

Life history of sea kraits in New Caledonia

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ABSTRACT

Two species of sea kraits (Laticaudidae) occur in New Caledonia. The yellow sea krait *Laticauda saintgironsi*, closely related to *L. colubrina* and *L. frontalis*, is endemic to the area. The blue sea krait (*L. laticaudata*) is widespread over the west Pacific, however an absence of careful taxonomic studies impedes to determine to what extent it might be also an endemic species. Paradoxically, despite their abundance, there is very little scientific information on the neo-caledonian sea kraits. Since 2002 we set up a mark recapture study on 10 islets. We gathered the most comprehensive data set on the morphology and ecology of these two species of snake. We captured and individually marked more than 4,000 snakes, and gathered more than 3,000 recaptures. We provide the mean values for the body size, body mass, number of rings of the two species. We also present the first information about the reproduction phenology. Despite superficial similarities, we detected significant difference between the two species for all the characteristics we investigated.

RÉSUMÉ

Histoire naturelle des serpents marins de Nouvelle-Calédonie.

Deux espèces de serpents marins (Laticaudidae) sont présentes en Nouvelle-Calédonie. Le “tricot rayé” jaune *Laticauda saintgironsi*, proche parent de *L. colubrina* et *L. frontalis*, est endémique de la région. Le “tricot rayé” bleu a une large répartition sur l'ensemble du Pacifique ouest, mais l'absence d'études taxonomiques détaillées ne permet pas de déterminer à quel point il pourrait également représenter une espèce endémique. De manière paradoxale et en dépit de leur abondance, il y a peu d'information scientifique sur ces serpents marins néo-calédoniens. Depuis 2002, nous avons entrepris une étude de marquage-recapture sur 10 îlots. Nous avons rassemblé le lot de données le plus complet à ce jour sur la morphologie et l'écologie de ces espèces de serpents. Nous avons capturé et marqué individuellement plus de 4000 individus, et obtenu plus de 3000 recaptures. Nous présentons des valeurs moyennes pour la taille du corps, le poids et le nombre d'anneaux chez ces deux espèces. Nous apportons aussi les premières informations sur la phénologie de la reproduction. Malgré une apparente similarité, les deux espèces sont bien différentes pour toutes les caractéristiques étudiées.

INTRODUCTION

Sea kraits (Hydrophinae, Laticaudidae) are among the most widespread sea-snakes. Large numbers occur over a geographic area broadly limited by India, Tongan archipelago, Japan and New Caledonia (Greer 1997; Heatwhole 1999). Such a wide distribution range offers ample opportunities to examine variations between contrasted environmental conditions within a narrow taxonomic range. In addition, sea kraits are characterised by an amphibious life style. They forage at sea, court, mate, lay their eggs, digest, rest, slough their skin on land (Greer 1997; Heatwhole 1999). The respective constraints of these two contrasted environments generate conflicting selective forces, notably to optimise locomotor performances at sea versus on land (Shine & Shetty 2001b; Shine *et al.* 2003b). Sea kraits are docile animals, easy to catch and to handle. Overall, sea kraits are interesting biological models to address several major evolutionary questions. Despite such combination of logistical and scientific advantages to set up studies on these species (high population densities, easiness of capture and for handling, paradisiacal study site, etc.), relatively little information is available on the ecology of the sea-kraits. Recently, two species (*L. colubrina* and *L. frontalis*) have been examined in detail in two localities, Vanuatu and Fiji (Shine & Shetty 2001a, b; Shetty & Shine 2002a, b, c, d; Reed *et al.* 2002; Shine *et al.* 2002a, b; Shine *et al.* 2003a, b). These studies confirmed that the peculiarities of the ecology of the sea kraits constitute an excellent substrate to explore important issues such as speciation, trade-offs between marine and terrestrial locomotor performances, diet, activity pattern on land, or sexual dimorphism for instance (Shine & Shetty 2001a, b; Shetty & Shine 2002a, b, c, d; Reed *et al.* 2002; Shine *et al.* 2002a, b; Shine *et al.* 2003a, b). However, many other major characteristics such as population dynamics, foraging ecology, growth rates, phenology of reproduction, annual variations for all life history traits for example, remain virtually not documented. Given the limited number of field studies there are very poor possibilities for comparisons between species and geographic areas over the distribution range of the sea kraits.

In New Caledonia, situated at the extreme south of the distribution range, two species of sea-kraits coexist: *Laticauda saintgironsi* (yellow sea krait, tricot rayé jaune, Fig. 1) and *L. laticaudata* (blue sea krait, tricot rayé bleu, Fig. 2). A single short term study provided preliminary data on the ecology of these two snake species (Saint Girons 1964). A book (Ineich & Laboute 2002) reviewed all the information available on the sea-snakes of New Caledonia, and in fact revealed a total cessation of investigation since the pioneer work of Saint Girons. Based on precise morphological criteria, Cogger & Heatwhole (2006) shown that *L. saintgironsi*, formerly regarded as part of the wide-ranging *L. colubrina*, was an endemic species to New Caledonia. The blue sea-krait, *L. laticaudata*, is also a widespread species (occurring on many islands of the indo-pacific). This snake exhibit marked variations across its distribution range. It should be noted that owing to a lack of careful morphological, ecological and genetic study, the taxonomic status of this species remains unclear.

Since 2002, in collaboration with the University of Sydney (Australia) and the Muséum national d'Histoire naturelle (Paris, France), we (CNRS, France) initiated a long term mark-recapture study on both species and we collected the most comprehensive data set available for this geographic area. In this paper, we present basic ecological data that aim to serve as a basis for future studies. Nonetheless, the large sample sizes on which we based the current analyses enabled to present new findings, to update previous data, and also to correct numerous errors that are still widespread in the scientific literature.

MATERIALS AND METHODS

STUDY SITES

All the study sites are situated in the south west lagoon. We surveyed 10 natural islets and an artificial one (a wreck lying on the barrier reef). The following sites, presented from the north to the south, have been visited on one to seven occasions (Fig. 5): Konduyo, Tenia, Mba, Signal, Larégnère, Amédée, Porc-Epic, Nouaré, Bayonnaise and Brosse. We also visited on two occasions the wreck of the Ever Prosperity which stands on the barrier reef near



FIGS 1-4. **1,** *L. saintgironsi* from the South of New Caledonia (Nouaré islet). This animal displays a colour pattern close to *L. frontalis* (Photo: Xavier Bonnet). **2,** *L. laticaudata* coming ashore at Signal islet (Photo: F. Brischox). **3,** Some examples of colour variation in the two species of sea kraits. From the top of the picture: a rusted *L. saintgironsi*, a normal *L. saintgironsi*, a normal *L. laticaudata* and a melanic *L. laticaudata* (Photo: X. Bonnet). **4,** Maitre islet, a natural reserve, during the construction of a huge tourism resort. The sign explain that it is forbidden to fish, capture, harvest or collect any animal or mineral; people must bring back their garbage; islet vegetation is fragile, it is forbidden to cut the trees, etc. It is still classified as a natural reserve (Photo: X. Bonnet)!

