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Accepted: 24 October 1993.

Seasonal Changes in Dorsal Reflectance of Two Species of Australian Elapid Snakes

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Color is an important aspect of the biology of most organisms. Several species of snakes have evolved genetic color polymorphisms in response to environmental heterogeneity (Camin and Ehrlich, 1958; Zweifel, 1981; Bechtel and Bechtel, 1985; Sweet, 1985; King, 1987, 1988). However, color change within individual snakes appears to be uncommon and/or to have gone largely unrecognized, even though this phenomenon has been well-documented in lizards (Norris, 1967; Hadley and Goldman, 1969).

Two types of color change have been recognized among reptiles (Bagnara and Hadley, 1973). Physiological color change involves rapid (minutes to hours) movement of melanosomes into (darkening) or out of (lightening) the processes of dermal melanophores, while morphological color change involves an increase (darkening) or decrease (lightening) in the number of melanosomes and melanophores over weeks or months. Physiological color changes have been reported in ten species of snakes in four families (Hedges et al., 1989; Shine, 1991). Rahn (1941) induced physiological color change in a crotalid and four species of colubrid by injection of intermedin following removal of the pituitary. Morphological color change has only been observed in three species of Australian elapids (Banks, 1981; Mirtschin, 1982) and one species of viperid (Rehak, 1987). In all four species the color change occurred seasonally.

I report spectrophotometric measurements made opportunistically on *Pseudonaja nuchalis*, *P. inframacula*, and *Oxyuranus microlepidotus* held in captivity at the Whyalla Fauna Park, South Australia. These data provide quantitative confirmation of earlier observations of seasonal color change in *P. nuchalis* (Banks, 1981) and *O. microlepidotus* (Mirtschin, 1982) and highlight a potential source of confusion in field recognition of *P. inframacula* and *P. nuchalis*.

The snakes used were two *O. microlepidotus* collected at Goyder's Lagoon (26°53'S, 139°00'E) in northeastern South Australia in 1980 and 1981, five *P. nuchalis* collected at Whyalla (33°04'S, 137°34'E) South Australia between 1979 and 1983, and two *P. inframacula* collected from Coffin Bay Peninsula (34°38'S, 135°29'E) South Australia in 1977. These snakes were sexually mature when collected. Most were kept in glass-fronted, wooden enclosures with a 1 m² cement floor within a brick building, but three *P. nuchalis* were kept in fiberboard enclosures with a fly wire top and a 1.5 m² cement floor in a corrugated iron building. The enclosures in the brick building were thermostatically maintained at 25 C and those in the corrugated iron building were maintained at 27–30 C. Heat was supplied by an infrared globe suspended from the top of each cage, to allow behavioral thermoregulation. Natural light was available through translucent roofing panels. All snakes were fed mice, rats, and day-old chickens.

Reflectance measurements were taken with an Evans Electroselenium reflectance spectrophotometer on 28 February (austral summer) and 13 July (austral winter), 1984. This instrument expresses light reflected from a surface as a proportion of light reflected by a magnesium carbonate blank (Benford et al., 1948). Reflectance was measured at nine wavelengths over the visible spectrum: 425 μm, 465 μm, 515 μm, 545 μm, 595 μm, 655 μm, and 685 μm. All measurements were taken dorsolaterally, one-third of the snout-vent length anterior to the cloaca. The spectrophotometer was calibrated prior to every measurement and care was taken to place the measurement port of the spectrophotometer over the same area of the snake for measurements at each wavelength to minimize errors due to changes in the range of angles of incidence of the light beam.

The effect of moving the measurement port of the spectrophotometer over the surface of a single snake was to vary reflectance by no more than 2%, provided the area sampled was evenly colored. If obvious color variations, such as darker or lighter spots or bands, were included in the area sampled, then greater variation in measurements was encountered. Care was therefore taken not to include any obvious variation in color in the area of the snake from which reflectance was measured. None of the snakes used in this study sloughed their skin during the ten days preceding or succeeding measurement. All measurements were taken between 1300 and 1600 h when the snakes were active, and had body temperatures of 30–35 C. Wilcoxon's signed-ranks tests (Sokal and Rohlf, 1981) were used to test for interseasonal differences in reflectance within each species and for differences in seasonal color shifts between species.

