METACHROSIS IN SNAKES [1]

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Little seems to be known about metachrosis in snakes; indeed, its very existence in this group has sometimes been denied. The pertinent literature is scanty and contradictory. Schmidt and Davis (1941) declared, "Snakes are unable to change color as many lizards can." However, Klauber (1931) had previously mentioned that the sidewinder, *Crotalus cerastes*, and the Pacific rattlesnake, *C. viridis oreganus*, were capable of changing color. Klauber (1939) had also stated, ". . . snakes . . . have little or no power of color change; in fact, there are those who say that no snake has any such power, although I am certain that it is evident to a slight degree in some species of *Crotalus*." Kauffeld (1943) denied the contentions of Klauber, suggesting that the latter had observed only a slow and progressive lightening of color in captive specimens. Klauber (1944) subsequently remarked, "There seems little doubt that the colors of live sidewinders are somewhat affected by temperature in the manner so much more evident in lizards." Neill (1951) described relatively rapid and marked color change in a sidewinder, thus verifying Klauber's findings.

Rahn (1941), in a study of the prairie rattlesnake, *Crotalus v. viridis*, found that a dark pattern, superimposed on a yellowish-white background, was produced by three types of melanophores, all of which could disperse or concentrate their melanin pigment. Such dispersion or concentration was dependent upon the presence or absence of the pars intermedia hormone of the pituitary gland, and when this organ was removed, the reptiles permanently assumed a cream color as the result of complete pigment concentration in the melanophores. In a later study of the prairie rattlesnake, Rahn (1942) reported that exposure to high temperatures produced a light coloration just as did hypophysectomy, and that low temperatures resulted in considerable darkening through melanin dispersion. Although Rahn did not so comment, his experimental temperatures were no higher or lower than those apt to be encountered by snakes in nature.

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In spite of the papers cited above, Werler and Smith (1952) stated, ". . . color change in lizards may be a response to . . . light, heat, excitement or death, but there is no information to indicate that the same factors will elicit a similar response in snakes." Werler and Smith then noted that the light bands of a captive cat-eyed snake, *Leptodeira mystacina,* became lighter and "opaque" during the night, and that a somewhat similar change had been observed by Robert Snedigar in captive reticulated pythons, *Python reticulatus.*

In the present paper we wish to emphasize that some snakes can and do change color under natural conditions, apparently as a result of temperature fluctuations.

At the Reptile Institute, eastern diamondback rattlesnakes, *Crotalus adamanteus,* are kept in an outside enclosure. This pen is roofed over to shield the reptiles from the hot summer sun, and is surrounded by a moat of running water to prevent them from freezing during the colder days of winter; but otherwise the captive rattlesnakes are exposed to local temperature conditions. Usually there is a good bit of individual color variation among these snakes (which are from widely scattered localities). The ground color may be whitish in one specimen, yellow in another, olive in a third; and the dark pattern may be much more intense in some examples than in others. Should the weather turn cold, however, overnight all the rattlesnakes become very dark, and no individual color variation is evident early the following morning.

Frequently, on cold mornings, several diamondbacks chance to be coiled in a shaft of direct sunlight, and these specimens will be noticeably lighter than those still resting in the shade. The lighter coloration of the basking individuals is definitely not an optical illusion produced by variation in illumination.

On one occasion a large number of western diamondback rattlesnakes, *Crotalus atrox,* were collected in Webb County, Texas. Some of the specimens were unusually colored, displaying a silvery-white or a golden-yellow ground color. After overnight exposure to low temperatures, however, all the snakes had become relatively dark, and no individual color differences could be detected.