Amédée islet (Fig. 5). Across the different sites, marked variations occur in terms of geomorphology, proportions of sandy beaches *versus* coral cliffs, vegetation, surface area, location between the main island and the barrier reef or human frequentation. Such diversity enables to better appreciate local variations and hence to obtain a general picture of the species under focus. The study sites were regularly surveyed in 2002, 2003, 2004, 2005 and 2006 by one to four peoples. We spent a total number of 199 days of surveys. In November 2002 a capture-mark-recapture program was set up with several hundreds of snakes individually and permanently marked (by XB from the CNRS, and Ivan Ineich from the MNHN) essentially on Signal island, but also to a lesser extent on Porc-Epic, and Amédée islets. The CMR program was intensified and extended the following year to Nouaré, Bayonnaise and Brosse (XB, II), and then to Konduyo, Tenia, Mba, and Larégnère in 2004, 2005 and 2006 (FB, XB).

CAPTURES AND MEASUREMENTS

As the snakes are mostly visible when they cross the shore, moving between the sea and the land, the whole perimeter of each islet was surveyed, both during the day and at night. The inland was also regularly surveyed. Most

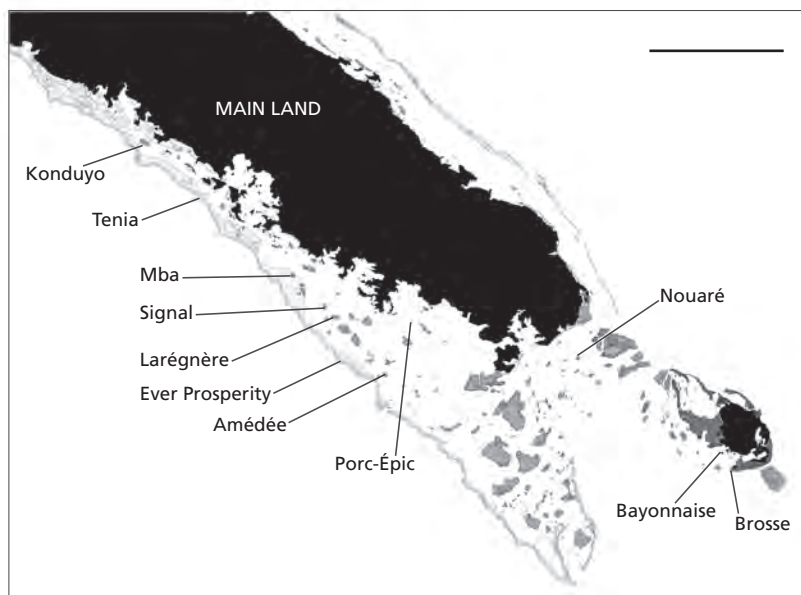


FIG. 5. Study area: the South-West lagoon of New Caledonia. Black areas indicate emergent land (mainland and islands), grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by the light grey areas. Scale bar = 40 km.

of the snakes were captured by hand and kept in cotton bags until processed. They were released after completion of the measurements 1 hour to 24 hours after capture. For each individual, the species, the sex, and the age class were recorded. We measured the size, snout vent length (SVL, ± 1 cm) by gently stretching the snake over a flexible ruler; the body mass (± 1 g) was gathered with a portable electronic scale. We carefully examined each animal, notably to count the number of black rings, the occurrence of abnormalities of the colouration, the number, the size and the shape of scars, we also counted the visible external parasites (ticks) and recorded a number of morphological details (see results and discussion). Most of the snakes were individually and permanently marked by scale clipping coupled with iron branding that often provokes a change in the colouration of the scales targeted. We noted an interesting divergence between the two species: iron branding entailed a colour change from black to white and from blue to black in the blue sea krait; but a change from yellow to dark orange and no change for the black scales in the yellow sea krait. A small proportion of the snakes were only observed by sight, notably during behavioural investigations, both on land or under water. The total number of snakes observed, pooling captures + recaptures, over the study period was 7,917 (4,823 *L. laticaudata* and 3,094 *L. colubrina*). The total number of individually marked snakes was 4,114 (1,913 *L. laticaudata* and 2,201 *L. colubrina*) with 3,598 recaptures (2,827 *L. laticaudata* and 771 *L. colubrina*). These values are among the highest for snake ecology, and given the fact that we set up the program in 2002, they show that the sea kraits of New Caledonia represent one of the best systems as stated in the introduction.

FEEDING HABITS

The abdomen of each snake captured was carefully palpated to check for the presence of prey in the stomach. As sea-kraits feed essentially on non-spiny fishes, it was easy to force them to regurgitate quickly their catch without risk of injury for the snake. On several occasions however, the preys were catfishes (*Plotosus lineatus*, see results), rendering this operation delicate; although still realisable with great care and patience (no snake was injured in these peculiar cases). On one occasion, the forced regurgitation provoked the death of the snake. Apparently the digested skull of a moray eel uncovered sharp teeth that probably cut a large blood vessel of the snake followed by a fatal haemorrhage. Except this regrettable case, we never observed any trouble directly caused by forced regurgitation and many of the manipulated snakes were recaptured later. In order to minimise the stress associated

with the loss of a large meal, we avoided collecting the stomach content on the same individual more than once. Similarly we discarded vitellogenic females and skinny snakes. The sampling bias hence introduced was partially compensated by spontaneous regurgitations and by a systematic collect of the preys during several weeks in 2005. We obtained 1,010 regurgitated prey items that were used for later identification. The preys collected were kept in 90% alcohol solution and identified to the nearest taxonomy level in the laboratory depending upon the state of the prey (*i.e.* presence of the dentition).

REPRODUCTION

The abdomen of adult females was carefully palpated to detect and count growing follicles and/or ovulated eggs. Well developed follicles still in the ovaries or ovulated eggs in the oviducts are easily recognisable at palpation; notably the seconds are more mobile. We also observed courtship behaviour (jerking, intensive tongue flicking, etc.) and mating with intromission of one of the hemipenises in the cloaca of the female on various occasions for both species. The timing of reproduction was inferred from those data. Laying periods were deducted from the comparisons between the periods during which vitellogenic females with large follicles or ovulated eggs have been observed and during which post laying females were detected. The post laying females were identified using recaptures (*e.g.*, a vitellogenic female being recaptured with an empty abdomen) or after the inspection of the posterior part of the body: very emaciated females with a very distended skin revealing a recent laying episode.

RESULT AND DISCUSSION

COLOUR PATTERNS

Both species exhibit important variations; however the precise parts concerned by the variations (rings, background colour, and back versus belly for instance) diverge between the two species.

