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Sexual Dichromatism in Snakes of the Genus *Vipera*: A Review and a New Evolutionary Hypothesis

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The sexes differ in color in many species of snakes, but these differences are generally subtle and their selective advantage (if any) remains obscure (Shine, 1993a). One phylogenetic lineage in which dichromatism occurs, and in which the degree of dichromatism varies among closely-related taxa, is in the Old World viperid snakes of the genus *Vipera*. These snakes are well-suited to an analysis of the adaptive significance of dichromatism because they are relatively well-known ecologically. In particular, the most strongly dichromatic species, *V. berus*, is arguably the

most intensively-studied species of snake in the world, and many populations of this species contain colour morphs (especially, melanistic individuals) that lack sexual dichromatism (e.g., Andren and Nilson, 1981; Madsen and Stille, 1988). In the present paper, we (i) review the distribution and evolution of dichromatism in *Vipera*, and (ii) evaluate a series of alternative adaptationist explanations for the sexual dichromatism.

Species of *Vipera* occur over a wide area of Europe and the Middle East, in habitats ranging from alpine meadows to deserts, and vary in mean adult body size from the diminutive *V. ursinii* (<50 cm) to the large *V. lebetina* (>150 cm). Females grow to larger body sizes than conspecific males in some taxa (e.g., *V. ursinii*, *V. berus*) but the reverse is true in others (e.g., *V. aspis*, *V. lebetina*; Steward, 1971). Although coloration varies among species, among populations, and among morphs within species (e.g., Nilson and Andren, 1986; Jøger et al., 1992), the most common pattern is a brown or grey background color with a series of cephalic lines running posteriorly into dorsal "zigzag" markings. In dichromatic taxa, females are generally duller in overall color and apparently well-camouflaged in the natural habitat. Males tend to be brighter-colored, especially after they slough their skins, and their dorsal zigzag lines (usually black, compared to brown in females) stand out more clearly against the background body color. For example, female *V. berus* are generally brownish overall with darker brown zigzag markings, whereas conspecific males are almost white with black zigzags during the mating season (Viitanen, 1967; Prestt, 1971). This bright coloration is evident as soon as males slough, before they commence mate-searching behavior (Madsen et al., 1992). Female *V. ammodytes* are grey-brown or reddish-brown with indistinct brown zigzags, whereas males are light grey with black-edged dark grey zigzag markings (Steward, 1971). Sexual dichromatism is less obvious in *seoanei*, and virtually absent in the *kaznakovi* complex (including *dinnicki* and *darevskii*), *ursinii* and *aspis* (Saint Girons, 1978; G. Nilson, pers. comm.). Although at least slight dichromatism probably occurs in all viviparous *Vipera* species, the oviparous *Vipera* (the *lebetina* group) lack dichromatism (G. Nilson, pers. comm.). Two other forms of dichromatism have also been reported in snakes of the genus *Vipera*: (i) in *V. xanthina*, ventral scales tend to be greyish in males, but yellow with dark marbling in females (Steward, 1971); and (ii) the frequencies of different color morphs may also differ between the sexes (e.g., Street, 1979; Andren and Nilson, 1981; Madsen and Shine, 1992a). However, the differences in this respect are generally minor, and no clear pattern is apparent. Thus, we will not consider these kinds of dichromatism in the following discussion.

Color differences between male and female vipers are often subtle, especially outside of the breeding season, and in some cases authorities disagree on whether or not a species is dichromatic (e.g. *V. aspis*; Noble, 1937 versus Steward, 1971). Some of these disagreements might reflect the time of year at which samples are taken (male colors are more intense during the breeding season) or the particular population

sampled. Geographic variation in the degree of dichromatism has been reported in some species. For example, dichromatism appears to be more extreme in some subspecies than in others within the species *V. ammodytes* (G. Nilson, pers. comm.), *V. ursinii* (Steward, 1971) and *V. berus* (Street, 1979). In some cases, the situation can be very complex. For example, northern specimens of *V. xanthina* tend to be darker than are specimens from more southern populations, and this trend is more pronounced in females than in males; thus, dichromatism is more evident in northern areas whereas snakes of both sexes from southern areas tend to be lighter in color (Nilson and Andren, 1986).