Oxyuranus microlepidotus and *P. nuchalis* showed clear changes in reflectance between winter and summer ($P < 0.01$ for both species) (Figs. 1, 2). *Pseudonaja inframacula* showed no such changes ($P > 0.05$). In-
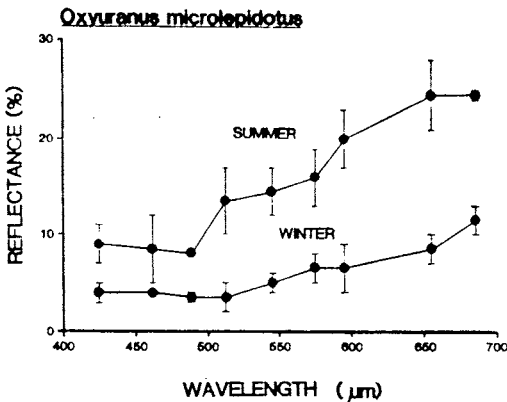
FIG. 1. Mean (dots) reflectance and range of values (bars) for *Oxyuranus microlepidotus* over the visible spectrum in summer and winter, showing change in reflectance.
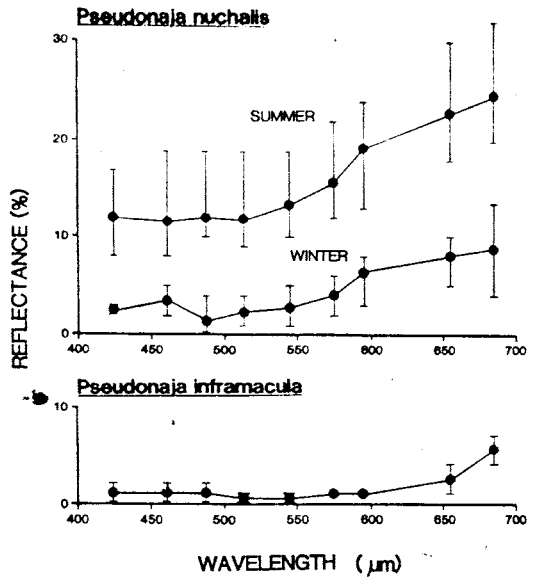

FIG. 2. Mean (dots) reflectance and range of values (bars) for *Pseudonaja nuchalis* (upper) and *P. inframacula* (lower) over the visible spectrum in summer and winter, showing change in reflectance in *P. nuchalis* but no such change in *P. inframacula*.

deed, reflectances in summer and winter were identical in this species (Fig. 2). In all three species and at both times of the year, the reflectance values increased with increasing wavelength. In both species that underwent shifts in reflectance, measurements taken in summer were higher than those taken in winter.

Interestingly, in summer there was no significant difference between reflectance values obtained from *O. microlepidotus* and *P. nuchalis* ($P > 0.05$), but *O. microlepidotus* had significantly higher reflectance than *P. nuchalis* in winter ($P < 0.01$), even though there was considerable overlap of the measurements obtained for each species (Figs. 1, 2). There was no significant difference between the reflectance values obtained for *P. inframacula* and *P. nuchalis* in winter ($P > 0.05$), but *P. nuchalis* were significantly more reflectant than *P. inframacula* in summer ($P < 0.01$) (Fig. 2).

The measured changes in reflectance were associated with visually obvious changes in color. The *O. microlepidotus* and *P. nuchalis* were pale straw-brown in February and dark chocolate brown in July 1984. The *P. inframacula* were dark grey-brown in both February and July. Subsequent to the reflectance measurements being taken, the same pattern of color changes were observed to occur seasonally over a period of four years in *O. microlepidotus* and *P. nuchalis*. The visual effect of the reflectance change reported here for *P. nuchalis* is shown in Fig. 3. The seasonal color change in *O. microlepidotus* has been illustrated previously by Mirtschin (1982, Figs. 1, 2).

