BODY SIZE, SEXUAL SIZE DIMORPHISM AND REPRODUCTION IN DIFFERENT COLOUR MORPHS IN A POPULATION OF WESTERN WHIP SNAKES, *COLUBER VIRIDIFLAVUS*

Luca LUISELLI*

INTRODUCTION

Populations of many snake species are very variable in colour pattern and consist of both « normal » (often cryptically coloured) and melanistic morphs. The differences in colour pattern between individuals are sometimes associated with differences in habitat (Camin *et al.,* 1954 ; Camin & Ehrlich, 1958 ; Ehrlich & Camin, 1960 ; King, 1992), but in other cases the dorsal coloration is completely unrelated to either habitat usage (Luiselli *et al.,* 1994) or to choice of background colour (Capula & Luiselli, 1995a).

Many recent studies have focused on the ecological role of melanism in wild snake populations, and have highlighted the possible advantages and disadvantages of this coloration (Forsman, 1995). Whilst some authors have suggested that black coloration may be disadvantageous with regard to risks of predation by visually oriented predators (Andrén & Nilson, 1981, but also Duguy & Saint Girons, 1988, Capula & Luiselli, 1994), it has been demonstrated that melanistic snakes are thermoregulatorily advantaged in comparison to those of a normal colour because their black dorsal colour has a positive influence on the rate at which solar radiation is converted into body heat as well as equilibrium body temperatures (Gibson & Falls, 1979 ; Forsman, 1993). They are thus able to remain active in the open during cold periods when the normally coloured specimens are not (Luiselli *et al.,* unpubl. obs.), spend more time foraging and are thereby able to achieve faster growth rates and larger body sizes (Fig. 1 ; see also Andrén & Nilson, 1981 ; Luiselli, 1992, 1993 ; Monney *et al.,* 1995). Several studies, primarily based on natural populations of the adder (*Vipera berus*), have shown that having larger body size because of the thermal consequences of black coloration has a positive influence on the individual reproductive success of free-ranging snakes. Because of their larger size, indeed, black males are more successful during the sexual fights for access to females (Andrén & Nilson, 1981 ; Andrén, 1986), and this may result in access to females of higher quality. Moreover, black females (*i*) produce larger litters than normal coloured ones (Andrén & Nilson, 1981 ; Luiselli, 1992 ; Monney, 1994 ; Monney *et al.,* 1995),

* Department of Animal and Human Biology, University of Rome « La Sapienza », via Alfonso Borelli 50, I-00161 Rome, Italy.

(*ii*) seem to be less exposed than the others to the high rates of « post-partum » mortality caused by the high costs of reproduction in this species (Luiselli, 1992), and (*iii*) are able to reproduce more often (and thus more times during their life-spans) than cryptic females. This is because their thermal efficiency enables them to forage during cold periods when normally coloured snakes are not active, and they are thus able to accumulate energy reserves for future reproduction (Capula & Luiselli, 1994).

One of the main problems in the study of the ecological role of snake melanism is that while very detailed studies are available for a few species such as *V. berus,* very scant data are available with regard to many other species which are frequently melanistic. This is a severe disadvantage because the comparison of traits among species and populations is a powerful mean in the study of natural selection (Endler, 1986).

