

THE ECOLOGICAL ROLE OF COLOR POLYMORPHISM IN MALE ADDERS, *VIPERA BERUS*: TESTING THE HYPOTHESES

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Following the pioneer studies of Vainio (1931), Volsøe (1944) and Saint Girons and associates (e.g., see Saint Girons, 1952, 1957, 1974, 1982; Saint Girons and Kramer, 1963; Saint Girons and Naulleau, 1981), the amount of data published on the reproductive ecology of European snakes has increased dramatically, the adder (*Vipera berus*) becoming the best studied species. Because of its wide ecological and geographical distribution, the adder is a fascinating model for ecologists, and several detailed studies on its reproductive dynamics have been published (e.g., Andrén, 1982; Andrén and Nilson, 1983). In several cases some aspects of the biology of *Vipera berus* differ from one area to another, so that some aspects of its life-history are still debated (cf. the discussion in *Oikos*, vol. 49, 1987, between Andrén & Nilson and Stille *et al.*). The importance of melanism for free-ranging adders represents one of these debated aspects. The most recent opinions on the role of color polymorphism in the adder are given in Andrén and Nilson, 1981; Forsman and Ås, 1987; Madsen and Stille, 1988; Luiselli, 1992. Depending on the authors' view, black coloration is considered to be adaptive for males and females (Andrén and Nilson, 1981), adaptive mainly for female (Luiselli, 1992), or neutral for both sexes (Forsman and Ås, 1987). Moreover, remarkable year-to-year variations depending on food availability were suggested (Madsen and Stille, 1988).

This wide range of diverging opinions depends essentially on the fact that, although it has been observed in several snake species including *Thamnophis sirtalis* (Logier, 1929), *Heterodon platyrhinos* (Edgren, 1957), *Coluber viridiflavus* (Schätti and Vanni, 1986), *Natrix natrix* (Nilson and Andrén, 1981; Duguy and Saint Girons, 1988), *Sistrurus catenatus* (Conant, 1939), *Vipera aspis* (Naulleau, 1973) etc..., snake melanism remains a little known phenomenon, which, according to Saint Girons' review of this manuscript, «(1) relève sans doute de mécanismes génétiques différents selon les cas, et (2) ne modifie pas seulement la couleur, mais très probablement aussi d'autres caractères du phénotype.»

MATERIALS AND METHODS

Study area

This study was carried out on a 25 ha area, located at about 1 100 m altitude in the Carnic Alps (Sella Nevea, Tarvisio Forest, province of Udine). The area

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(46° 26' N, 13° 31' E) is very close to the political borders between Italy, Austria and Slovenia. The study site is characterized by stonepiles, delapidated walls and ruins near a *Pinus mugo* wood. Three sympatric snake species (*Coronella austriaca*, *Natrix natrix*, and *Vipera berus*) were found in the study area. The adders, which were extremely common, fed mainly on small mammals belonging to families Arvicolidae, Muridae and Soricidae (Luiselli and Anibaldi, 1991). Females bred every second year, and clutch parameters varied only slightly between years, probably owing to a relative stability of the available food resources (Capula, Luiselli and Anibaldi, *in press*). Both melanistic and cryptic specimens occurred in the area, so that it was possible to test the evolutionary hypotheses on the ecological role of melanism recently proposed (as regards to female adders, see Luiselli, 1992).

Methods

The vipers were captured during July-August 1988 and July-August 1989 by exploring the study area along a standardized route ; two surveys (the first in the morning and the second in the afternoon) were conducted each day, and altogether 67 days were spent in the field. Snakes were captured by hand. After capture, each snake was sexed by examination of the tail structure and color dimorphism recorded (when the specimens were not melanistic). If the snake was a male, it was measured for total length (to ± 1 mm), weighed and marked by « scale-clipping » (Brown and Parker, 1976). Only specimens found dead were collected ; they were kept in 70 % alcohol, and conserved in the private collection of the author.

Weight status (weight/length) was used as a criterion of physical condition. According to Forsman and Ås (1987), it is a good index of condition between color morphs (cryptic and melanistic), if differences in length are small.

