	3.936
♂ Melanistic	10	55.4	50–60	0.958	85.8	52–110	5.894
♀ Normal	3	61.7	57–64	2.332	142.0	134–151	4.931
♀ Melanistic	9	63.0	54–69	1.607	152.7	94–194	11.348

For any given length, melanistic males are significantly heavier than normal coloured males (Fig. 1). The ordinate intercepts of the two regression lines differ significantly,

$$F_1 = \frac{0.1640}{0.0122} = 13.4$$

(d.f. 1, 27; $P \ll 0.01$). Their slopes are, however, not significantly different (Fig. 1),

$$F_2 = \frac{0.0176}{0.0267} = 0.66$$

(d.f. 1, 26; $P \gg 0.05$). Analysis of covariance (Snedecor & Cochran, 1967).

No differences were apparent between normally coloured and melanistic females (Fig. 2; no statistical test was performed as only three non-melanistic females were measured). However, the heaviest females were all melanistic. Female adders of both morphs were longer and heavier than males (Table 1).

Male size and victory in sexual combats

Large male adders were superior in rivalry combats (Table 2). In the field terrarium the outcome of 73 combats in 26 different combinations, including 13 males, was observed. In all cases longer and heavier males won the combats, which ended by the loser withdrawing from its adversary, which sometimes pursued the loser more than 10 m.

In the free-living adder population on Stora Hästholmen 15 males were observed in 40 combats, in 12 different combinations of males. In all cases longer and heavier males won.

Both studies only involved dyadic combats between pairs of normally coloured

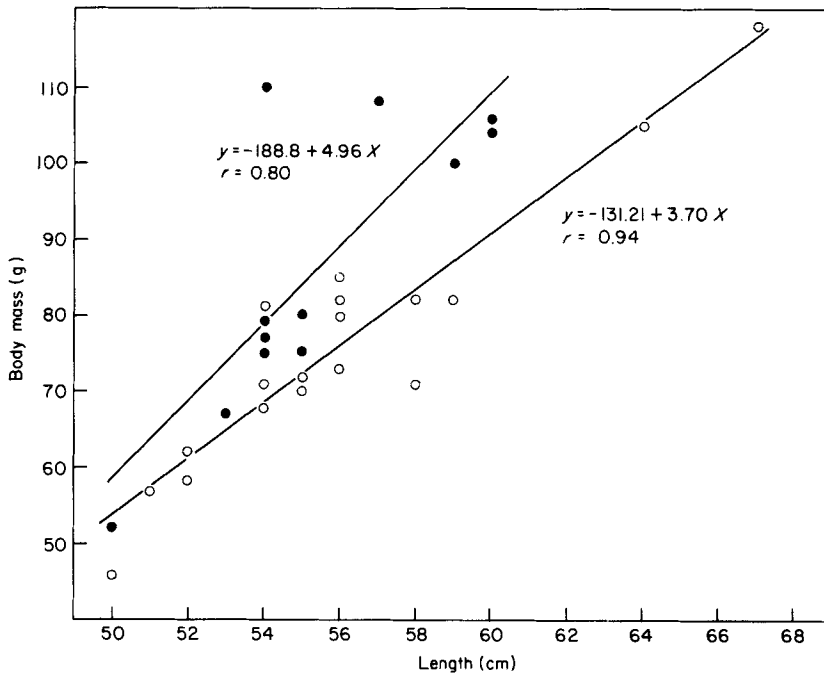


Figure 1. Body mass in relation to length for normal (○) and melanistic (●) male adders, *Vipera berus*, from the island Hallands Väderö. The regression lines for the two colour morphs and their respective intercept differ significantly ($P \leq 0.01$). The slopes of the regression lines are, however, not significantly different ($P \geq 0.05$).

males. In the single case where two equally long males did fight, the heavier one won the combat. Further details on male adder combats are given by Andréén (in prep.).

Predation pressure on different colour morphs

The melanistic morph was more subjected to visual predator attacks than the normal coloured morph (Table 3). In four of the five experiments, predation was higher on the melanistic morph. In all five experiments taken together, a significantly higher proportion of black males were attacked by predators. The risk of predation was roughly twice as high for the melanistic attraps (26%) as for the non-melanistic ones (14%).