These observations were casual ones, and there was an obvious need for experimentation under controlled laboratory conditions. Accordingly, studies were made of metachrosis in a captive adult sidewinder, *Crotalus cerastes laterorepens.* Thirteen areas of the snake's body were examined and their color noted. These areas were as follows: (1) right postorbital stripe midway of its length, scale tip; (2) right postorbital stripe midway of its length, scale base; (3) last dark tail ring at dorsal midline; (4) light tail ring preceding last dark one, at dorsal midline; (5) first dark tail blotch posterior to level of vent, at midline; (6) center of third blotch on body, at midline (all body blotches counted forward from the level of the vent); (7) posterior dark border of third blotch on body, at midline; (8) ground color of dorsum between the third and fourth dorsal blotches; (9) proximal lobe of rattle-matrix; (10) ground color of side at a level midway between the ninth and tenth dorsal blotches; (11) side of snout midway between gape and postocular dark stripe; (12) small spot in parietal region, one of many such spots on the head; (13) midline of venter, near midbody. For convenience these areas will be referred to hereafter by number. Parenthesized color names and notations are from Maerz and Paul (1950).

With the snake's cloacal temperature at 31° C., the various areas of the body were colored as follows: (1) yellowish-cream (9 G 2); (2) medium brown (14 D 11); (3) black; (4) whitish; (5) light brownish (12 D 7, bran); (6) light brownish (12 D 7, bran); (7) inconspicuously gray- and black-stippled; (8) light flesh color (a little lighter than 9 B 2, polar bear); (9) black; (10) tannish-beige (11 B 3, champagne) with faint gray stippling; (11) very light flesh color (a little lighter than 11 A 2, flesh); (12) light brownish (12 E 8); (13) white. The color notations were made indoors at a window, under direct sunlight on a winter morning.

The snake's temperature, as determined cloacally by a mercury thermometer, was then lowered. This was accomplished by placing the snake, cage and all, out of doors in fairly bright but not direct sunlight, and allowing it to remain there for four hours. At the end of this time the snake's cloacal temperature was approximately 8° C. Color notations were then made out of doors in direct sunlight. Several areas of the reptile's body had altered in appearance. (1) had become duller yellow (11 G 3); (2) was a darker brown (15 E 11, new bronze); (4) had a faint buffy cast (a little lighter than 12 A 2, moonmist); (6) seemed a slightly duller brown (13 D 6, cracker); (7) had become more intensely stippled with dark gray and black; (8) had darkened slightly (11 B 2, putty); (10) was more conspicuously stippled; (11) had become so heavily gray-stippled as to obscure most of the previously recorded color; (12) had not perceptibly altered, yet appeared much less distinct owing to a slight darkening of the ground color of the head.

The snake was then brought into a heated room and allowed to remain there, in direct sunlight near a window, for two hours. At the end of this time its cloacal temperature was about 35° C. Color notations were made in direct sunlight. Several areas of the body had lightened. (2) had become a somewhat lighter brown than ever (13 D 7, oakbuff); (4) was again whitish; (5) was light brownish (12 B 5, fallow); (6) was light brownish (12 B 4, Long Beach); (7) again showed but inconspicuous stippling; (8) had returned to light flesh color (a little lighter than 9 B 2, polar bear); (10) was but faintly stippled; (12) was again in sharp contrast with the head. However, (1) was slow to lighten, and (11) remained for a time rather heavily stippled. Throughout the experiment, areas (3), (5), (9), and (13) were not observed to alter in coloration.

It is not contended that all of the apparent color changes were significant. The precise matching of colors may be hampered by several factors, particularly by diversity of surface textures. It is especially difficult to compare small areas of a living reptile with the plates of a color chart and achieve absolutely accurate results. The same color might conceivably be recorded as, say, (11 B 4) on one occasion and (11 D 3) on another, the apparent difference arising from variation in the environment or in the observer rather than in the color itself. Nevertheless, some of the recorded color changes in this case were too great to be explained away in any such fashion.