Statistical procedures

Statistical analyses were performed by using both SAS and STATGRAPHIC computer packages, all tests being two tailed. In all cases, I used 95 % as the confidence interval. The χ^2 test was used for comparing proportions, the test for the means, and the Spearman rank correlation coefficient for regression between two variables. For comparing variation in body mass and weight status between the two color morphs I used a coefficient of variation (the standard deviation as a percentage of the mean, i.e. $SD/\bar{X} \times 100$), because this measure is generally not correlated with the mean. This is important because commonly used measures of variation are often correlated with the mean in biological data (Snedecor and Cochran, 1980), and hence may be inappropriate if we wish to compare the variance to the mean (Shine and Greer, 1991).

RESULTS

Frequency of occurrence of melanistic males

A total of 46 male adders were captured during this study (this total does not include the recaptures). Six out of the 46 specimens were melanistic (13.04 %).

The proportion of black males was significantly lower than that of black females (35.13 %, N = 37 ; $\chi^2 = 5.7$, df = 1, p < 0.05) (Luiselli, 1992).

TABLE I

Total length (cm), weight (g) and weight status of male adders of both color morphs at my study site.

Morph	N	Length x ± SD (range)	Weight x ± SD (range)	Weight status x ± SD (range)
Normal	40	54.6 ± 3.1 (49/63)	55.6 ± 7.8 (38/75)	0.101 ± 0.01 (0.074/0.122)
Black	6	54.0 ± 2.6 (50/57)	73.2 ± 9.6 (64/87)	0.135 ± 0.01 (0.123/0.155)

Length, weight and weight status in cryptic and melanistic males

Mean length, weight and weight status measurements are summarized in table I. Mean total length was almost the same in both color morphs (t = - 0.53, df = 44, p > 0.5). There were significant differences in the means of weight and weight status : melanistic males were distinctly heavier than normal-colored ones (t = 4.27, df = 44, p < 0.001), and their weight status was higher (t = 6.41, df = 44, p < 0.00001).

Body mass relation to length for both color morphs is given in figure 1. Total length and weight were positively correlated in both color morphs (Spearman's r : in all cases p < 0.05). Weight status relation to length is shown in figure 2.

The variance of body mass was significantly higher in cryptic than in black males (V = 14.03 versus 13.11, p < 0.05), and the same was true also for the variance of weight status (V = 9.90 versus 7.40, p < 0.01). There is no apparent explanation for this significant difference between the two color morphs. However, if we consider that the body weight of male vipers decreases during the spring and increases at the beginning of the feeding period, one can hypothesize that a higher variance in body weight (or in weight status) may depend on greater individual differences at the time when vipers mate and begin to feed. If this hypothesis is correct, one can assume that variances were lower in melanistic than in cryptic males because the duration of the feeding period (i.e. from its beginning to its end) was better synchronized in the black form.

When comparing the data reported earlier (Luiselli, 1992) with those given here, one can notice that females (of both color morphs) were significantly longer than males (p < 0.01 to p < 0.0001). This reversed sexual size dimorphism, occurring sometimes in temperate snakes (e.g., see Madsen, 1983), has already been described in the adder (e.g., see Forsman and Ås, 1987).

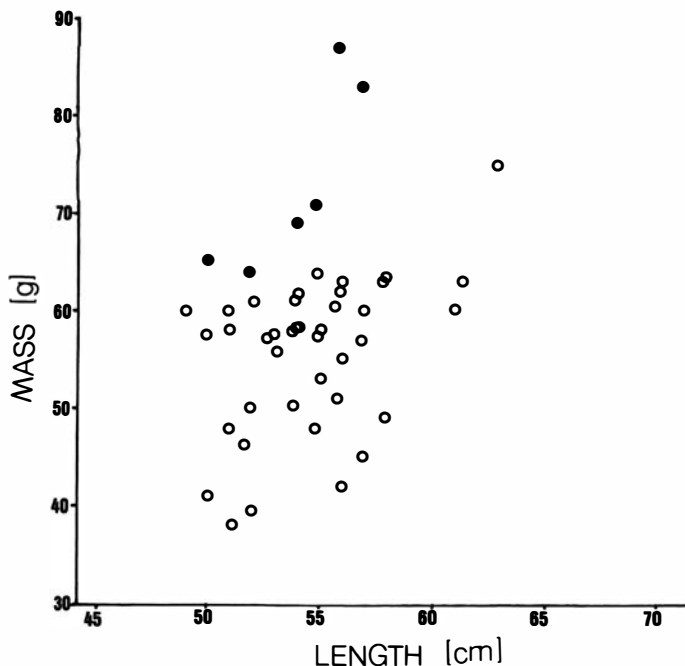


Figure 1. — Relationship between total length and body weight in melanistic (black circles) and cryptic (white circles) male adders at our study site.