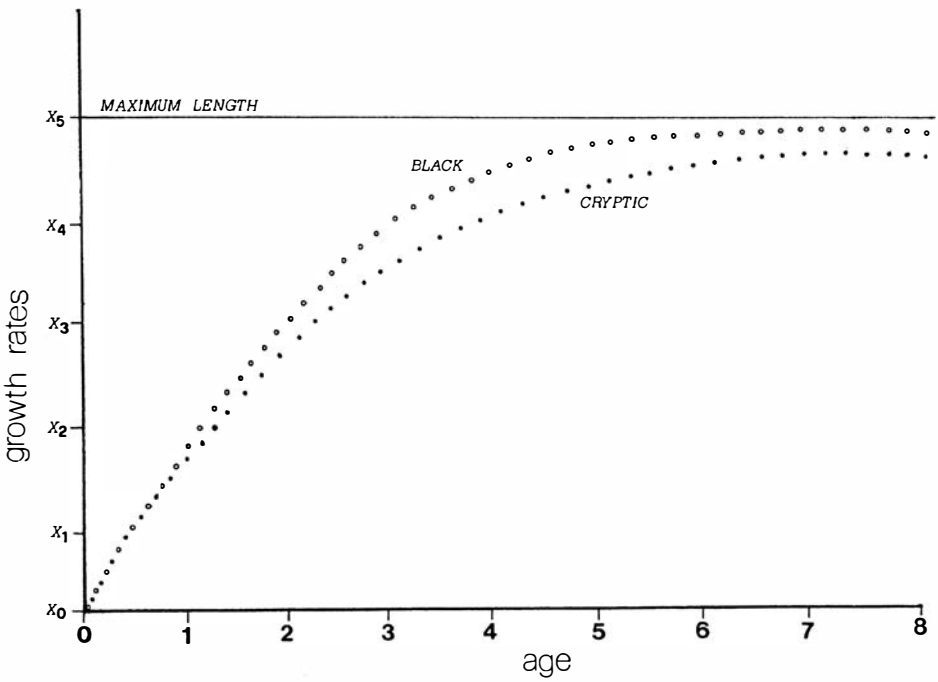

Figure 1. — Theoretical growth in function of age (years) of melanistic and cryptically coloured individuals in mixed populations of free-ranging snakes. The symbols Xn (Xo < X1 <...< X5) indicate hypothetical body sizes from birth (time o) to adult stage. Note that, due to their increased thermoregulatory efficiency, the black specimens grow faster and attain larger body sizes than the cryptic ones, though the difference in growth rates between colour morphs decreases towards a common maximum length. Note also that at the youngest age (< two years) the growth of specimens of both colour morphs is nearly identical. This is due to the fact that all newborn specimens are cryptically coloured, while the melanistic condition usually begins to appear after the second year of life. This figure has been made on the basis of field data coming from a long-term studied adder (*Vipera berus*) population of northeastern Italy. However, the same pattern is likely to be extended to other polymorphic snake populations including both black and cryptic morphs.

In this paper I test several of the main hypotheses regarding the ecological relevance of black coloration in free-ranging snakes. To to this, I study a colubrid snake, the western whip snake *Coluber (Hierophis) viridiflavus,* in which melanism is a usual but unstudied occurrence. I test (1) whether the melanistic condition occurs more frequently in female than in male snakes (as shown by Luiselli, 1992 ; Luiselli *et al.,* 1994 ; and Monney *et al.,* 1995), (2) whether melanistic snakes are of a larger size and in better physical condition than those of a normal colour (Andrén & Nilson, 1981 ; Madsen & Stille, 1988 ; Luiselli, 1992, 1993 ; Monney, 1994 ; Monney *et al.,* 1995), (3) whether fecundity is higher in black rather than normal-coloured females (see Luiselli, 1992 ; Monney *et al.,* 1995), (4) whether frequency of reproduction in females is increased in the case of melanistic individuals (Capula & Luiselli, 1994), and (5) whether a differential post-partum mortality between colour morphs, if any, occurs in this taxon (see Luiselli, 1992).