L. laticaudata: although the typical colouration is banded pattern of regularly spaced black rings on a blue background (Fig. 3) our large sample size enabled to detect several cases of melanism (Fig. 3) and a relatively high proportion of incomplete or divided black rings. The blue background is weakly variable and ranged from light to dark blue. The period previous sloughing provokes a change in the blue colour, from a bright blue to a light (milky) blue. The total (body + tail) number of rings is highly variable, ranging from 35 to 55. Such values extend the previously documented patterns (from 36 to 44: Ineich & Laboute 2002; Saint Girons 1964 figure 2). The coloration tends to evolve with age as many large (presumably old) individuals present a dark (blackish) back with a fusion of the rings sometimes forming a line above the back spine (Lorioux *et al.* 2008). However melanic and melanistic individuals appear at low frequency. We observed one fully melanic male (absolutely black) and five melanistic individuals where the chin, or a small proportion of the belly where clear; All these six animals were large (> 1m in snout vent length). Melanism is assumed to take place during the juvenile phase. In the sea kraits, such changes can occur during adulthood. We observed a rapid colour change, a marked specimen shifted from a “normal” blue coloration to a melanistic phase in 9 months (Lorioux *et al.* 2008). The black rings were almost entirely fused in a general black background. The background colour of the belly is generally clear (whitish). Most of the individuals present white dots on the ventral part of the black bands and/or black dots on the white ventral space between the rings. Sometimes these black dots join the rings, forming a ventral black line. Although most of the dots (black or white) are situated in the mid body, the position is very variable making unique combinations for each individual (sometimes helpful for individual identification).

L. saintgironsi: this species is also characterised by a banded pattern (hence the name *tricot rayé*). The background colour is far more variable compared to *L. laticaudata*. It ranges from greyish to bright red, with light brown and orange individuals (Fig. 3). In the south of the area (around the île des pins) the background is sometimes blue-grey, leading to possible confusion between the two species by many peoples (hence the occurrence of each species based

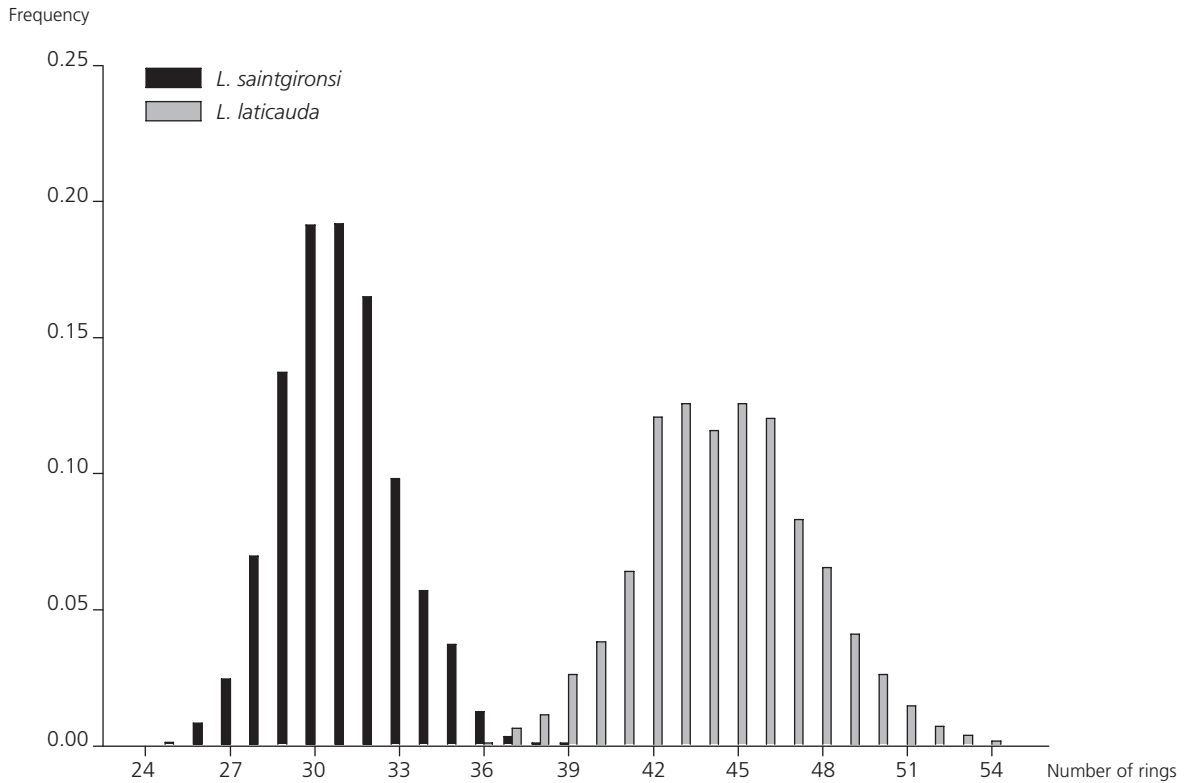


FIG. 6. Distribution of black ring number for *L. saintgironsi* (black) and for *L. laticauda* (grey).

on interviews becomes unreliable). Most of the individual exhibit a dark yellowish background colouration. Some individuals (mostly on Signal islet but also on Mba, Larégnère, Porc-Epic and Amédée) present a rusted coloration, the background appearing bright orange or red (Fig. 3). Interestingly, our mark-recapture study shows that this is a temporary coloration, disappearing suddenly after sloughing. A high proportion of rusted animals occurs on the Ever Prosperity wreck, suggesting that this place is used as a resting site during long periods; at least for the superficial layers of the skin to be deeply impregnated by the rust. Most of the snakes captured on the wreck are digesting or in the shedding process, preparing their slough (*e.g.*, the eye is opaque) or actually loosing the superficial layers of the skin. Many slough skins are observed on the wreck. For unknown reason, a number of yellow sea kraits were spotted on the highest metallic structures of the wreck, therefore displaying surprising climber abilities (see Bonnet *et al.* 2005). Several blue sea kraits also visit the wreck, their blue background do not turn into obvious rusted colour and they remain all on the lowest levels of the old vessel. The snakes that rest on the wreck originate from distant islets, for instance Signal Island is distant from 20 km (Fig. 5). Based on recaptures, our data show that sea kraits can travel over long distance: for instance individuals marked on signal islet have been recaptured on Amédée islet (Fig. 5). The yellow sea kraits present fewer black rings relative to *L. laticaudata*; and the number of rings is less variable ranging from 25 to 39 (Fig. 6). We never observed any case of melanism in this species, and the colouration apparently does not change with age (at least not in an obvious manner as observed in the blue sea krait). The belly is clear (whitish) and most of the individuals present some black dots between the black bands. The size of these white dots sometimes interrupt the black ring ventrally.

