The colouration and displays of venomous reptiles: a review

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SOME years ago, my friend Malcolm Coe inadvertently stepped on a large Gaboon viper (*Bitis gabonica*) whilst scrambling along a narrow track up Mount Cameroon. Fortunately for Malcolm, the snake was apparently as anxious as he was to terminate their brief encounter as quickly as possible. It slithered away down the slope without making any attempt to strike at him. In captivity, Gaboon vipers show dramatic colouration – beige, browns, yellow, purple and black are interwoven in a manner that has been described as having the effect of an oriental carpet. These bright colours are disruptive (Mehrtens, 1987), and in their normal environment Gaboon vipers – like the majority of venomous snakes – are extremely cryptic. Their silvery eyes are located at the apex of black or dark brown cheek patches (Fig. 1). This marking not only disguises the eyes but it also conceals the mouth very effectively! (Cloudsley-Thompson, 1999a).

The thesis of the argument outlined below is that venomous snakes are almost always, if not invariably cryptic (Cott, 1940). None of the species illustrated by Greene (1957), Mattison (1986) or Mehrtens (1987) for example shows aposematic (conspicuous or warning) colouration with the exception of sea snakes and coral snakes which appear to be special cases. Other possible exceptions may include the juveniles of a few species such as the King cobra (*Ophiophagus hannah*) which have black and white stripes and the Bandy-bandy (*Vermicella annulata*) (see below). The rarity of warning colouration in venomous snakes was first emphasised by Poulton (1890) and by Hingston (1933).

Concealing colours

Back in 1890, E. B. Poulton concluded that whereas it may be 'to the advantage of certain venomous snakes to advertise publicly the fact that they are dangerous, retaining the poison to use if necessary; and others would gain by concealing themselves by Protective Resemblance, while they also use their poison fangs if detected and attacked'. On balance, crypsis is more beneficial than aposematism in assisting venomous reptiles to avoid attack (Ruxton *et al*., 2004).

According to Cott (1940) the methods by which concealment is obtained in nature are: (1) General colour resemblance to the environment, (2) Variable colour resemblance, (3) Obliterative countershading, (4) Disruptive colouration, (5) Coincident disruptive colouration and (6) Concealment of shadow. Not all of these are found among venomous reptiles. When present, their function may be concealment in defence, in offence so that they are not seen by the prey, or both. Good examples of the latter are provided by Green mambas (*Dendroaspis viridis*) and the vine snakes, of which four distantly related genera are known. They are all 'sit and wait' foragers which stalk their prey with lateral swinging of the head: they are generally extremely cryptic and difficult to see (Cloudsley-Thompson, 1989; Henderson & Binder, 1980). More common among venomous reptiles than general colour resemblance to the environment are obliterative countershading and disruptive colouration. Light and shade make objects apparent even when seen against backgrounds whose colour and texture exactly match their own. For this reason the ventral surfaces of nearly all animals are lighter in colour than the rest of their bodies. Concealment of shadow is achieved by pressing the body onto the substrate whenever possible. The Sidewinder (C*rotalus cerastes*) illustrated in Fig. 2 is doing this. As well as to day-active snakes, cryptic colouration is important to nocturnal species, such as the Horned adder (*Bitis caudalis*) (Fig. 3) and the Saw-scaled viper (*Echis carinatus*) (Fig. 4). Even these may bask in the sunshine during the hours of daylight and many snakes, nocturnal during the summer, become day-active in winter.

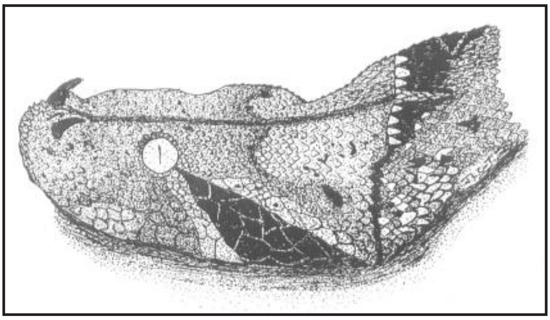

Figure 1. Head of Gaboon viper (*Bitis gabonica*).

Figure 2. Sidewinder (C*rotalus cerastes*).

Figure 3. Horned adder (*Bitis caudalis*).

Figure 4. Saw-scaled viper (*Echis carinatus*).

Few venomous snakes are able to adjust their colour rapidly to match their environment, but the Western rattlesnake (*Crotalus viridis*) has been reported to become lighter or darker within a minute or two, while the European adder (*Vipera berus*) becomes brighter after sloughing its skin prior to the breeding season (Ernst & Zug, 1996).