The reflectance of a snake at visible wavelengths is a direct inverse measure of energy absorbed because no visible light is transmitted entirely through the snake's body (Porter, 1967). Thus, in summer, *O. microlepidotus* and *P. nuchalis* are absorbing about half the thermal energy that they are in winter over the range of wavelengths measured (Figs. 1, 2). The importance of this observation is reduced, however, because only reflectance in the visible portion of the spectrum (400–700 μm) was measured. Visible wavelengths contain approximately half of the energy in

solar radiation at the surface of the earth; most of the remainder is contained in the infrared.

Norris (1967) has demonstrated that color change in reptiles is a functional adaptation which is related primarily to concealment at visible wavelengths and to thermoregulation at infrared wavelengths. With this in mind, there is clearly a need to measure changes in reflectance at both visible and infrared wavelengths in snakes that undergo seasonal color changes to determine the reason(s) for such changes. Although I measured reflectance at visible wavelengths only, a likely hypothesis to explain the color changes reported here is that they are related to thermoregulation. *Oxyuranus microlepidotus* and *P. nuchalis* both show a reduction in reflectance in winter concomitant with a reduction in mean temperature and solar radiation over all of their geographic ranges in central and southern Australia, whereas *P. inframacula* occurs coastally and at higher latitudes than the other two species where it is subject to lower temperatures and solar radiation throughout the year. This hypothesis could be tested directly by measuring the heating rates of snakes in summer and winter.

The seasonal variation in color of the snakes reported here also has implications for correct identification of the two species of *Pseudonaja*. *Oxyuranus microlepidotus* and *P. nuchalis* are essentially pale brown with darker flecks in summer and are a considerably darker brown in winter. *Pseudonaja inframacula* is very dark brown throughout the year. In some parts of South Australia where *P. inframacula* and *P. nuchalis* are sympatric this similarity in color in winter makes identification problematical. Hitherto color and morphology of the rostral scale have been used to separate these species (Waite, 1925). In *P. nuchalis* the rostral
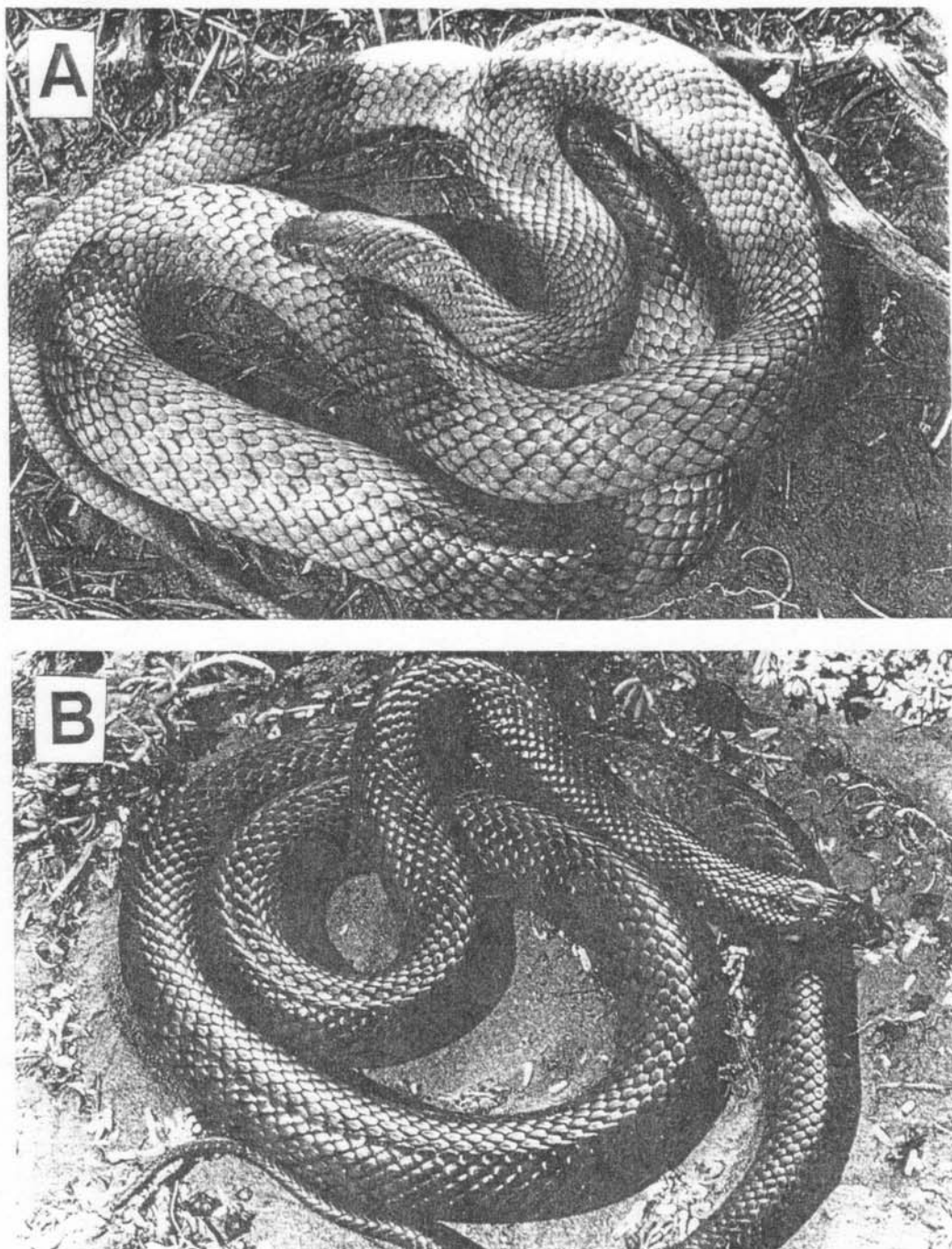
FIG. 3. A *Pseudonaja nuchalis* from near Whyalla in South Australia, showing pale color in summer (A) and darker color in winter (B) in the same individual.