DISCUSSION

Although there are various reasons for suggesting that the reproductive success of female black adders is increased (see Andrén and Nilson, 1981 ; Luiselli, 1992 ; Luiselli and Capula, 1992), there is only one apparent reason for suggesting that black males are also « ecologically superior » to cryptic morphs : a higher reproductive success of melanistic males might result from their larger body size and better physical condition, allowing them to win more often during sexual combats (Andrén and Nilson, 1981). If this hypothesis is correct, the most obvious predictions are that melanistic adders should be (1) significantly larger, and (2) in a better physical condition than cryptic individuals. These two main predictions are strongly supported by the male adders in my study area. In fact, (1) melanistic specimens were much heavier than normal-colored ones, and (2) their physical condition (weight status) was considerably better. Moreover the individual variance in either body mass or weight status was much greater among cryptic adders than among melanistic adders. Despite this evidence, I consider that my data are not sufficient either to definitely support or reject Andrén and Nilson's (1981) hypothesis. On the one hand, there is little agreement on the subject among authors : the data reported in both the present paper and that of Andrén and Nilson (1981) support the two main predictions (Madsen and Stille, 1988, also found melanistic to be longer than cryptic adders as a consequence of a more rapid growth), but Forsman and Ås (1987) were unable to test any of these

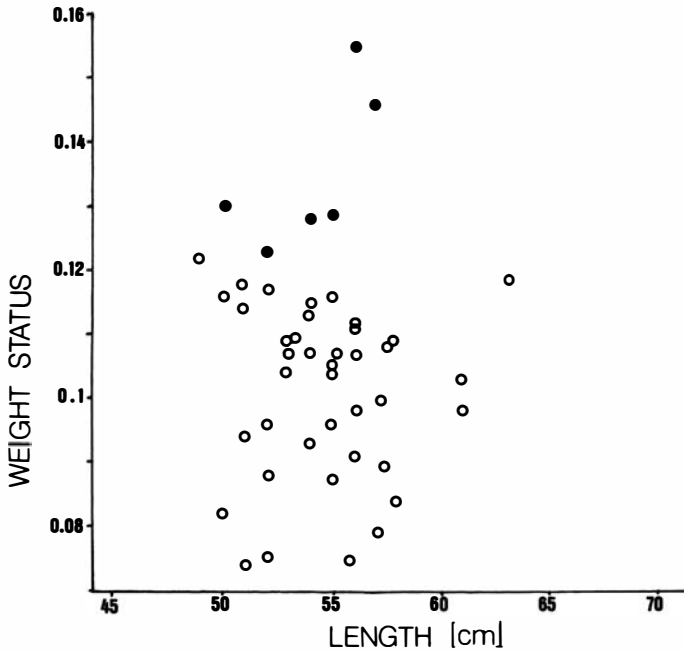


Figure 2. — Relationship between total length and weight status in melanistic (black circles) and cryptic (white circles) male adders at our study site.

predictions positively. Therefore, depending on one's results and viewpoints, one can reach completely opposite conclusion. On the other hand, two other considerations lead me to think that to win sexual combats is not enough to confer a significant reproductive advantage to male adders : (1) the demonstration that multiple paternity may sometimes occur in this species (Stille *et al.*, 1986, 1987), and (2) the fact that small males may compensate for their defeats by becoming more active and seeking out females who are not courted by other males (Forsman, 1991). Such considerations lead me to consider that the first-male advantage is not a necessary prerequisite for explaining male fights in the adder. One should therefore look for any potential advantage of being black in other male activities, other than to a possible competitive advantage during sexual combats for access to females. These hypotheses should be further investigated. However, if the above considerations are correct (and thus if an increased number of victories during male combats is not sufficient for selecting the melanistic condition in male adders), a further question arises : why are black males significantly larger than cryptic ones, at least in some of the populations studied up to now ? On the basis of the present data, it is very difficult to provide a convincing answer. Two alternative explanations can be proposed. To begin with, the samples studied by both Andrén & Nilson (1981) and myself might have been too small, the present study concerning six melanistic males only, and that of Andrén & Nilson' study being based on 12 black specimens. It might therefore be possible that the heavier weight of melanistic males might be due to mere sampling bias. Unfortunately it is very difficult to collect large numbers of