Metachrosis in the present specimen might be summarized as follows: At the beginning of the experiment, under a warm temperature, the scales of the postorbital stripe were brownish except for yellowish tips. Upon exposure to cold, the brown became darker through the development of a minute but dense stippling, and the brown areas encroached upon the yellowish scale tips which themselves seemed to darken. The brownish dorsal body blotches were edged with a grayish-black stippling which intensified when the reptile was chilled; and the actual blotches appeared to darken slightly. At warmer temperatures, the side of the snout, between the postorbital stripe and the gape, appeared almost white on gross inspection; faint grayish stippling was present but evident only on close examination. Under the influence of cold, the stippling intensified to a marked degree. The lateral ground color of the body also became more heavily stippled at lower temperatures. The whitish interspaces between the dorsal blotches seemed to darken slightly in the cold-induced phase, but they did not darken as markedly as did the areas bordering them. Consequently, the interspaces stood out rather sharply, like a row of small, light spots, when the snake was cold, and were much less conspicuous when it was warm. The brownish spots of the head did not alter with temperature, but in the cold-induced phase they contrasted less strongly with the ground color of the head. The whitish tail rings seemed to darken very slightly under the influence of cold. No one area of the body changed color to a really pronounced degree, but the small changes of value were sufficient to alter the snake's general appearance considerably.

A color sensation is generally considered to have three attributes, sometimes called hue, value, and saturation. In the sidewinder, value was the only one of these attributes to vary with temperature. In other words, the observed metachrosis involved only a darkening or a lightening, presumably resulting solely from expansion or contraction of melanophores.

Metachrosis in the above-mentioned specimen was far less pronounced than in the one previously reported on by Neill (*op. cit.*). However, the former was a *Crotalus cerastes laterorepens* with a dull buffy ground color and dull brownish blotches, while the latter was a very light *C. c. cerastes* with shades of cream, orange, and pink in the pattern. Expansion of melanophores would probably be more impressive, visually, in very light specimens.

Habits, habitat, and temperature tolerances of *Crotalus cerastes* have been discussed by Cowles and Bogert (1944) and by Klauber (1939). Sidewinders are inhabitants of certain western desert areas. In portions of the species' range, summer air temperatures may rise to 55° C., while winter nights may be freezing. During a 24-hour period the temperature may vary as much as 30° C. Although primarily nocturnal, sidewinders are sometimes found abroad in daylight, particularly during eary spring and late fall, or in the early morning hours. They are occasionally active in quite cold weather, and have been noted on desert roads at night when the cold wind was so strong as literally to sweep them across the smooth highway. Their spring season of activity is as early as that of any snake found within their desert range, and they are among the last snakes to go into hibernation in the fall. On the other hand, they are occasionally found coiled and fully exposed to the midsummer sun. Nevertheless, under captive conditions approximating those of their normal habitats, sidewinders were noteworthy for their ability to maintain a constant body temperature within the narrow limits of 31-32° C. From these observations, it might be suspected that metachrosis in the sidewinder is of considerable importance as a thermoregulatory mechanism, permitting longer periods of activity both daily and seasonally.

Klauber (1939) stated that sidewinders tend to match the hues of the sand on which they dwell. This circumstance may have arisen through natural selection; but conceivably, metachrosis might be involved. Clearly there is a need for intensive field study of this interesting reptile.

Rahn (1941) found that hypophysectomy, and concomitant concentration of melanin in the melanophores, resulted in paling, not only in the prairie rattlesnake, but in two species of garter snakes, genus *Thamnophis;* in the bull snake, *Pituophis melanoleucus sayi;* and in the Florida banded water snake, *Natrix sipedon pictiventris.* In all these reptiles, the pigmentary effects of hypophysectomy could then be largely neutralized by the injection of intermedin. Evidently, in various colubrid snakes as well as *Crotalus,* there is a pituitary regulation of melanophores; and one might suspect that this physiological mechanism is not completely useless to the species involved, even though its precise function is not known at present.