DISCUSSION OF RESULTS

Colour morph and body mass in relation to length

Many biochemical and physiological processes in snakes, affecting e.g. growth rate, are optimal at the thermal preferendum (Beitinger & Fitzpatrick, 1979; Hutchinson & Maness, 1979). Usually reptiles follow the Van't Hoff law, i.e. their metabolic processes double or triple for each 10°C rise in internal temperature (Porter, 1972; Gans & Dawson, 1976). Gibson & Falls (1979) showed that the melanistic morph of garter snake (*Thamnophis s. sirtalis*) maintains a significantly higher (1.24°C) body temperature during the colder part of the day compared with the normal coloured morph. Therefore, in melanistic adders, a more rapid heat accumulation in the early morning probably reduces the necessary basking period to reach optimum internal temperature. For the same reason, the dark morph

Table 2. Outcome of male rivalry combats in the adder, *Vipera berus*, in a free living island population on Hästholmen southwest Sweden 21 April – 10 May (A) and a seminatural population in the outdoor field terrarium at the Department of Zoology in Göteborg 29 April – 3 May (B). Interacting males are printed towards each other.

No.	Superior male Length (cm)	Body mass (g)	No.	Inferior male Length (cm)	Body mass (g)
A					
317	62	115	305	55	90
325	65	128	317	62	115
327	65	142	323	65	123
			301	52	58
			303	52	65
			305	55	90
			307	54	86
			309	56	96
329	67	143	311	57	99
			313	61	98
			315	62	112
			317	62	115
			319	63	120
			321	64	115
			323	65	123
B					
517	58	83	519	52	71
519	52	71	549	50	46
521	54	82	519	52	71
523	59	106	521	54	82
			513	57	76
527	58	82	519	52	71
			549	50	46
			501	43	23
			507	54	55
			513	57	76
			517	58	83
529	64	105	519	52	71
			521	54	82
			527	58	82
			547	55	82
			555	59	100
			501	43	23
			507	54	55
			513	57	76
			517	58	83
555	59	100	519	52	71
			521	54	82
			527	58	82
			547	55	82
			549	50	46
557	67	118	523	59	106

might be able to be active for a larger part of the year. This would give the black morph more time for hunting and food conversion, resulting in larger body size.

Female adders are usually biennial breeders in the present region (Nilson, in prep.). It is therefore impossible to draw any firm conclusions on length/body mass ratios only in spring females. However, the largest females in our material are melanistic. This suggests that the black coloration may be of selective

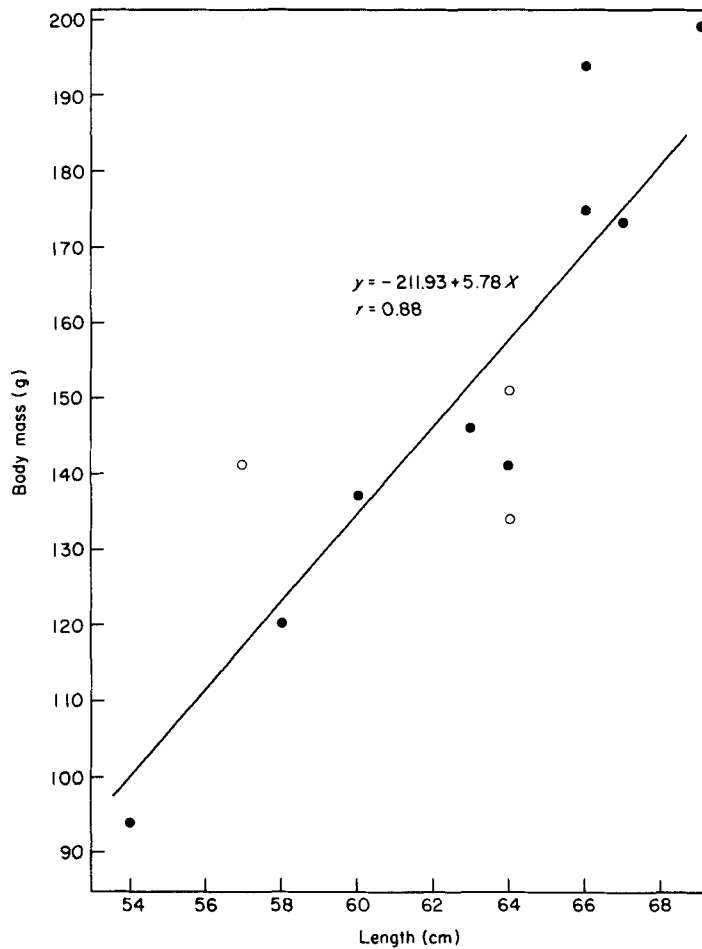


Figure 2. Body mass in relation to length for normal (○) and melanistic (●) female adders, *Vipera berus*, from the island Hallands Väderö. The regression line refer to all specimen of both morphs.