scale is flattened and extends well onto the dorsal surface of the snout. In *P. inframacula* the rostral is rounded and does not extend onto the dorsal surface of the snout. Southern populations of *P. nuchalis* have been separated from *P. inframacula* by their pale brown, rather than dark coloration. The phenomenon of seasonal color change in *P. nuchalis* in areas where it coexists with *P. inframacula* necessitates reliance upon morphology of the rostral scale alone for identification in the field, even though there is little doubt that

these taxa are separate biological species (Mengden, 1985). *Pseudonaja inframacula* and *P. nuchalis* are both large and highly venomous species; consequently, correct identification of these snakes may be important for medical reasons.

Pseudonaja nuchalis is a composite taxon which exhibits great variation in color and pattern (Gillam, 1979), some of which reflect electrophoretic and chromosomal variation (Mengden, 1985). Seasonal color changes must now be taken into account when describing the color variation among populations currently identifiable as *P. nuchalis*. All of the *P. nuchalis* in which seasonal color changes were observed by Banks (1981), and those quantified here, belonged to the 'southern' group of taxa recognized by Mengden (1985). It is unclear whether other taxa within the *P. nuchalis* complex exhibit seasonal color changes.

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Impact of Artificial Lighting on the Seaward Orientation of Hatchling Loggerhead Turtles

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Under natural conditions marine turtle hatchlings emerge from their nest primarily at night and immediately crawl seaward. They are guided by the optical cues provided by the relatively bright horizon over the ocean (as reviewed by Mrosovsky and Kingsmill, 1985). Experiments have demonstrated the relative effects of light intensity and color on hatchling orientation (Mrosovsky and Kingsmill, 1985; Witherington and Bjorndal, 1991). One implication of the dependence on photic cues is the possible disturbing effect of photopollution. The presence of artificial lights at a nesting beach can cause mortality in hatch-