Interestingly, some of the characteristics used to discriminate *L. frontalis* (a closely related species occurring in Vanuatu and the Loyalty Islands) from *L. saintgironsi* (Cogger & Heatwole 2006) are actually shared by the two species (Fig. 1). Notably, the absence of a lower lateral connection between the black ring of the head and the first black ring of the neck, assumed to be typical from *L. frontalis* has been regularly observed in *L. saintgironsi*. Similarly the interruption of the ventral parts of the black rings, essentially in the front portion of the body, was commonly observed in *L. saintgironsi*. Interestingly, although observed in all our study sites, these problematic traits were very common in the south part of the lagoon (Bayonnaise and Brosse islets). This suggests that the boundary between *L. frontalis* and *L. saintgironsi*, in terms of colouration tends to be particularly unclear in the areas where the two species are the most likely to meet: Bayonnaise and Brosse islets are both relatively close to the Loyalty islands. Further studies are necessary to determine to what extent the two species are inter related through a gradient or are clearly separated through mating system frontier for example as demonstrated in the case of the closely related *L. colubrina* and *L. frontalis* (Shine *et al.* 2002a).

In both species, we observed incomplete or divided black rings. The most widespread anomalies are the half rings, the z-shaped and the y-shaped rings, they can occur either on the right or the left side of the snake. Other anomalies occur at a lower frequency: totally or partly fused rings (the y-shaped ring could be assimilated to a fusion between half and z-shaped rings), either on the back or the belly, a succession of thin and large rings instead of the regularly spaced rings, etc. We observed an individual with a belly with almost no ring visible. The bands were replaced by a succession of black squares (somewhat similar to the belly of *Natrix natrix*), the occurrence of y-shaped rings on the back was very high. All these peculiarities reinforce the confidence during individual identification.

BODY SIZE

The ranges of body sizes of the two species are given in the Fig. 7.

L. laticaudata: relative to *L. saintgironsi*, the blue sea krait is a slender species that also attains larger size (Fig. 7). The largest body size, 149 cm for total body length (137 cm SVL), was recorded on a female. This is a greater value compared to the other published maximal sizes for the species: 136 cm total length by Greer (1997), 96 cm SVL by Heatwole (1999), and 108.7 cm total length by Ineich & Laboute (2002).

L. saintgironsi: it is a medium sized, heavy bodied snake which makes it an intermediate sized species in the *L. colubrina* complex (in between *L. frontalis* and *L. colubrina*). The maximum SVL recorded for *L. saintgironsi* was 131 cm total length (120 cm SVL; Fig. 7). This value is greater than the maximum body size of 109 cm SVL provided by Cogger & Heatwole (2006), but slightly smaller than a specimen of 135.8 cm total length examined by Ineich & Laboute (2002). The fact that *L. saintgironsi* is more heavily built compared to *L. laticaudata* has been examined by Bonnet *et al.* (2005). The yellow sea snake is also relatively stronger as measured in terms of pulling-strength corrected by body mass (Bonnet *et al.* 2005), suggesting that the proportion of muscles is greater in this later species.

DIET

Accordingly to other studies, *L. saintgironsi* is highly specialized on anguilliform fishes, 100% of the prey were moray eels or fishes with a similar gross morphology (anguilliform fishes, Shetty & Shine 2002a; Heatwole 1999; Ineich & Laboute 2002; Reed *et al.* 2002). *L. laticaudata*, is often described as a snake that feed regularly on non-anguilliform fishes in the literature (Greer 1997; Heatwole 1999; Ineich & Laboute 2002). Our data provide a different picture to this widespread view; the diet of the blue sea krait was constituted by 96% of anguilliform fishes in New Caledonia. We nonetheless found several non-anguilliform fishes, *Ptereleotris* sp., *Plotosus lineatus* and an unidentified species. The discrepancy between previously published data and our findings is probably due to the fact that our observations are based on a large data set compared to several anecdotic observations recorded under water.

The list of the species consumed by the sea kraits is provided in the Table 1. Such diversity of preys is likely among the most important in comparison with all the other species of snakes. As suggested in Vanuatu by Reed *et al.* (2002), sea kraits are extremely efficient natural samplers of the anguilliform fish communities. In New Caledonia,

the analyses of the stomach content of the two species of sea kraits show that the anguilliform fish community was far more abundant and diverse than previously suspected (Ineich *et al.* 2007; Table 1). Through the snake's diet, we recorded 15 new fish species for the area. Studying the diet of the two neo-caledonian sea kraits offers enormous potential for monitoring the fish biodiversity of the lagoon, and to better understand how the species, and within species the sexes exploit the feeding resources. Notably to appreciate to which extend the species and the sexes compete or not during foraging activities.

REPRODUCTION

The few data available on the reproduction of the Neocaledonian sea kraits were incorrect. Therefore, the information presented below, although limited, provide the first basis that clearly show divergences between the two species.

The presence of follicles and/or eggs in the abdomen of the females combined with the time during which we observed females with a very emaciated posterior part of the body, and courtship or mating enabled to characterize the timing of reproduction in both species (Fig. 8). For *L. saintgironsi*, courtship and mating were observed in November (Fig. 8). Unfortunately, our field work never began before November; it is likely that we missed the beginning of the mating period (Fig. 8). Vitellogenic females were detected from November to February with a peak in November-December. A three-four month period for vitellogenesis is a normal value in snakes, and thus was expected (Bonnet *et al.* 1994); however we cannot exclude the fact that the process might start earlier in October. Notably, our estimate for the duration of vitellogenesis may contain different cohorts of females; several starting earlier (October or before?)