Phylogenetic hypotheses for *Vipera* suggest that the degree of sexual dichromatism is phylogenetically labile. For example, the two most strongly dichromatic taxa (*V. ammodytes* and *V. berus*) are only distantly related, whereas the nondichromatic *V. ursinii* is the sister-taxon to the highly dichromatic *V. berus* (e.g., Herrmann et al., 1992). Thus, the dichromatism seen within this lineage cannot be dismissed as being due to phylogenetic conservatism (retention of ancestral features). A molecular phylogeny for the viperine snakes indicates that the outgroups (*Cerastes* and *Echis*) and basal taxa in the ingroup (*lebetina*, *xanthina*, *ursinii*) are essentially nondichromatic (fig. 2 of Herrmann et al., 1992). This phylogenetic hypothesis suggests that dichromatism has evolved independently at least twice: once in *berus* and once in the *ammodytes* group. Alternatively, dichromatism may have evolved only once (basal to the *berus*-*ammodytes*-*aspis* clade) and subsequently been lost twice (in *aspis* and the *dinnicki*-*kaznakovi* lineage). Two lines of evidence indicate that it is the coloration of adult males rather than adult females that has become modified through viperine phylogeny: (i) females in dichromatic *Vipera* species resemble both sexes of related nondichromatic viperine species in color, and (ii) bright male colors in dichromatic taxa are restricted to the mating season. Thus, we proceed to consider adaptationist hypotheses for the evolution of bright colors in reproductive male viperines.

Evolutionary theory suggests two processes—sexual selection and/or natural selection—that could confer a selective advantage to bright coloration in male *Vipera*. In turn, sexual selection is divisible into two main forms, intrasexual and intersexual. Bright nuptial colors in several species of male lizards are clearly attributable to intrasexual selection: for example, the "green badge" of reproductive male sand lizards (*Lacerta agilis*) serves as a signal of a male's fighting ability, and is used by other males to evaluate the probable outcome of a combat bout (Olsson, 1992). Male *Vipera* of several species (probably, all species) do show male-male combat (review in Shine, 1993b), but field studies provide no indication of color assessment by rival males prior to combat, or any increment in combat success due to bright colors. The most detailed data in this respect come from comparisons of male adders of two color morphs in a small population at Smygehuk in extreme southern Sweden (Madsen and Shine, 1992a). Although "blue" males are duller in color than "normal" males, they show no decrease in reproductive success (Madsen and

Shine, 1992a). Success in combat appears to depend almost entirely on a male's body size, with color being irrelevant in this respect (Andren and Nilson, 1981; Madsen and Shine, 1992a). These data thus suggest that intrasexual selection is not responsible for the dichromatism observed in *V. berus*.

Intersexual selection might also favor dichromatism, if receptive females actively select more brightly-colored males. Female preferences may well have been responsible for the evolution of bright male colors in many types of animals (e.g., Krebs and Davies, 1991), but seem unlikely to be important in snakes. Color discrimination has not been shown in these animals, and our studies at Smygehuk show that the dull "blue" males are more successful than similar-sized "normal" males (Madsen and Shine, 1992a). Indeed, "blue" males can actually induce mating (female receptivity) after briefer courtship than can "normal" males (Madsen and Shine, 1992a). Comparisons of "normal" and melanistic males have also failed to reveal any advantage to the more brightly-colored morph (Andren and Nilson, 1981). In combination, these data suggest that dichromatism in *Vipera* cannot be attributed to sexual selection. We also note that mating systems appear to be phylogenetically conservative within *Vipera* so that the high degree of interspecific and intraspecific variation in the degree of dichromatism observed in this group would not be expected of a sexually selected trait.