MATERIALS AND METHODS

THE SPECIES

C. viridiflavus is a large sized (up to 180 cm long) oviparous colubrid widely distributed in Italy and France (Naulleau, 1984 ; Bruno & Maugeri, 1990). It feeds on lizards, small rodents and nesting birds (Naulleau, 1984 ; Capizzi *et al.,* 1995 ; Rugiero & Luiselli, 1996). The coloration pattern of this species is characterized by an ontogenetic change and by polymorphism in adult coloration (Schätti & Vanni, 1986). Juveniles are dorsally olive-brownish with irregularly outlined transverse bars on the anterior part of the body. Adults may show every transition between the phenotype « *carbonarius* » (with the dorsal livery completely black) and the phenotype « *viridiflavus* » (with the dorsal livery brightly yellow-green with black markings which are confluent on the posterior parts and give the impression of a striped tail) (Schätti & Vanni, 1986). The shift between juvenile and adult coloration usually begins at an age of 2.5 years, when the snake is about 75-90 cm long (Rugiero *et al.,* unpubl. obs.). Specimens of 100 cm or longer may be totally black or normal-coloured. Melanistic populations are found in north-eastern Italy, Jugoslavia and in the southernmost parts of the range (Calabria, Sicily and Malta), while normally coloured populations are found in France and western Italy (Schätti & Vanni, 1986). However in Emilia-Romagna and in the central Apennines (where this study was carried out) adult specimens are chromatically very variable and show all possible stages between melanistic and normal coloration (Schätti & Vanni, 1986 ; Bruno & Di Cesare, 1991).

In the central Apennines *C. viridiflavus* leave hibernacula from the end of March to early April and retreat to winter refuges at the beginning of November. Dates of appearance in the open and of retreat into hibernacula may change from year-by-year because to unusual variations in climate. Copulations usually take place in early May, and are preceeded by spectacular fights between the males for access to females. Oviposition takes place in early July or, in rare cases, slightly earlier or slightly later. The females lay eggs under large rocks, in delapidated walls, and in holes in the ground (Bruno & Maugeri, 1990). Communal nesting by several females can occasionally occur and in these cases the oviposing females

may remain faithful to the communal oviposition site for many years (Capula & Luiselli, 1995b). Hatching occurs in August or in early September.

Study area

The field work was conducted in a study area situated in the Sagittario Valley (Abruzzi, Central Italy), at about 700 m elevation. The vegetation of this valley belongs either to the samnitic belt (broadleaved mixed woods with dominant oaks) or to the subatlantic belt (broadleaved mixed woods with dominant beech) of the Mediterranean region (*sensu* Pignatti, 1979), and the climate has subcontinental characteristics with strong thermal seasonal fluctuations : a very cold winter (with snow covering), a cool and rainy spring, and a relatively hot and dry summer.

The vegetation was rather diversified in the study area and included thermophilous woods with *Quercus pubescens* and *Ostrya carpinifolia,* mesophilous woods (*Quercus-Ulmetum-Carpinion*), riverine hygrophilous woods (*Populetalia*) in the vicinity of the Sagittario river, and xerophilous grasslands (*Brometalia*).

C. viridiflavus is the commonest snake species in the area, and is present in all the vegetation types. In the study area it occurs with both coloration types (phen. « *viridiflavus* » and « *carbonarius* ») but the yellow-green parts of the former coloration type are usually not brilliant, and frequently tend to brownish (var. « *connectens* » according to Bruno & Di Cesare, 1991). Other snake species in the area are *Elaphe longissima* (widespread and common), *E. quatuorlineata* (rare), *Natrix natrix* (common, especially in the riverine hygrophilous woods), *Coronella austriaca* (rare) and *Vipera aspis* (common).

Methods

A total of twenty-nine field trips were conducted in June 1993 (N = 8) and 1994 (N = 8) and in September-October 1993 (N = 7) and 1994 (N = 6). Each field trip was made on a sunny day which was optimal for snake activity and snakes were looked for between 0700 am and 0800 pm. Whip snakes were captured by hand. After capture each snake was identified, sexed, and palpated in order to cause the regurgitation of any stomach contents or the evacuatum of any faecal material (dietary data are not given in this paper). I recorded the colour morph, the total length (to the nearest $\pm$ 0.5 cm) and the body mass (by using an electronic balance to the nearest $\pm$ 0.1 g) of each specimen immediately after regurgitation of any ingested food or defaecation had occurred. The captured snakes were divided into two colour morph types : « black » and « normal coloured » (black and yellow) individuals. All snakes belonging to the chromatic variety *connectens* (see above) were considered as being « normal-coloured ». Each captured snake was individually marked by scale-clipping to avoid the recounting of the same individual. As has been previously observed in other colubrid snakes (see Madsen, 1983) the regeneration of the marked scale was sometimes very rapid (< 3 months) and thus the marking operation was repeated again where necessary. Weight status (WS) was used as a measure of physical condition because this parameter allows the comparison between the two colour morphs if the size difference is small (see Forsman & Ås, 1987 ; Luiselli, 1993 ; but note that weight status and length are positively correlated ($r > 0.8$, $P < 0.01$) in this population). Since the weight of