Warning colours

The most venomous lizards, the Gila monster (*Heloderma suspectum*) (Fig. 5) and the Mexican beaded lizard (*H. horridum*) provide striking contrast to other lizards which depend for safety upon cryptic colouration, alertness and speed. Not only are they brightly coloured, but they are slow, defiant, and defend themselves with their powerful jaws and poisonous bite (Cloudsley-Thompson, 1999). According to Greene (1988), the black and yellow colour pattern of *H. horridum* is primitively cryptic, whereas the black and pink colouration of *H. suspectum* is derived and probably aposematic. The Komodo dragon (*Varanus komodoensis*) is not only venomous but its bite is poisonous and often lethal to the prey on account of toxins and the noxious bacteria in its saliva (Fry *et al*., 2006, summarised in *The Natterjack* No. 131: 4–5, December 2005). Whether or not the same is true of the Perentie (*Varanus giganteus*) does not appear to be known but, like those of the Lace monitor (*V. varius*), its bright colours could well be aposematic. In the course of my research in Sudan during the 1960s I was not infrequently bitten without ill effects by young Nile monitors (*V. niloticus*) which, likewise are brightly coloured (Fig. 6). In threat (see below) monitors of several species rear up to display alternatively dark and light stripes on much of their belly surfaces (Hingston, 1933).

Possibly the only adult venomous snakes with brilliant body colours whose function may be to warn possible predators that they are dangerous are sea snakes (*Pelamis platurus*) and coral snakes of the genera *Micrurus* and *Micruroides* (Elapidae). Not only are these readily detected but they have burrowing habits, dull sight, and are not stirred to irritability unless restrained (Ditmars, 1944). Not surprisingly, they are mimicked by various harmless or mildly poisonous ‘false’ coral

Figure 5. Gila monster (*Heloderma suspectum*).

Figure 6. Nile monitor (*Varanus niloticus*).

snakes (e.g. *Atractus, Erythrolamprus, Lampropeltis, Pseudoboa* and *Rhinobothryum* spp.; Colubridae). Coral snakes are so deadly that some investigators have expressed doubts as to whether they could actually serve as models, since potential predators are almost invariably killed and therefore never learn to avoid them. Alternatively, Mertens (1966) suggested that rear-fanged and mildly venomous species of snakes with coral snake patterns may be the models while nonvenomous and front-fanged species are respectively their Batesian and Müllerian mimics. The name Mertensian mimicry has been applied to this hypothesis (Wickler, 1986). It is doubtful, however, whether any snake is so venomous that all animals bitten by it are invariably killed. Moreover, many predators have both natural and acquired mimicry against snake and other venoms (Cloudsley-Thompson, 1994, 1999a). The paradox of the deadly model has also been discussed by Cloudsley-Thompson (1994), Engelmann & Obst (1984), Greene & McDiamid (1981), Mattison (1986), Pough (1988) and Roze (1996) among others. Mertensian mimicry is now generally regarded as a version of Müllerian and not as a completely different category of mimicry. The relationships are evidently extremely complicated and some 'false' coral snakes are found in regions where there are no venomous models. Since scavenging birds, which quickly consume other snakes killed on the roads, apparently leave the corpses of coral snakes undisturbed it may well be that their aposematic colouration is related more to distastefulness or an unpleasant smell than to venom (Cloudsley-Thompson, 1999a). Perhaps 'false' coral snakes and the most venomous species both display the simple Müllerian mimicry of distasteful species.

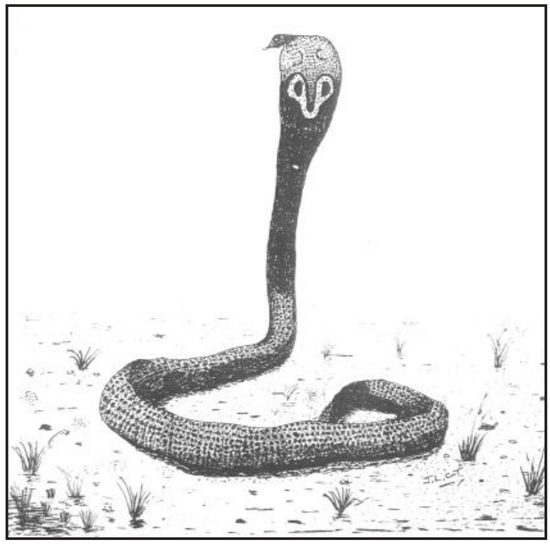

Figure 7. Indian cobra (*Naja naja*).