Could viperine dichromatism evolve via natural selection rather than sexual selection? At first sight this possibility seems unlikely, because the only selective forces that would favor the dichromatism would involve ecological differences between males and females. Dietary analyses show no consistent differences in prey types taken by male and female adders (Prestt, 1971): indeed, males do not even feed during the mating season, when the dichromatism is most intense (Madsen and Shine, 1993). Thermoregulatory differences between males and females are also likely to be minor at this time of year, and studies on garter snakes suggest that dorsal reflectances (and thus, heating rates) will differ only slightly between the sexes (Gibson and Falls, 1979). However, male and female adders do differ substantially in movement patterns during the mating season. Males move large distances in search of receptive females, often across relatively open habitats, whereas females are highly sedentary and tend to remain in more sheltered areas (e.g., Viitanen, 1967; Prestt, 1971; Andren, 1985, 1986; Madsen and Shine, 1992b). Moving adders are more vulnerable to predators (especially, birds) than are stationary adders (Andren, 1985; Madsen and Shine, 1993).

Is there any plausible reason why bright colors might enhance a moving snake's ability to evade predators? Superficially, it seems as though bright coloration would be a particularly great *disadvantage* to a reproductive male adder: at least to a human observer, males are very obvious during the mating season (Andren, 1985; pers. obs.). Nonetheless, snakes of many species have evolved brightly-banded patterns that apparently function to confuse visually-hunting predators by inducing "flicker-fusion." This phenomenon occurs when the images of the bands move across the predator's eyes at such a speed that

it becomes difficult to focus on the moving object or to assess its velocity or direction of movement (Jackson et al., 1976; Shine, 1980). In the course of our fieldwork on adders, we noticed the same effect with fast-moving male snakes. The black zigzag marks stand out against the pale background color, and function like bands as the snake moves rapidly. The end result is a blur in which the snake's exact position is difficult to ascertain. If natural predators experience the same phenomenon, the bright contrasting colors of male adders may actually enhance the snakes' survival as they move about rapidly in search of mates.

The "flicker-fusion" hypothesis is consistent with the fact that the bright colors are shown only by adult males, and only during the mating season. Mate-searching males have been reported to show very extensive movements in several studies of adders (e.g., Viitanen, 1967; Andren, 1985, 1986; Madsen et al., 1993). Juveniles, adult females, and non-reproductive male snakes all adopt more sombre hues, and our observations at Smygehuk suggest that these animals are relatively sedentary and hence rely on camouflage rather than predator deception (e.g., Madsen and Shine, 1992b). The seasonal timing of male sloughing relative to mating activity may also be important in the evolution of dichromatism. If mating follows sloughing (as in *V. berus* and the dichromatic montane populations of *V. ammodytes*; G. Nilson, pers. comm.), males will tend to be brighter than females even without any adaptive modifications of male color. Thus, there will be abundant color variation upon which natural selection can operate, and the evolution of dichromatism may be facilitated. We predict that the extent of color variation among males will be lower in taxa (such as *V. aspis*) in which mating is not linked to male sloughing (Saint Girons, 1957).

Although the "flicker-fusion" hypothesis thus offers a plausible explanation for the adaptive significance of sexual dichromatism in *Vipera berus*, the hypothesis is a difficult one to test. Experimental manipulation of male colors, with monitoring of survival rates, would be the best technique for such a test but imposes major logistical difficulties. Plasticine models of different colors have proven useful in testing similar hypotheses (Andren and Nilson, 1981; Andren, 1985; Olsson, 1992), but are inapplicable in the present case because our hypothesis relies on movement by the snakes. Comparative behavioral studies on supposedly non-dichromatic populations of *V. berus*, or on other *Vipera* species with both dichromatic and non-dichromatic subspecies would be useful also. *Vipera ammodytes* looks to be particularly interesting in this respect, because it shows geographic variation both in the degree of dichromatism, and in the seasonal timing of its mating activity (G. Nilson, pers. comm.). We predict that populations with differing degrees of dichromatism will differ also in the degree to which mate-searching males experience mortality due to visually-hunting predators.

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