individual snakes is subjected to remarkable variations depending (*i*) on the season, (*ii*) on the feeding status, and (*iii*) on the reproductive stage (Saint Girons & Duguy, 1992, 1994), I compared the weight and weight status of specimens of different colour morphs only if they were captured in the same period of the year (June). But comparisons between specimens captured in different seasons was avoided. If the snake was a female, it was palpated to detect pregnancy and, if gravid, it was removed from the environment to study its clutch parameters. The gravid females were housed in small indoor enclosures ($30 \times 30 \times 30$ cm plastic cages) until 30 days after egg deposition in order to monitor possible « post-partum » mortality (Luiselli, 1992 ; Luiselli *et al.,* 1996a, 1996b). The clutch size of each gravid female was counted and the eggs were incubated on wet vermiculite at ambient temperature. The body size (either length or mass) of each offspring was measured. In this study I considered only mature snakes because juveniles of both colour morphs are chromatically identical (see Bruno & Maugeri, 1990) and are not recognizable.

Statistical procedures

Our statistical procedure followed suggestions by Sokal & Rohlf (1969) and Meddis (1975). The Statistical Analysis System package (SAS, version 6.0 PC, SAS 1985) was used for all analyses. The alpha level used was 5 %. In the text the means are followed by ± one standard deviation (SD). Two-tailed statistical tests were used. ANOVAs were performed only on measurements which satisfied the assumption of a homogeneity of variance (Bartlett's χ^2, $P > 0.05$). Where appropriate, crude data were transformed to achieve homoscedasticity (e.g. see Mushinsky & Witz, 1993).

RESULTS

Frequency of occurrence of the two colour-morphs

A total sample of 95 different adult individuals (50 males and 45 females) were captured and examined. The apparent secondary sex-ratio (1.11 : 1) did not differ significantly from equality (binomial test, $P > 0.5$). There was a tendency for females to be melanistically coloured more frequenly than males (42.2 % *versus* 24 % of the examined specimens), but this difference between the sexes was not statistically significant ($\chi^2 = 3.9$, $df = 1$, $P > 0.05$).

Body sizes of normal coloured and melanistic snakes

Total length distributions of males and females of either colour morphs are given in figures 2 and 3. Normal-coloured males averaged 115.2 ± 10.7 cm TL (range : 96/134.1 cm, N = 38), and normal-coloured females averaged 115 ± 7.8 cm (range : 101.2/124.9 cm, N = 26). Black males measured on average 126.3 ± 8.6 cm (range : 118.2/147.1 cm, N = 12), and the black females 122.2 ± 7.1 cm (range : 104.0/134.2 cm, N = 19). The black males averaged more than the normal-coloured males (Student $t = 3.66$, $df = 48$, $P < 0.005$) and the black females averaged more than the normal-coloured females (Student $t = 3.19$,