Although there are few published accounts of metachrosis in snakes, several herpetologists have witnessed this phenomenon and have kindly permitted us to mention their observations. Among colubrids, the glossy snake, *Arizona elegans,* is capable of changing color. This fact was brought to our attention by Charles M. Bogert. Dr. Bogert stated that specimens collected by him darkened considerably overnight, probably as a result of the lowered temperatures that prevailed after sunset. Cowles and Bogert (*op. cit.*) found that the glossy snake was exposed in nature to wide fluctuations of temperature; and, like the sidewinder, seemed markedly tolerant of cold. Howard Campbell stated that a juvenile Great Plains rat snake, *Elaphe guttata emoryi,* collected by him in a desert situation of Mexico, seemed capable of metachrosis; at times it appeared reddish, at other times dull brownish. L. Neil Bell informed us that the eastern hog-nose snake, *Heterodon platyrhinos,* had been observed to darken under the influence of cold.

William E. Duellman called our attention to metachrosis in a Mexican boa, *Constrictor constrictor imperator,* which darkened most noticeably when chilled. This boa was in the possession of Arthur E. Damman, who generously permitted us to keep it for several days, and to observe the way its coloration varied with temperature. The snake was a very light example of its kind, at least at summer room temperatures, being marked with shades of pinkish and fawn; this circumstance may explain why its metachrosis was so impressive visually. Most Mexican boas are dark, being patterned with blackish, chestnut, and wood brown. Metachrosis in such dark snakes might be overlooked, or dismissed as an optical illusion resulting from variations in lighting. L. Neil Bell has also observed that some boas of this species become much darker when cold.

Metachrosis seems to be much more widespread among snakes than is generally realized, some sort of color change having been noted in crotalid, colubrid, and boid species. In *Crotalus* and probably in *Arizona* and *Elaphe guttata emoryi,* metachrosis may function chiefly as an aid to thermoregulation, permitting longer periods of activity. As for the common hog-nose snake, it has been described as "the last reptile to go into hibernation" in Georgia; young of the year have been found foraging as late as November and December (Neill, 1948). Metachromatic thermoregulation might therefore be quite useful to the species. The Mexican boa ranges from northern South America northward almost to the United States border in Sonora, Mexico; in the northern part of its range, at least, it is exposed to extremes of temperature and so might profit by a thermoregulatory mechanism. According to Werler and Smith (*op. cit.*), the light crossbands of *Leptodeira mystacina* became decidedly lighter at night although there were but negligible temperature fluctuations, and so another explanation must be advanced for color change in this species. An hypothesis may be offered. By day the pattern of this rear-fanged snake affords a remarkable example of disruptive coloration through constructive shading. However, in the absence of metachrosis the light (grayish) bands would not especially contrast with the dark ones by night, when the snake is most active. Actually, the light bands become paler by night and so continue to maintain somewhat the same degree of contrast with the dark ones, thus breaking up the snake's outline and helping to conceal the reptile from keen-eyed nocturnal predators or from potential prey. A similar situation might exist with *Python reticulatus,* which is elaborately camouflaged and largely nocturnal.

The slow and progressive lightening of captive snakes, mentioned by Kauffeld (*op. cit.*), might be explained as loss of "suntan." Nothing much seems to have been recorded about "tanning" in reptiles. We have previously mentioned its occurrence in alligators (Allen and Neill, in press). At any rate, this type of color change is not metachrosis and need not be discussed here.

The pituitary regulation of melanophores, reported in *Thamnophis, Natrix,* and *Pituophis,* might function on a seasonal basis, darkening the snakes as winter approaches. In this connection, the senior author is under the purely subjective impression that several common colubrid snakes are apt to be unusually dark when unearthed from shallow hibernating sites in cold weather.

Metachromatic responses in snakes appear to be somewhat unpredictable; they may be affected by visual stimuli or other factors, as well as by temperature. This, however, remains to be demonstrated. At any rate, the subject of metachrosis in snakes merits much further study, from the standpoints of physiology, ecology and animal behavior.

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