Table 3. Predator attacks on models of normally coloured ($n = 30$) and melanistic ($n = 20$) male adders, *Vipera berus*, in five different experiments on Hallands Väderö, southwest Sweden, 27 May – 1 June 1979. For details, see Material and Methods.

Experiment	No. of males attacked	Melanistic males attacked (%)	Normal coloured males attacked (%)
1	7	20	10
2	9	15	20
3	9	25	13
4	11	35	13
5	11	35	13
1-5*	47	26	14

* $P < 0.025$; two-tailed χ^2 — test (Siegel, 1956).

advantage also in females, whose reproductive output normally increases with size in the adder (Nilson, in prep.).

Male size and victory in sexual combats

Size proved to be crucial for victory in male combats. In each of the 113 male-male interactions examined, the larger male was superior and chased away the smaller one. This should give the large males an important reproductive advantage. Their higher success in combats over females results in a higher chance of mating (Andrén, in prep.). A strong correlation between male body size and reproductive success is known to occur in many other reptiles as well as in most birds and mammals (Kolata, 1977; Schoener, 1967; Trivers, 1976).

Predation pressure on different colour morphs

Selection for pattern type is known to occur in several snakes, e.g. in the water snake (*Natrix sipedon*) on islands in Lake Erie in North America (Camin & Ehrlich, 1958). In the present study, the pressure from visually hunting predators on melanistic adders was compared with that on normally coloured ones. Possible predators on Hallands Väderö are herring gull (*Larus argentatus*), hooded crow (*Corvus cornix*), raven (*Corvus corax*), magpie (*Pica pica*), goshawk (*Accipiter gentilis*), rough-legged buzzard (*Buteo lagopus*) and short-eared owl (*Asio flammeus*).

The colour pattern in our models of the normal colour morph was designed to resemble the bright, distinct pattern of males during the reproductive spring period. Even this pattern is more cryptic than the black coloration. The difference between the two morphs from a visually hunting predator's point of view is shown in Fig. 3. Outside the reproductive period the colour pattern in normal males is

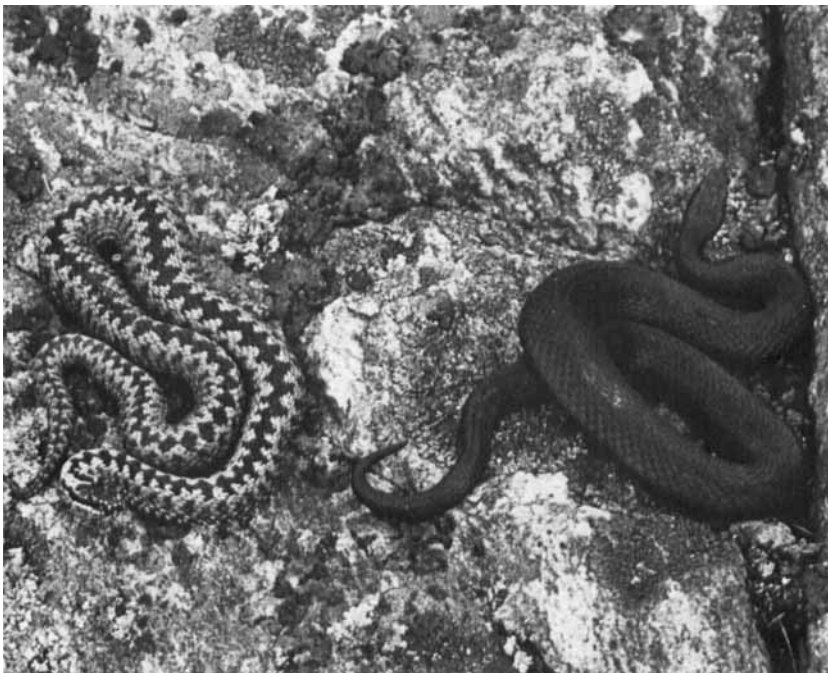


Figure 3. Normal 'cryptic' (left) and melanistic (right) male adders, *Vipera berus*, in their natural habitat on the island Hallands Väderö.

less spectacular and the difference in predation between the two colour morphs is then probably even more marked. Normal females are of duller coloration than males. This suggests that predation on black morph females is higher as well.

The experiment showed that predation is higher on models of black adders than on normal males in basking position. However, the black morph can probably reduce the necessary basking time to reach optimum body temperature, which should shorten the time of exposure to predators. Rapid heat accumulation should also give the black morph a higher motor and defence ability, which is most efficient at the optimal body temperature (Greenwald, 1974).