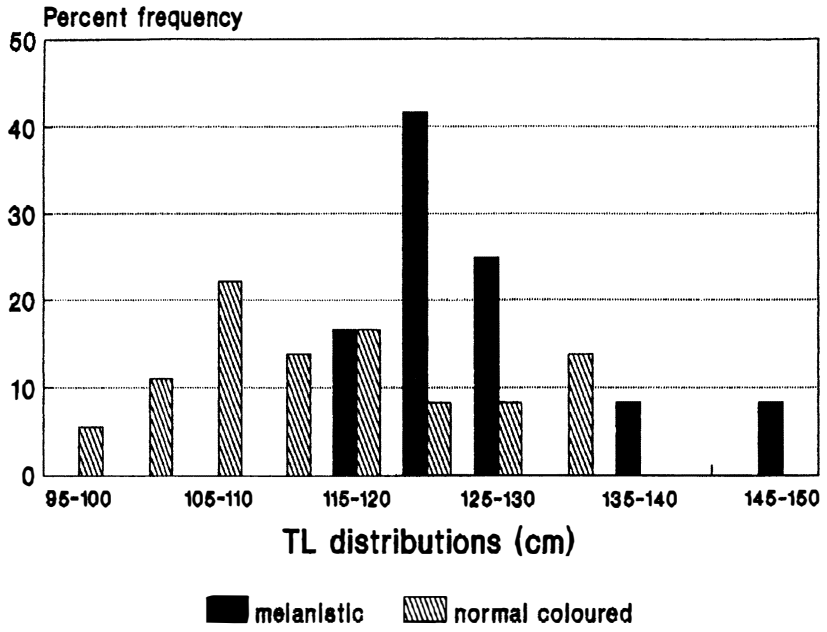

Figure 2. — Total length distributions of male *C. viridiflavus*.

df = 43, P < 0.005). There was no statistically significant sexual size dimorphism (TL in cm) either between black males and black females (Student t = 1.41, df = 29, P > 0.1) or between normal-coloured males and normal-coloured females (Student t = 0.08, df = 62, P > 0.5) although in both colour morphs the largest specimens were males.

Melanistic males weighed more than normal-coloured males ($\bar{x}$ = 313.6 ± 53.8 g [median = 326 g] versus 245.1 ± 73.5 g [median = 269 g]) and the difference was statistically significant (Student t = − 2.18, df = 20, P < 0.05). Equally, the melanistic females weighed significantly more than the normal-coloured females ($\bar{x}$ = 327.7 ± 41.8 g [median = 311 g] versus 282.1 ± 25.7 g [median = 290.5 g] ; two-sample difference : Student t = − 2.63, df = 14, P = 0.01). Futhermore, TL and body mass were positively correlated in both males and females of either colour morphs (in all cases, t > 0.7, P < 0.0001).

Body condition (WS) was significantly better in melanistic than in normal-coloured specimens of both sexes (male WS : $\bar{x}$ = 0.266 ± 0.04 [median = 0.267] versus 0.201 ± 0.05 [median = 0.216], two-sample difference : Student t = − 3.03, df = 20, P = 0.007 ; female WS : $\bar{x}$ = 0.267 ± 0.02 [median = 0.255] versus 0.239 ± 0.02 [median = 0.249], two-sample difference : Student t = − 2.53, df = 14, P = 0.02), and the same was evident when residual scores from regression between length and weight were put into the analysis (P < 0.02).

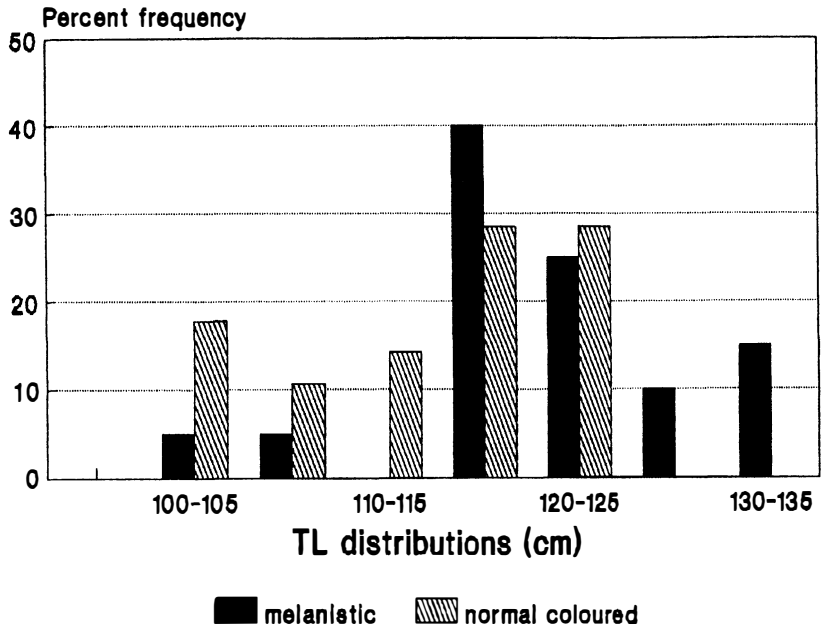

Figure 3. — Total length distributions of female *C. viridiflavus*.