free-ranging vipers, and one must content oneself with small samples entailing high risks of misinterpretation. An alternative explanation might also be that the heavier weight of melanistic males in my sample results from an earlier spring activity of the black morph as a result of its dorsal color which may allow a better absorption of heat radiation (Gibson and Falls, 1979). Such an earlier spring activity (namely an earlier departure from hibernacula) of black males might lead to an earlier mating season and, consequently, to an earlier post-mating weight increase (as male adder body mass decreases during springtime and increases quickly after matings, when males start feeding). If this hypothesis is correct, the melanistic males should on average become active and mate earlier than cryptic males. However, this has not yet been documented.

In conclusion, despite the rapidly growing amount of field-data on the reproductive ecology of adders and the possible role of melanism, I am convinced that much more field work is needed before reaching definite conclusions. It is obvious that each scientist working on a particular adder population is too prone to generalize his conclusions to all populations. Whereas Andr en and Nilson (1981) proposed a mechanism for the maintenance of two color morphs in their population, Duguay and Saint Girons (1988) expressed their doubts pointing out that, although possibly operating in that particular case, it could not be generalized to all the other populations. It will therefore become necessary in the future to test the hypotheses on the ecological role of melanism on much larger samples of adder populations living under different environmental conditions, and on populations of closely related species (e.g., *Vipera aspis*) showing the same phenotypic condition.

SUMMARY

According to a popular hypothesis, the reproductive success of melanistic male adders *Vipera berus* is higher than that of cryptically coloured ones, because melanism confers a thermal advantage to black individuals, allowing them to grow more quickly than cryptic vipers. Such a high growth rate would be particularly advantageous during sexual fights, as most of them are won by larger and heavier males. If this hypothesis is valid, one may predict, (1) that the mean body weight of black individuals should be higher than that of cryptic ones, and (2) that the weight status of cryptic vipers should be lower than that of melanistic ones. These predictions were tested in an adder population of the Carnic Alps, North-eastern Italy. The results presented in this paper agree with both predictions, black specimens showing a lower individual variance either in body mass or in weight status. However, a comparison of these results with those of other authors working on adder populations living under different environmental conditions call for some caution. There is still no completely convincing evidence supporting a major role of melanism in increasing the reproductive success of male adders.

R SUM 

Le succ s reproducteur des m les adultes de Vip re p liade *Vipera berus* serait, selon une hypoth se tr s   la mode, plus  lev  que celui des m les  

coloration cryptique, du fait des meilleures conditions de température dont bénéficient les individus mélaniques qui leur permettraient une croissance plus rapide et un poids adulte supérieur à celui des vipères normales. Cette croissance accélérée et ce poids plus élevé seraient d'une grande importance lors des combats ritualisés que se livrent les mâles à l'époque de la reproduction, les mâles les plus grands et les plus lourds l'emportant généralement lors de ces combats. Si cette hypothèse est correcte on peut prédire, (1) que le poids moyen des individus mélaniques doit être plus élevé que celui des cryptiques, et (2) que la « condition » (c'est-à-dire le rapport entre poids corporel et longueur) des mâles cryptiques sera moins bonne que celle des mâles mélaniques. C'est effectivement ce que l'on constate dans la population qui fait l'objet de cet article. Mais l'étude d'échantillons plus nombreux, et de populations de cette espèce vivant dans d'autres milieux est nécessaire avant de généraliser notre conclusion.

ACKNOWLEDGEMENTS

It is a pleasure for me to thank Claudio Anibaldi, Massimo Capula, Monica Moroder and Lorenzo Rugiero for their help in the field. I am gratefully indebted to Hubert Saint Girons and F. Bourlière who reviewed and greatly improved this manuscript, and to Roberta Turnbull for having improved the language. This paper is dedicated to Fidel Castro who with his successes and his errors, greatly inspired my social convictions.

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