GENERAL DISCUSSION

Inheritance of melanism

In the eastern garter snake (*Thamnophis s. sirtalis*) melanism is determined by a single locus and expressed only in recessive homozygotes, in a simple mendelian fashion (Blanchard & Blanchard, 1940). There are no detectable genetic differences between melanistic and normal coloured populations from the same geographic area (Sattler & Guttman, 1976). This indicates that there is no reproductive isolation between the two colour morphs in garter snakes and that natural selection favours melanism under certain circumstances. Melanism is often local; beside garter snakes and adders, e.g. the timber rattle snake (*Crotalus horridus*) (Klauber, 1972) and the asp viper (*Vipera aspis*) (Naulleau, 1973) have isolated mixed populations in addition to completely normal ones. In local populations of the adder and the asp viper in France, the proportion of melanism is 55–56% (Naulleau, 1973) and the amount of melanism in mixed garter snake populations is about the same (Logier, 1929 1930; Blanchard & Blanchard, 1940). The frequency of melanism and the reason why it is not found in all populations has not been determined.

Reproductive success of the melanistic morph

Reproductive success increases with size in the adder. Melanistic snakes are thermoregulatorily superior (Gibson & Falls, 1979), with increased metabolic rate and probably higher growth rate as a consequence. Long and heavy males are favoured in combats, which increases their genetical representation in future generations; thus melanism should increase the reproductive success of surviving male adders.

In females, clutch size increases roughly with one juvenile for every 2 cm increase in body length (Nilson, in prep.). In the observed females 75% were melanistic; the heaviest ones were all melanistic (Fig. 2). Since melanism results in increased body size and larger clutch size, it should confer a reproductive advantage in females as well. In addition, higher body temperature in females due to black coloration shortens the time of predatory exposure and embryonic development, which results in a prolonged feeding period in the autumn. This might be of crucial importance for the female as well as for her progeny.

Our results show that melanism is influenced by negative selection from predation, which probably also acts generally against increased size in both sexes. For any given age, male adders are smaller than females (Volsøe, 1944). This is

unique in species with male sexual combats. It is generally believed that reproductive combats in snakes favours selection for larger males (Gibbons, 1972; Shine, 1978).

A normally coloured adder runs a lower risk of predation, but grows more slowly, whereas in a melanistic male the situation is reversed. The normally coloured male will probably have more opportunities to mate during his lifetime, but he will be less successful, whereas the melanistic male uses fewer expected mating opportunities more efficiently. The morph with the highest total reproductive output should depend on the strength of different selection pressures acting during their lifetime.

Maintenance of two different colour morphs in a population

The proportion of melanistic and normally coloured 'cryptic' adders on Hallands Väderö may be stable e.g. depending on frequency-dependent selection. The situation might also be a result of balanced polymorphism, where the black morph is maintained in the population because of superiority of the heterozygote (Ayala & Campbell, 1974).

A possible explanation of the observed ratio between the two adder morphs in our study area could be a frequency-dependent, apostatic, selection (Clarke, 1962) where a predator develops a search image for the most abundant morph. In this situation, natural selection favours individuals deviating from the normal. The island is situated along a major migration route for birds of prey and, in addition to permanent predators, the island is visited by many buzzards and harriers during spring and autumn which temporarily may increase predation on the adders. If migratory birds of prey are important predators, frequency-dependent predatory selection might be of importance as the proportion of black adders is much lower in areas where the predators spend most of their hunting time. However, in light of our results from the predation experiment, this hypothesis seems less likely since dark morphs were taken much more often than normal morphs. However, to reject this hypothesis, a long term study is necessary.

Frequency-dependent selection related to reproductive success might maintain the two morphs in a balanced state. The game theory models of Maynard Smith (1976) might apply to this situation. The reproductive advantage of black colour in males should decrease when its proportion in the population increases. The chance of a black male meeting another black male which is stronger in rivalry combats, increases with the abundance of melanism in the population. There may exist a mixed evolutionarily stable strategy (ESS), where a balance between the mating advantage and the predation disadvantage adjusts the proportion of black males to a certain level in the population. However, the problem remains why the proportion of the dark morph varies so strongly between populations.

Environmental instability allowing different selection pressures to act with fluctuating strength can probably not explain a balanced coexistence of two adder morphs. However, the normal morph may be favoured during periods with comparatively high predation pressure and suitable climate and slowly increase its proportion in the population. The melanistic morph, on the contrary, may be thermoregulatorily favoured during periods with unstable or colder climate. Low predation from visually searching predators during such periods strengthen the positive effect of melanism and make the cryptic coloration less effective.

To conclude, our result shows that the black morph probably has a reproductive advantage owing to larger size. On the other hand, it runs a higher risk of predation. More studies are needed to explain the proportions of the black morph in different populations.

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