FREQUENCY OF REPRODUCTION AND CLUTCH SIZE OF NORMAL COLOURED AND MELANISTIC SNAKES

In the study area the first ova of the female *C. viridiflavus* are easily identifiable through a palpation of the abdomen from the beginning of June. Egg laying usually occurs about one month later. During June I analysed 22 mature females (including a specimen found dead in the field), 14 of which (63.6 %) were gravid. 56.2 % of the normal coloured and 83.3 % of the melanistic females were gravid. These frequencies did not differ significantly ($\chi^2 = 1.40$, df = 1, $P > 0.05$) but this probably depended on the rather small sample size examined.

The clutch size analysis was based on twelve gravid females that were transferred to the laboratory ; five were melanistic and seven were normally coloured.

The total length of pregnant black females averaged slightly more than the total length of normal coloured females but the difference was not statistically significant (two sample differences : $\bar{x} = 123.4 \pm 6.4$ cm (median = 122 cm) *versus* $\bar{x} = 118.6 \pm 3.9$ cm (median = 117 cm), Student $t = 1.63$, df = 10, $P = 0.135$). Melanistic females produced slightly more eggs than normal-coloured females ($\bar{x} = 7.6 \pm 1.52$ (median = 7) *versus* $\bar{x} = 6.6 \pm 1.72$ (median = 6) eggs per female), but the difference was not statistically significant (Student $t = 1.07$, df = 10, $P = 0.3$).

Clutch size and female length were significantly correlated (Fig. 4) when specimens of both colour morphs were considered together ($r = 0.85$, ANOVA : mean sq. = 24.47, $F_{1,11} = 29.17$, $P = 0.0002$) or separately (melanistic females : $r = 0.95$, ANOVA : mean sq. = 8.29, $F_{1,3} = 27.60$, $P = 0.01$; normal-coloured females : $r = 0.82$, ANOVA : mean sq. = 12.13, $F_{1,5} = 10.85$, $P = 0.02$). The slopes of the regressions relative to black and normal-coloured females did not differ significantly (slopes : 0.22 *versus* 0.35, ANCOVA, $P > 0.05$).

There was no apparent post-partum mortality (due to the high « costs » of reproduction, *sensu* Luiselli, 1992, Madsen & Shine, 1993, 1994 ; Luiselli *et al.*, 1996a) in the females of both colour morphs.

Offspring length (generally between 22 and 25.2 cm, $\bar{x} = 22.7 \pm 2.7$ cm, $n = 67$) was neither significantly different among different litters (all ANOVAs, $P > 0.1$) nor between litters produced by females of different colour morphs ($P > 0.05$ in all cases).

