

Is melanism adaptive in sea kraits?

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Abstract. Ontogenic melanism (progressive darkening of the skin) has been documented in snakes. Black coloration of the skin often compromises the cryptic effects associated with other patterns (e.g. zigzags) and exposes individuals to predation; however, the mortality risk can be balanced, for example by a thermoregulatory advantage during sun basking. Such adaptive context has been proposed to explain the appearance and the maintenance of melanism within snake populations. Based on a very large captures and re-captures sample (>8000 observations) gathered on two species of sea-kraits (*Laticauda saintgironsi* and *L. laticaudata* in New Caledonia), we observed that melanism occurred in only one species (*L. laticaudata*), was infrequent and concerned adult snakes solely. None of three adaptive hypotheses respectively linked to thermoregulation, predation, or protection against sun radiations, provided a satisfactory account for the occurrence of melanism in our study populations. Therefore, we suggest that melanism was a fortuitous phenomenon.

Keywords: adaptation, colouration, *Laticauda*, melanism, sea snakes.

Introduction

Melanism is one of the most obvious and widespread examples of polymorphism in animal populations (Kettlewell, 1973; Futuyma, 1986). Black individuals are often conspicuous, subject to increased predation; consequently, some benefits somehow counterbalance the deleterious effect of melanism. Notably, the thermoregulatory advantage of a dark colouration during sun basking has been documented in ectothermic species (Andren and Nilson, 1981; Gibson and Falls, 1988; Madsen, 1988; Madsen and Stille, 1988; Luiselli, 1992; Bittner et al., 2002). For instance, In *Vipera berus*, black females reproduce more frequently compared to those exhibiting a zigzag dorsal pattern (Capula and Luiselli, 1994). Such advantage likely explains why the frequency of melanism increases with latitude and altitude in many reptiles and amphibians (Monney et al., 1995).

In snakes, melanism is a common, complex and highly variable phenomenon. The expression of melanism varies both in terms of the

parts of the body affected (back, head, tail, etc.) and in terms of frequency among populations. Black colourations (e.g. tiger snakes [*Notechis* sp.]; black swamp snake [*Seminatrix pygaea cyclops*]) or black patterns (e.g. grass snakes [*Natrix natrix*]; coral snakes [*Micrurus* sp.]; Timber Rattlesnake [*Crotalus horridus*]) are often partly established at birth and remain permanent throughout lifespan. Rapid changes of colouration (minutes, hours), well documented in many animal species (squids, fish, lizards, owing to the displacements of melanin granules within the melanocytes), may also occur in snakes; however, their moderate intensity cannot be associated to melanism (Bagnara and Hadley, 1973; Hedges et al., 1989). Progressive and marked melanism over time has been observed in different snake species. Therefore, the frequency of black individuals increases within older age classes. In fact, the neonates exhibit cryptic colourations (e.g. complex patterns of spots and zigzags); they tend to become darker over time and apparently acquire their final colour at sexual maturity (Naulleau, 1997). In different species, the occurrence of melanism has been documented in the adults solely, suggesting that the juveniles retain a cryptic coloration until maturity (e.g. *Vipera berus*, *Vipera aspis*, *Hierophis viridi-*

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flavus). Such ontogenetic changes of colouration are likely adaptive (Booth, 1990) as small snakes are more vulnerable to predation than larger ones, which in turn need to reach high body temperatures during reproduction (e.g. during vitellogenesis; Nagy, 2000; Creer, 2005). In the current manuscript, we report cases of relatively rapid melanism that took place after maturity in already large and sexually mature snakes.

Materials and methods

Since 2002, we set up a long-term mark recapture study in eight islets in the south-west lagoon of New Caledonia: Tenia, Mba, Signal, Larégnère, Porc-Epic, Amédée, Bayonnaise and Brosse (from north to south). We have individually and permanently marked more than 4700 sea kraits belonging to two species (>2200 *Laticauda laticaudata* and >2550 *L. saintgironsi*). Each individual was sexed and measured (snout-vent length SVL \pm 1 cm; body mass \pm 1 g).

SVL permitted to assign to each individual an estimated age-class: snakes smaller than 50 cm in SVL were classified as neonates; snakes above the minimal size for maturity were classified as adults; snakes in between were classified as juveniles. However, females attained maturity at a larger body size (female and male were considered as adult when exceeding 75.5 cm and 63.0 cm and 88.5 cm and 70.0 cm in SVL for *L. saintgironsi* and *L. laticaudata* respectively, unpublished data).