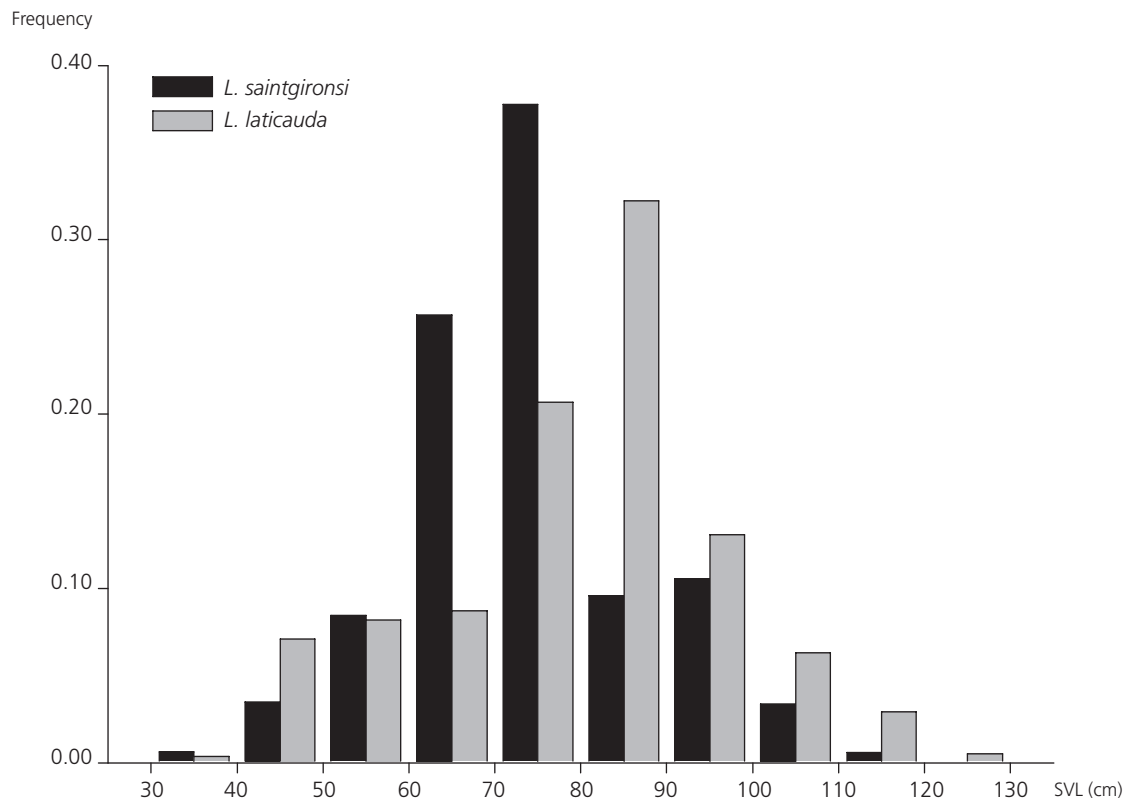


FIG. 7. Distribution of body length (SVL, cm) for *L. saintgironsi* (black) and for *L. laticauda* (grey).

TABLE 1. List of the fish species identified from sea kraits stomach contents.

Family	Species
Muraenidae	<i>Anarchias allardicei</i>
	<i>Anarchias</i> sp.
	<i>Cirrimaxilla formosa</i>
	<i>Echidna</i> sp.
	<i>Echidna unicolor</i>
	<i>Enchelycore pardalis</i>
	<i>Gymnothorax australicola</i>
	<i>G. albimarginatus</i>
	<i>G. buroensis</i>
	<i>G. chilospilus</i>
	<i>G. cribroris</i>
	<i>G. dorsalis</i>
	<i>G. eurostus</i>
	<i>G. favagineus</i>
	<i>G. fimbriatus</i>
	<i>G. fuscomaculatus</i>
	<i>G. gracilicauda</i>
	<i>G. meleagris</i>
	<i>G. moluccensis</i>
	<i>G. monochorous</i>
	<i>G. margaritophorus</i>
	<i>G. nudivomer</i>
	<i>G. pindae</i>
	<i>G. pseudothyrosideus</i>
	<i>G. reevesi</i>
	<i>G. reticularis</i>
	<i>G. richardsoni</i>
	<i>Gymnothorax</i> sp.
	<i>G. undulatus</i>
	<i>G. zonipectis</i>
	<i>Scuticaria tigrina</i>
	<i>Scuticaria okinawae</i>
	<i>Stophidon sathete</i>
<i>Uropterygius alboguttatus</i>	
<i>U. concolor</i>	
<i>U. fuscoguttatus</i>	
<i>U. macrocephalus</i>	
<i>Uropterygius</i> sp.	
<i>U. cf. xanthospilus</i>	
Ophichthidae	<i>Muraenichtys</i> sp.
	<i>Myrophis microchir</i>
	<i>Myrichthys maculosus</i>
	<i>Ophichthus</i> sp.
<i>Schismorhynchus labialis</i>	
Congridae	<i>Conger cinereus</i>
Muraenesocidae	<i>Muraenesox cinereus</i>
Microdesmidae	<i>Ptereleotris</i> sp.
Plotosidae	<i>Plotosus lineatus</i>

and the other later (December). Post reproductive females were detectable from December to late February with a peak in January, suggesting that the laying period ranged from December to February (Fig. 8). For *L. laticaudata*, courtship or mating were observed much later, from early December to mid-March (Fig. 8). Similarly, growing follicles or eggs were detected between December and March with a peak in January (Fig. 8). The presence of post-reproductive females from January to March suggests that the laying period ranges from January to March (Fig. 8). If so, this means that vitellogenesis may sometimes require only two month (Fig. 8); reinforcing the notion that the females are not highly synchronised in the timing of reproduction. Overall, the respective reproductive period of the two species of sea kraits differ. Broadly *L. saintgironsi* breed earlier (last months of the year) compared to *L. laticauda* that breed essentially at the beginning of the year. Nonetheless, there is some overlapping between the two reproductive seasons from November to February (Fig. 8).

The two species diverge for other reproductive characteristics. For instance in terms of behaviour during courtship or mating. *L. saintgironsi* was always observed in couple while *L. laticaudata* was always found in larger group with at least 2 males and up to 5 males attempting copulation. Courtship and mating was observed under large rocks or logs on a dry substrate in *L. saintgironsi*. By contrast, amorous *L. Laticaudata* were observed very close to the sea (partly under water), on a wet substrate and sometimes in the open (but at night). In both species we never observed male to male combat and the typical jerking of the male was displayed at a very low intensity compared to what can be observed in terrestrial snakes.

Meristic data on the size of the reproductive females and on clutch size are summarized in the Table 2. The smallest (presumably youngest) reproductive females attained 75.5 cm in SVL in *L. saintgironsi* and 88.5 in *L. laticaudata*. These body sizes correspond broadly to the minimal size at maturity. For both species, clutch sizes are far smaller than previously stated (Saint Girons 1964; Ineich & Laboute 2002; Heatwhole 1999). For example, Saint Girons (1964) inferred from dissection and palpation that a clutch size of 15 eggs might be a minimal value for *L. saintgironsi*. We obtained a 5 times smaller value with a mean clutch size of 3 eggs (Table 2). However, Saint Girons did not had at its disposal fully vitellogenic females, and its count might be more related to the initial number of follicles recruited (or ready to be recruited) rather than to the actual number of

TABLE 2. Meristic data on reproductive female *L. saintgironsi* and *L. laticaudata*.

	<i>L. saintgironsi</i>	<i>L. laticaudata</i>
SVL (cm)	92.08 ± 7.56 (75.5-107.5)	107.28 ± 7.94 (88.5-129.5)
N	80	102
Clutch size	3.25 ± 1.27 (1-8)	3.61 ± 0.88 (1-5)
N	72	90

follicles that will develop until ovulation stage. The data we provide for *L. laticaudata* are likely to be the first available for the area. Although the clutch size of the blue sea krait was slightly greater relative to the yellow sea krait, it was also less variable. As expected in a species where reproductive females are spread over a large range of body size (SVL from 75.5 cm to 129.5 cm pooling the two species) we found a positive correlation between maternal size and the number of follicles palpated (Fig. 9).