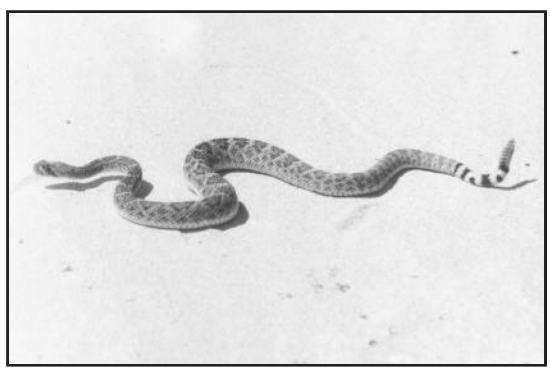

Figure 8. Rattlesnake (*Crotalus* sp.).

Snakes are probably vulnerable to different predators at different times and under different conditions. Defence may be effective in some cases, but none is invariably successful except possibly that of the aposematically coloured sea snake (*Pelamis platurus*) mentioned above. This is very conspicuous when not floating in the debris of drift-lines, its distinctive tail being especially noticeable. Greene (1997) suggested that this species might be one of the few vertebrates with no regular enemies – even among predators such as sea eagles that regularly feed on other marine elapids (Healwole, 1987). Seabirds occasionally seize but invariably drop them. Under experimental conditions Pacific Ocean fish rejected them as food and, although naïve Atlantic Ocean fishes ate them, they were later regurgitated (Rubinoff & Kropache, 1970).

Startling behaviour

When discovered by an enemy, many animals respond by adopting intimidating postures or making sudden, threatening sounds. Such behaviour is known as 'deimatic' (from the Greek word meaning 'I frighten') (Edmunds, 1974). Deimatic behaviour is extremely common among cryptic venomous snakes. Before striking in defence, most adopt characteristic positions. The Indian cobra (*Naja naja*), for instance, rears up with its conspicuous hood spread (Fig. 7), thereby increasing its apparent size. The hood of the Black-necked 'spitting' cobra (*Naja nigricollis*) has scarlet patches on its ventral side, while the ventral part of the body of Ringhal's cobra (*Hemachatus haemachatus*) displays black and white stripes below its black hood when the snake rears up.

Expansion of the neck region may be horizontal, as in cobras, or vertically as in the gular expansion of the Twig snake (*Thelotornis kirtlandii*) which flattens its head like an ace-of-spades. It is usually accompanied by the sudden exhibition of conspicuous colouration. Apparent increase in size is not limited to the hoods of cobras, however. The Boomslang (*Dispholidus typus*) can inflate its trachea and lung until it looks like an enormous sausage, the Eastern diamondback rattlesnake (*Crotalus admanteus*) to a lesser extent and the same kind of device is practised by numerous other animals (Cott, 1940). Defensive reactions of rattlesnakes such as *Crotalus cerastes* (Fig 3) and *C. viridis* in the presence of King-snakes (*Lampropeltis getulus*) may consist of the formation of a broad loop or band in the body which is then lifted from the ground (Cowles, 1938). The Australian Bandy-bandy (*Vermicella annulata*), so named from its conspicuous white bands on a black body, elevates single or multiple body loops which are held immobile. Burrowing elapids, these snakes only emerge at night or after rain when their colouration may be aposematic.

The tongue and lining of the mouth are often brightly coloured among lizards and snakes. This internal colouration is associated with opening the jaws widely when threatened. Examples among venomous species include Hog-nosed snakes (*Heterodon* spp.), the Vine snake (*Oxybelis acuminatus*), the Long-nosed tree snake (*Ahaetulla prasinus*) and the Fer-de-Lance. (*Bothrops atrox*) which have brightly coloured linings to their mouths, and the Cottonmouth (*Agkistodron piscivorous*) in which it is white. Among venomous species, deimatic exposure of mouth colours may serve as a threat but, in harmless species, it is just bluff (Cloudsley-Thompson, 1994). Defensive tail displays are characteristic of rattlesnakes, coral snakes, sea snakes and other venomous serpents (Greene, 1988).

The Shield-nosed 'cobra' or Cape coral snake (*Aspidelaps lubricus*) rears the forepart of the body and neck when molested, thereby exposing a row of black and yellow bands. It does not have a hood as do true cobras, but is capable of producing extremely loud hisses accompanied by an exhalation of air that is quite explosive (Mehrtens, 1987). The King cobra or Hamadryad (*Ophiophagus hannah*) has a narrower hood than those of other true cobras. Whereas the hisses of most snakes are in the region of 3,000-13,000 Hertz, with a dominant frequency of 7,500 Hz, however, the 'growl' of the King cobra consists entirely of frequencies below 2,500 Hz with a dominant frequency near to 600 Hz. This sound is produced by tracheal diverticula functioning as low-frequency resonating chambers (*The NatterJack* No. **128**, 3-4; Sept 2005).

Instead of hissing, a few venomous snakes stridulate by rubbing together the modified lateral scales of the trunk. Deimatic sounds are produced in this way by Saw-scaled vipers (*Echis* spp.) (Fig.