The typical colouration of sea kraits is a banded pattern of regularly spaced black rings on a coloured background. The background is blue for *L. laticaudata* and greyish to bright red for *L. saintgironsi* (Brischoux and Bonnet, 2007). For each individual, we also carefully described the distinctive colour pattern: the colour of the background (e.g. light blue, grey, orange), we counted the number of black rings and noted the abnormalities such as y-shaped rings, and we also recorded the number and the position of the small colour marks such as the small dots or dashes (either dark or light). The number, size and position of recent injuries were recorded. For simplicity, we categorized the individuals into three colour morphs (fig. 1; table 1):

- 1) Snakes with a normal banded pattern (= normal snakes): a well-defined alternation of coloured and black rings;

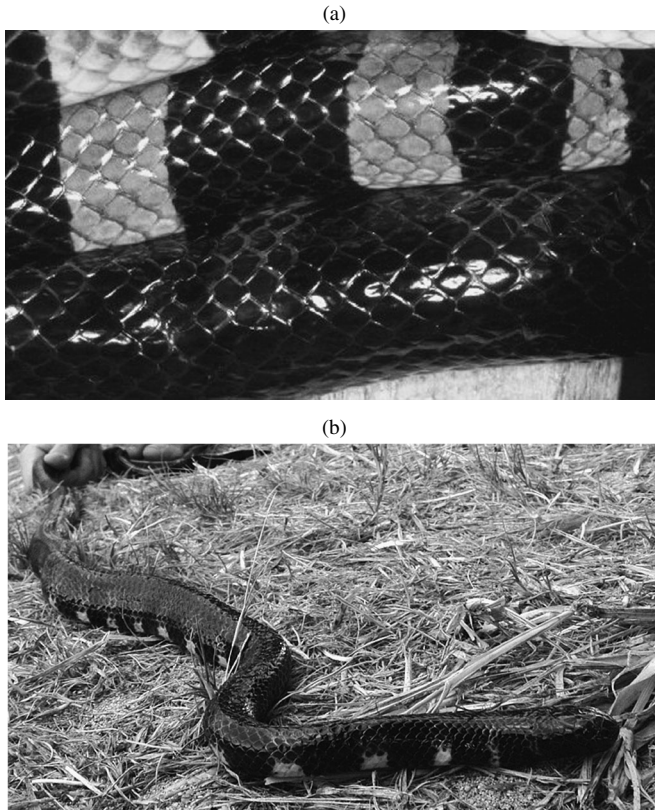


Figure 1. (a) Comparison between the normal banded pattern (top) and a melanic snake (bottom). (b) The melanic adult male (# 463) pictured here exhibited a normal banded pattern 312 days before, without any sign of darkening.

Table 1. Occurrence of three main colour patterns in *Laticauda laticaudata* with respect to sex and age. Banded pattern refers to the normal coloration (blue background and black rings); dark individuals exhibited a dark dorsal coloration but the rest of the body was normally banded; in melanic snakes the blue background colour was replaced by a very dark or black pigmentation (see text for details). The values refer to captures only.

	Females			Males		
	Neonates	Juveniles	Adults	Neonates	Juveniles	Adults
Banded	89	349	261	66	195	1107
Dark	1	10	61	0	0	66
Melanic	0	0	1	0	0	8

- 2) Individuals with a dark dorsal colouration (= dark snakes), but with the rest of the body presenting a normal pattern (e.g. lateral and ventral parts with a blue or yellow background and black rings);
- 3) Melanic individuals (= melanic snakes) where the black rings became almost or fully invisible at least on the dorsal and lateral parts of the body, individuals totally black were included in this category.

We never observed any snake with a black, or nearly black pigmentation, on the lateral parts of the body but with the back still normally banded. Therefore, we assumed that the categories 2 and 3 above were representative of two successive stages for a progressive establishment of melanism, starting from the back and spreading progressively towards the ventral parts of the snake.

Results and discussion

The very large sample sizes gathered of both snake species provided a satisfactory level of confidence in our ability to detect black individuals. We never observed dark or melanic individuals in *L. saintgironsi*. By contrast, we recorded a substantial number of dark snakes, and several melanic individuals in *L. laticaudata* (table 1). The occurrence of melanism was low, only 0.4% of captured snakes were melanic (eight individuals) and only one snake was totally black. The absence of dark, or melanic snakes, in *L. saintgironsi* precluded further analyses in this species.

In *L. laticaudata*, the proportions of different colour morphs varied significantly between the sexes (table 1; $\chi^2 = 21.3$, $df = 2$, $P < 0.001$) and between the age classes (table 1; $\chi^2 = 44.2$, $df = 4$, $P < 0.001$). None of the immature male (neonates or juveniles) presented a dark or melanic coloration; conversely, several immature females ($N = 11$) had a dark

dorsal coloration. In adults, the occurrence of a dark dorsal pattern was greater in females (23%) relative to males (6%). We recorded only one melanic female versus eight males. However, both proportions were low (0.3% versus 0.6% respectively). Overall, our results were somewhat puzzling. However, under the hypothesis that melanism is a progressive phenomenon, the differences between the sexes became easily explainable. Males reach maturity at a smaller body size, and thus before the females (see above). Consequently, most of the males are represented by adults whilst many females remained juveniles for much prolonged time periods. Such sex difference for maturity generated the sex biased proportions of individuals with an equilibrated sex ratio among neonates, but an overrepresentation of the juvenile females and a very large number of adult males (table 1).