Despite intensive field work during the putative laying period of both species, we still ignore where the females lay their eggs (and we thus still ignore incubation duration or embryonic stage at laying). Due to the configuration of the islets, the potential laying sites are not very diverse. The burrows of sea birds (Procelariforms) and the large block fields that are both intensively used as shelters by the sea kraits are the best laying sites identified yet. In the two places, the temperatures are stable and theoretically suitable for incubation (unpublished data). Although humidity is another crucial parameter we did not record accurately, the sand remained relatively wet in these two potential laying sites. As we never found any clutch deposited in its natural place, we also ignore the incubation time, and consequently we have no accurate data on the neonates. A three-four month period is assumed to be reasonable (Guinea 1986). Given our large sample size, the smallest snakes observed likely provide a reliable estimate of the size of the neonates. The mean body size of the ten smallest sea kraits was 39.5 ± 1 cm (19 ± 6 g) in *L. laticaudata* and 37.5 ± 2 cm (21.5 ± 7.5 g) in *L. saintgironsi*. Such a relatively large size for the very young individuals corresponds probably to the minimal dimensions of the body and of the head necessary to catch and to swallow the smallest preys available to the neonates who also feed on anguilliform fishes.

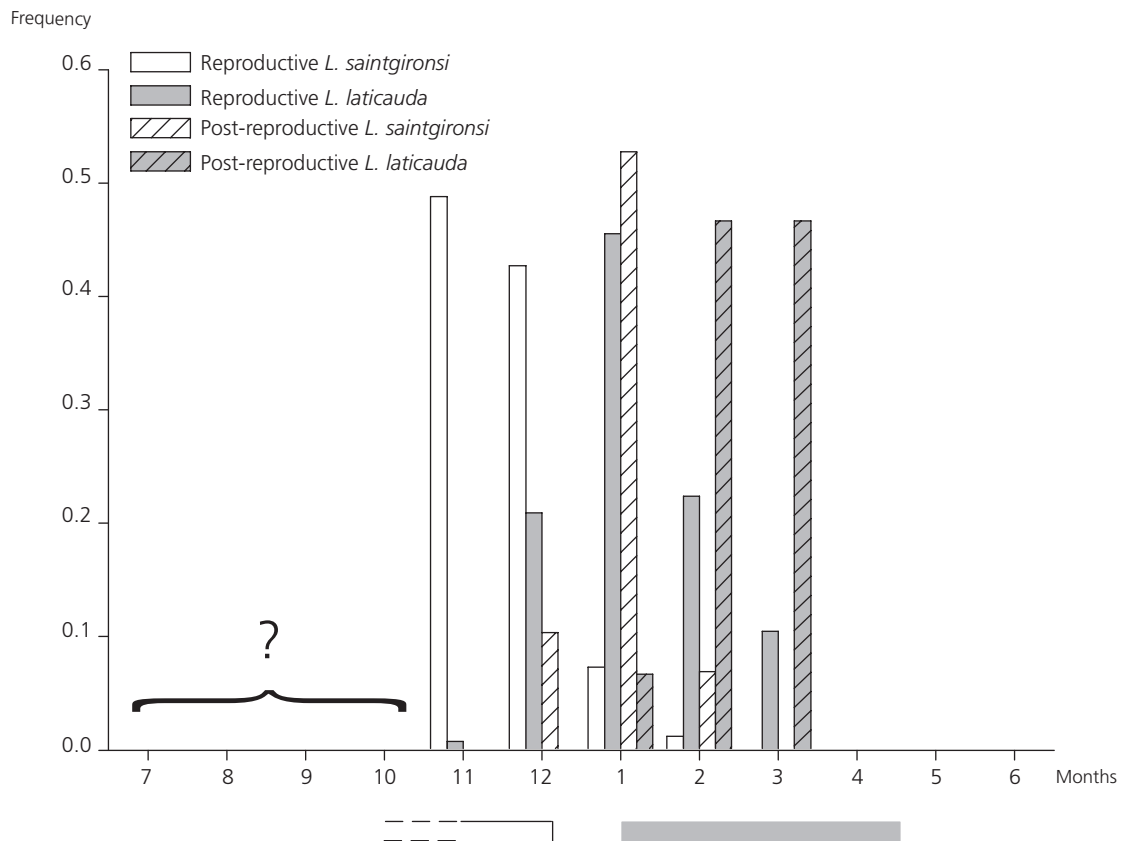


FIG. 8. Reproductive periods of sea kraits in New Caledonia. The white and grey boxes on the “Y” axis represents periods where courtship behaviour has been observed for *L. saintgironsi* and *L. laticaudata* respectively. The question mark represent period where no field work occurred.

In contrast to what has been stated, our information show that reproduction is very seasonal in New Caledonia for the sea kraits (Greer 1997). Most of the studies on the sea kraits have been carried out on equatorial populations. Geographic variations are likely to occur in the characteristics of reproduction accordingly to changes in environmental conditions (food availability, temperature, etc.). Our study populations are situated at the extreme south of the distribution range of the *Laticauda* genus. The winter is relatively cold in south New Caledonia. Perhaps that the ambient temperatures (of the water, air, and substrate) are not favourable to meet the physiological requirements of reproduction (*i.e.* high metabolic activity for vitellogenesis, mating, and incubation). In the same vein, perhaps that the high energetic and plastic demands of vitellogenesis are better covered in summer (high food availability, favourable temperature to catch and to digest the preys). Finally, the availability of small preys for the neonates might also be an important parameter that determines the seasonal character of reproduction of the sea krait. Teasing apart the respective contribution of these different factors will require an intensive field work.

HABITAT

Broadly speaking, our numerous observations on the terrestrial habitats used by the neo-caledonian sea kraits are in accordance with the observation previously done by Saint Girons (1964). The snakes come on land to digest, slough their skin, mate, rest, and lay their eggs. Most of the time they remain invisible to human observers. As typical snakes, they choose the roots of large trees, cavities, crevices, burrows, logs and large rocks to hide themselves. When the air is cool (*e.g.*, $< 20^{\circ}\text{C}$), they can also be observed basking in the grass, or immobile in small puddles of hot water ($> 28^{\circ}\text{C}$) left by the tide on the flat beach rocks. As expected from sea snakes, the sea kraits tend to use mostly the habitats