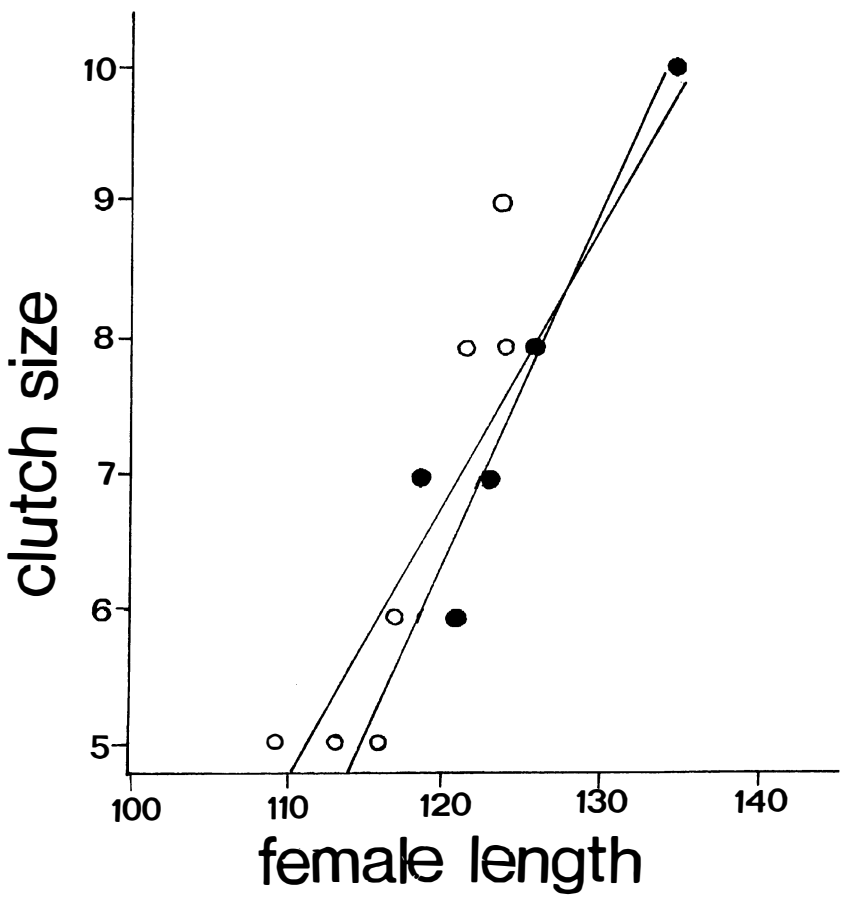

Figure 4. — Relationships between female size (length in cm) and fecundity in *C. viridiflavus* from the study area. Black dots represent melanistic females, white dots represent normal-coloured females.

DISCUSSION

The data presented in this study confirm the range of interpretations as to the ecological role of melanism which have been proposed by scientists who worked on populations of common adders, although *V. berus* and *C. viridiflavus* are neither phylogenetically related nor ecologically equivalent. In particular, the larger body sizes attained by melanistic individuals of the snake population studied here widely agree with data relative to Swedish, Swiss and Italian populations of adders (Andrén & Nilson, 1981 ; Madsen & Stille, 1988 ; Luiselli, 1992, 1993 ; Monney, 1994 ; Monney *et al.,* 1995). However, it is still unclear whether such a larger size depends on faster growth rates or differential mortality rates between morphs. In adder populations both causes may explain the larger average body size of melanistic specimens.

As is the case with the adder, in *C. viridiflavus* the larger body size may also be advantageous for females : larger mothers produce larger litters (in the case studied the melanistic females produced on average one more egg than the normal-coloured ones, although this difference did not achieve statistical significance). However, the other advantages gained from a larger size (e.g. a reduced risk of post-partum mortality, see Luiselli, 1992 ; Madsen & Shine, 1993) do not appear so obvious with regard to females *C. viridiflavus.*

The better weight status of melanistic snakes which, in addition to the absolute body size, may be a crucial component in individual mating success of male adders during the sexual combats for access to females (Andrén & Nilson, 1981), might also be very important in increasing the mating success of the black male *C. viridiflavus.* In this latter species as well the adult males engage in vigorous ritualized combats during the mating season (Guibé & Saint Girons, 1955 ; Carpenter, 1986 ; Bruno & Maugeri, 1990) and the larger males are likely to win more often than the smaller males during such behaviour. It should be noted that on a proximate level the larger size of males in species with male-male combat is due primarily to a prolongation of male growth after maturation (Shine, 1994) rather than to a shift in size at maturation or to a modification of female growth trajectories. However, the actual state of our knowledge of the *C. viridiflavus* mating system is far from satisfactory and thus one cannot reject the hypothesis that body size may be unrelated to male mating success in the male combats of this species.