These interpretations are testable: if we were correct, significant differences of body size should be detected. Notably, darker (presumably older) individuals should be larger than the normally coloured ones because growth requires time. Among adults, the dark individuals (dark or melanic) were larger than those exhibiting a normal banded pattern (in females: ANOVA, $F_{1,2380} = 14.16$, $P < 0.001$, mean SVL: 104.1 ± 0.46 cm and 108.1 ± 0.97 cm for blue banded and dark individuals respectively; in males: ANOVA, $F_{1,463} = 89.9$, $P < 0.001$, mean SVL: 84.6 ± 0.13 cm and 89.3 ± 0.48 cm for blue banded and dark individuals respectively). This supports the notion that the amount of black pigmentation progressively increased over time. Interestingly, the snakes be-

came melanic only after sexual maturity, a pattern not well described in snakes (it is usually assumed that melanism takes place around maturity, not long after). The data and analyses above provide a picture where melanism is a slow process that requires several years after maturity to be expressed. However, our capture-recaptures led to a different perception. Two individuals shifted from a normal blue and black pattern to a melanic pattern within a year time period: one male captured on Signal islet (99 cm SVL), and another male caught on Amédée islet (92 cm SVL) were recaptured after 312 and 373 days respectively: both became melanic. Their identification was confirmed using the number of black rings (still visible on the ventral part) and the number and disposition of scars. All the dark or melanic snakes recaptured later ($N = 36$; 1-3 years later) kept their colouration, or exhibited a darker pattern over time: melanism was irreversible.

The permanent marking of the snakes required scale clipping (following a code) associated to a superficial burning of the targeted scales. In snakes, this technique usually translates into regenerated scales with a distinguishable and permanent novel colour. Interestingly, the new colours of the marked scales were different between the two snake species. In *L. laticaudata*, the black scales sometimes turned into white, but the blue ones became black. Similarly, the scared injuries led to black marks on the blue background. In *L. saintgironsi*, the black scales remained black, the orange (or grey...) scales re-grew with a dark orange colour (Brischoux and Bonnet, 2007). Such species difference in the modification of the coloration for accidental causes accords well with the fact that melanism was observed only in *L. laticaudata*.

Our data clearly demonstrate that moderate to marked melanism (from dark dorsal coloration to full melanism) occurred in the adults of at least one species of sea-kraits, but not in another one. The two species of sea-kraits share many ecological features: they occur on the

same islets, they feed on the same prey types (anguilliform fish; Ineich et al., 2007), and they exhibit relatively similar body sizes (Brischoux and Bonnet, 2007). Although they diverge for many traits (exact diet, activity pattern, morphology, reproductive periods...) we found no satisfactory explanation for the melanism in *L. laticaudata*. Below we review the main hypotheses favouring melanism in snakes:

- 1) Thermoregulation: when the snakes are at sea, their colouration has no influence on their body temperature (Shine et al., 2003). When on land the situation is different. However, *L. laticaudata* remain sheltered under large rocks or under seabird burrows and were never observed exposing their body to the sun. In addition, they are not active during the daylight phase (Brischoux and Bonnet, 2007). On the other hand, *L. saintgironsi* is often observed basking in the sun. The advantage associated with melanism for thermoregulation hypothesis can be confidently rejected.
- 2) Anti predation: in many aquatic animals a dark dorsal coloration combined with a light (mirrored) ventral pattern afford an effective crypsis against predators (Johnsen and Sosik, 2003). The low frequency of such a putative camouflage in *L. laticaudata*, along with its total absence in *L. saintgironsi* do not support the notion that melanism is an efficient anti-predator strategy in sea-kraits. Furthermore, the sea kraits with dark back still exhibited a banded belly and the full melanism produced totally black individuals; two patterns incompatible with a cryptic coloration.
- 3) Protection against sun damages: suntan is an adaptive response to the deleterious effects of solar radiations (Herbert and Emery, 1990). However, melanism occurred in the nocturnal species (*L. laticaudata*) and not in the diurnal species

that often bask in the sun (*L. saintgironsi*). It is unlikely that the dorso-ventral spreading black pigmentation of the skin, documented in the sea kraits, was a response against the damaging effects of the sun.

None of the above hypotheses provided any support to the melanism displayed by *L. laticaudata*. In the absence of explanation, we suggest that this phenomenon is non-adaptive. Overall, at least part of the colour polymorphism of the sea kraits may be fortuitous and may not require an adaptive context.

Acknowledgements. We thank François Devinck, Claire Goiran and Dominique Ponton (Aquarium de Nouméa, DRN Province Sud, IRD). We are indebted to Rex Cambag who recovered the bâton de mort. We thank the CNRS and the University François Rabelais for funding. The study was carried out under permit number 6024-179/DRN/ENV and # 6024-3601/DRN/ ENV.

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Received: March 19, 2007. Accepted: May 25, 2007.