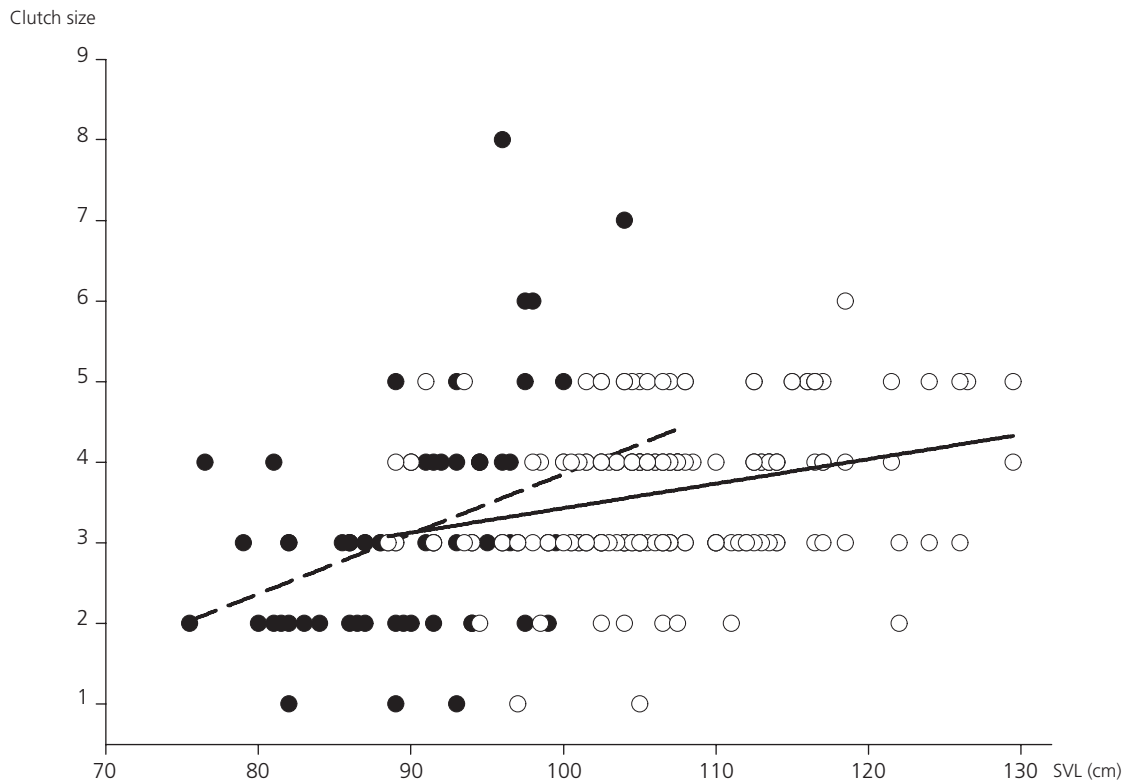


FIG. 9. Body length (SVL, cm) in relation to clutch size in *L. saintgironsi* (black circles) and *L. laticaudata* (white circles). SVL was positively correlated to clutch size in *L. saintgironsi* (dashed line, $F = 15.57$, $df = 1.70$, $r^2 = 0.18$, $p < 0.001$) and in *L. laticaudata* (black line, $F = 31.65$, $df = 1.87$, $r^2 = 0.27$, $p < 0.001$).

close to the shore. However, the yellow sea kraits sometimes undertake relatively long trips on land. *L. saintgironsi* notably tends to climb on the top of the hills (e.g., Porc Epic), on the trees and on any elevated structure that offers sufficient shelters. In comparison to *L. laticaudata*, this species is a better crawler and is an excellent rock climber (Bonnet *et al.* 2005). It also moves more frequently within the herbaceous vegetation that covers the inland, cruising during long periods, visiting different burrows. By contrast, the blue sea krait is never observed far from the sea. This species displays poor abilities to move on land over long distances or to climb (Bonnet *et al.* 2005). Interestingly, it uses intensively the large rocks that are submerged at high tide.

To date, no extensive data is available about the submarine habitats used by the sea kraits (*i.e.* foraging areas). We do have relatively long (> 20 hours) observations of the snakes foraging in the vicinity of the islet, exploring the coral matrix. However, this concerns solely the yellow sea kraits. All the blue sea kraits spotted under water were swimming in a strait direction toward or from the sea further than the reef flat. We know from the analyses of the stomach contents combined with numerous recaptures that the time spent at sea is devoted to foraging. We also know the spectrum of prey consumed by the snakes. However, as the ecology of the anguilliform fishes predated by the snakes is barely unknown, it is impossible to infer the foraging sites of sea snakes through their diet. We are currently setting up a study on diving behaviour.

ACTIVITY PATTERN

Surprisingly, Saint Girons (1964) noticed that the sea kraits of New Caledonia do not exhibit any particular activity pattern. In contrast, our very first observations and our analyses revealed that the snakes decide to leave their shelters, to come on land, to mate or to swim parallel to the shore at very precise time periods. For example, there are sharp peaks of the locomotor activity displayed by the snakes with strong differences between the two species (Fig. 10). *L. saintgironsi* began to move to or from the sea at the end of the afternoon (sunset) whereas *L. laticaudata* are mostly active after nightfall. This could be due to either predator avoidance or thermoregulation (to prevent overheating while crossing the beach).

When rain occurs after a dry period, the usual activity pattern of snakes is disrupted. In these conditions, whatever the time of the day, the two species stop their usual activity to drink (Bonnet & Brischoux 2008).

PREDATORS

Data on predation are scarce. The docile behaviour of sea kraits both on land and under water suggests that predation rates are low. Perhaps that the sea kraits rely on their spectacular banded pattern associated with potent venom as a main anti-predator tactic. A large fish was instantaneously killed after having swallowed a sea krait (Aquarium of Nouméa, pers. comm.) However, when on land the sea kraits flee away under the threat caused by rapidly approaching humans (Shine *et al.* 2003a); similarly, when moving under water a gentle touching of the snake triggers a fast swimming towards the nearest cavity in the coral. These behaviours reveal that the sea kraits still display the main anti-predator behaviour of most snake species. Clear predation cases are available on both habitats. On land, sea-eagles, and reef herons have been observed catching the snakes (Leach 1928; Bauer & Devaney 1987). Analyses of the stomach content of tiger sharks and of large cods indicate that the sea kraits are not excluded as food items by these large fishes (Rancurel & Intès 1982; Kulbicki pers. comm.) Sea-anemone (Ineich & Laboute 2002; Devincq pers. comm.), and crabs (Guinea, Voris & Jeffries in Heatwhole 1999) are able to capture juveniles and adult sea kraits as well (direct observations). Although important, all that information remains anecdotic and does not permit any quantitative evaluation of the impact of predation. Indirect data show that the conflict between the sea kraits and the fishes are quite common. The injuries (sometime impressive) and the scars that display many sea kraits (the majority of them in certain areas) reveal frequent attacks by fishes. The teeth marks and the jaw shape of the bite are easily recognisable. However, teasing-apart predation from defensive bites inflicted by potential preys is almost impossible. Indeed, it is likely that while prospecting for eels in the coral matrix, the coveted prey retaliate; moray eels notably are renewed for their defensive abilities. Alternatively, the sea kraits might be attacked and sometimes