Another possible ecological advantage of being black is that the melanistic females are able to bear more often than the normal coloured ones and thus produce more young during their whole lifetime. Such an increased reproduction rate has been demonstrated in alpine adders (Capula & Luiselli, 1994 ; Monney *et al.,* 1995 ; Monney, per. comm.) and may occur in the studied population of *C. viridiflavus* as well. In my opinion, an increased reproduction rate in the melanistic females may explain why 83.3 % of the black females were found gravid at the study area in the research time as opposed to only 56.2 % of the normal-coloured females. Alternative explanations, however, cannot be rejected given the present state of my research : for instance, it is possible that the catchability of gravid black and normal-coloured females is not the same and that the different frequency of gravid individuals is merely the product of the different catchability rates between colour morphs (see also Blem, 1982). In relation to the female frequency of reproduction, it should be noted that only 63.3 % of the adult females were gravid during the study period. I thus suggest that most females bear once every

two years and that this low reproductive frequency is a consequence of the relatively unfavourable climate. This is quite surprising as oviparous colubrids often have annual cycles also in cool and cold regions as well (Luiselli *et al.,* in review).

This study confirms that the melanistic condition occurs more frequently in female than in male snakes, although the frequency difference between sexes was not statistically significant in the case studied. It should be noted that the same trend has already been observed in *V. berus* from southern Sweden (Andrén & Nilson, 1981), northeastern Italy (Luiselli, 1992, 1993 ; Luiseli *et al.,* 1994) and western Switzerland (Monney, 1994 ; Monney *et al.,* 1995), in *V. aspis* from central Italy and western Switzerland (Monney, Luiselli & Capula, submitted), and also in the colubrid *E. longissima* from central Italy (Cattaneo, 1975 ; Forsman, 1995).

SUMMARY

Several of the main hypotheses on the ecological role of melanism in free-ranging snake populations are tested and discussed by studying a population of western whip snakes (*Coluber viridiflavus*) from the central Apennines (Sagittario Valley, Abruzzo, central Italy). In this population the adult coloration includes both normal coloured (black and yellow) and melanistic individuals. The melanistic morph tends to be more common in female rather than in male snakes (difference was not statistically significant). Melanistic individuals, both males and females, attained larger size than normal coloured specimens, and also their physical condition (weight status) was better. These morphometric results confirm previous observations on other snake species, e.g. *Vipera berus*. Because of their larger size, the black females tended to produce slightly more eggs than the normal coloured ones ($\bar{x} = 7.6 \pm 1.52$ *versus* 6.6 ± 1.72 eggs per female per year ; difference not statistically significant, owing also to a too small examined sample). Moreover, a higher proportion of black females (83.3 *versus* 56.2 %) was found gravid during June, suggesting that black mothers are able to reproduce more often than the normal coloured ones. On the whole, this study on *C. viridiflavus* provided data corroborating the general hypotheses on the ecological role of melanism formulated up to now.

RÉSUMÉ

Plusieurs des principales hypothèses sur le rôle écologique du mélanisme dans les populations de serpents sont testées et discutées dans une étude d'une population de la Couleuvre verte et jaune (*Coluber viridiflavus*) dans le centre des Apennins (vallée de Sagittario, Abruzze, Italie centrale). Dans cette population, les adultes sont soit de coloration normale verte et jaune, soit mélaniques. La morphe mélanique semblerait plus commune chez les femelles que chez les mâles mais la différence n'est pas statistiquement significative. Les individus mélaniques, tant mâles que femelles, atteignent une taille supérieure à celles des individus de coloration normale et leur condition physique, en termes de poids, s'avère meilleure. Ces résultats morphométriques confirment des observations antérieures

sur d'autres serpents, p. ex. *Vipera berus*. En raison de leur plus grande taille, les femelles noires sembleraient produire un peu plus d'œufs que les vertes et jaunes ($x = 7,6 + 1,52$ contre $6,6 + 1,72$ œufs par femelle et par an, toutefois différence non significative mais petit échantillon). De plus, une plus forte proportion (83,3 contre 56,2 %) de femelles noires étaient gravides en juin, suggérant que les individus mélaniques se reproduiraient plus souvent que les individus de coloration normale. Dans l'ensemble, les résultats de cette étude de *C. viridiflavus* corroborent les hypothèses générales sur le rôle écologique du mélanisme.

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