4), Horned vipers (*Cerastes cerastes*) and the Sand viper (*C. vipera*) of North Africa. They enable acoustic warning to be produced without the loss of respiratory water as occurs in hissing (Cloudsley-Thompson, 1999a) and are characteristic of desert species. Rattlesnakes (Fig. 8) also produce warning sounds without loss of water. A comparison of the power spectra and intensity of rattling in six species revealed conformation to the same general pattern – medium density broad-band sounds (2–20 k Hz) (Fenton & Licht, 1990). By drawing the attention of enemies or potential prey to their conspicuous tails, rattlesnakes must increase the chance of success when their heads strike unexpectedly from the opposite end of their bodies.

Vine snakes produce warning sounds by vibrating their tails in the vegetation, as does the Bushmaster (*Lachesis muta*) and other ground living snakes when they rattle their tails among dry leaves. Among the strangest sounds made by a snake are the cloacal ‘pops’ of the Sonoran coral snake (*Micruroides euryxanthus*) (Ernst & Zug, 1996). These are evenly spaced, of low amplitude (*c.* 50 decibels) and limited in pitch (442-5523 Hz) and frequency. They are made by contracting the cloacal sphincter and expelling air. Multiple pops are created by relaxing the sphincter, drawing air in, and contracting the sphincter again (*The NatterJack* No. **128**, 11; Sept. 2005).

The similarity of deimatic sounds throughout the animal kingdom may well result from Müllerian mimicry, so common in warning colouration. In addition to the usual repertoire of visual displays and sounds, some venomous snakes are able to jump – not only for the capture of prey but also in defence. Examples include *Porthidium [Bothrops] nummifier* (Crotalinae) and various *Bitis* spp. This type of behaviour also occurs among non-venomous snakes (Cloudsley-Thompson, 1996; 1999a). In this context, the flight of back-fanged tree snakes of the genus *Chrysopelia* deserve mention, but this is a way of escaping or merely travelling rather than deimatic display. The defences of reptiles have been reviewed by Bellairs (1969), Cloudsley-Thompson (1994; 1999a) and Greene (1988) among others.

DISCUSSION

Evolutionary adaptations resulting from natural selection are often the result of more than one factor. This is particularly apparent in the adaptive colouration of animals. The colours of reptiles may, for instance, combine elements of crypsis, aposematism (based on formidable defences of which venoms are the more important, mimicry, or both), epigamic display and climatic factors (Cloudsley-Thompson, 1999b). Deimatic displays may be bluff, based on real threats or mimicry or either of these. Moreover, selection may be influenced overwhelmingly by factors that operate only for a brief period during the life of an animal – for example, during the breeding season or in twilight (Cott, 1940). Thus, the colour pattern of *Echis carinatus* (Fig. 4) has multiple functions. Initially it is cryptic but, after the viper has been annoyed and begins coiling around itself and stridulating, its colours become aposematic and have a warning function. The light coloured lines that cross the black are outlined by black scales. These, and the pale dorsal patches, render the Saw-scaled viper more conspicuous than snakes with unicoloured dark patches on a light background; while inflation of the body emphasises the contrast of the cross bands (Cloudsley-Thompson, 1994).

The functions of the colours of venomous reptiles are not always obvious. Frequently they can only be interpreted by herpetologists who have practical experience and knowledge of the animals in their natural environments. Some Egyptian cobras (*Naja haje*) are banded, some are black, and some uniformly brown. At night, the banded form is almost invisible, but the significance of the other colours is uncertain. Furthermore, different colour patterns may be found among siblings from the same batch of eggs. Beaded lizards (*Heloderma horridum*) too are very variable in colour. In general, snakes with horizontal stripes tend to be harmless, whilst banded snakes are dangerous. Stripes are less distinct among the snakes that inhabit regions with luxuriant vegetation than among those of more open country (Cloudsley-Thompson, 1994).

In this short review, an attempt has been made to draw attention to some of the outstanding problems presented by the colouration of venomous reptiles. The solutions to these can only be supplied by herpetologists familiar with the animals concerned, and particularly those working in the field.

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EDITORIAL

Ammendment

When considering the significance of the colours of venomous reptiles (*Herpetol. Bull*. **95**, 25–30, 2006), I suggested that possibly the only adult venomous snakes with conspicuous coloration whose function might be to warn possible predators to leave them alone are sea snakes (*Pelamis platurus* and *Laticauda* spp.), coral snakes of the genus *Micrurus* and *Micruroides* and the burrowing Australian bandy bandy (*Vermicella anulata)*. In this context I should also have mentioned the kraits (*Bungarus fasciatus* and *B. multicinctus*). The avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica was recorded by E. D. Brodie (1993, *Evolution* **47**, 227–235).

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