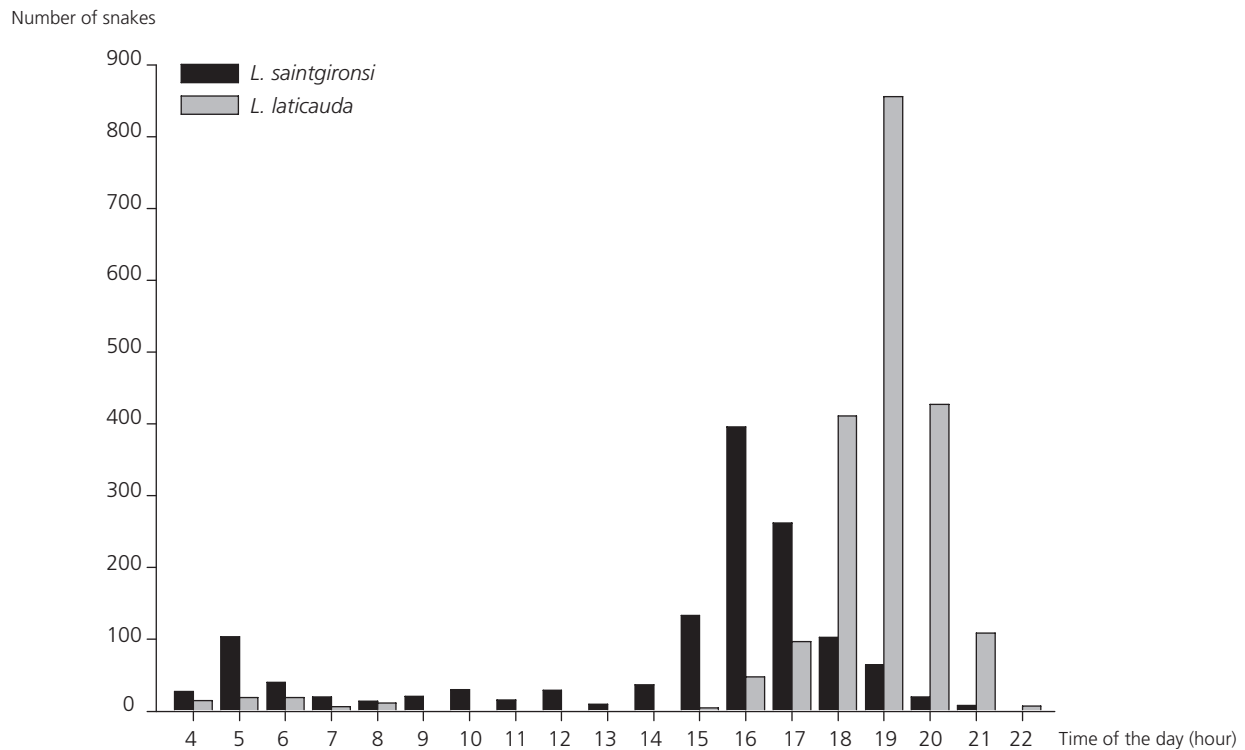


FIG. 10. Comparative pattern of catchability of *L. saintgironi* (black bars) versus *L. laticauda* (grey bars). Each bar represents the total number of snakes observed per-hour.

consumed by the larger eels, some of them being largely out of their prey size range (> 1m). Predation on land is far more mysterious. During our intensive field work we never saw any capture or predation attempt by the birds supposedly dangerous to the snakes. Both reef herons and ospreys occur in large number in our study sites. One dead (mummified) sea krait has been found in an osprey nest (Signal Islet, 2003), but the skeleton of the snake was intact and the birds sometimes use strange items as nest ornamentation (P. Villard pers. comm.). We acknowledge that our presence may deter the avian predators from trying to catch the snakes: indeed the birds are systematically threatened from relatively long distance by human walking on the beaches. Overall, the influence of the predators on the sea kraits is largely an open field.

VENOM AND BITES

A common trait displayed by nearly all sea snakes (except the fish egg eater *Emydocephalus annulatus*) is a very potent venom that permits to kill the preys almost instantly. A very fast action of the venom might prevent the loss of the prey in the ocean; trailing a prey in such an environment might be very complicated for the snakes. Direct observations of sea kraits hunting moray eels confirm the extreme rapidity of the venom in killing the fishes. The venom of the sea krait is often described as one of the most dangerous, potentially lethal to the humans (Heatwhole 1999; Ineich & Laboute 2002). However, these snakes are extremely docile; the occurrence of the bites to the humans is virtually equal to zero. Few cases of envenomations by sea snake have been recorded in New-Caledonia. Imprecise identification of the species of snake impedes to appreciate to what extent the sea kraits inflicted serious or fatal bites to humans.

In the course of our field study we manipulated thousands of snakes. Assuming that the snakes have been handled at least 3 times: at capture, during measurements and during releasing (we discard the many other manipulations, forced regurgitation, locomotor performances tests, etc.), we handled the snakes on more than 20,000 occasions. The vast majority of the snakes remained fully defenceless. A small proportion of them opened the mouth during handling. We experienced only 2 real defensive bites. Surprisingly, we noticed only moderate local and general troubles following the bites. It is impossible to state if the venom was injected in sufficient amounts to produce a strong effect. Greer (1997) noticed that bites are infrequent and are not considered dangerous to human. Overall the docile behaviour of the sea kraits is one of their prime traits in front of humans. Nonetheless, real bites are not fully impossible and the effects of a strong bite remain unknown. Therefore, the sea kraits must not be manipulated unless necessary.

STATUS OF POPULATIONS IN NEW CALEDONIA

New Caledonia is one of the very rare spot on earth where very large numbers of venomous snakes cohabit successfully with human populations. The tricots rayés benefit from a positive image and most of the local people and tourists respect the snakes (although the snakes are very often considered as threatening creatures). The situation is not totally idyllic however as many sea kraits are still killed for totally unjustified reasons (Saint Girons 1964 and information below). Unfortunately, long term data are not available, rendering very delicate any attempt to assess the status of sea kraits. However, a number of examples permit to show that sea krait population can be negatively affected by human activities.

First, according to local people, the sea kraits were common on the 2 major beaches of Nouméa: Anse Vata and Baie des Citrons. Since 2002, despite intensive sampling, we never saw any sea kraits crossing these two sites. Few sea kraits can be observed under water nearby these beaches or resting in the sea water pumping room of the aquarium indicating that several individuals still cruise around. Both beaches have been completely modified to make them more attractive to the tourists. Not only the human frequentation is very high, but also all the potential shelters for the animals, rocks, or logs have been removed.

Second, on Maître islet (near Nouméa), an officially classified natural reserve where hunting, plant collecting are prohibited, a recent construction of huge tourism infrastructure was preceded by the destruction of most of the natural islet on the side usually employed by the snakes (Fig. 4). The substrate, both on land and under water has been removed (sometimes using dynamite). Many buildings, concrete pathways, swimming pool, restaurant, bungalows etc. form a totally unsuitable habitat for the flora and the fauna. While the sea kraits were easily found until 2002, it is now barely impossible to observe any. The disappearing of the sea kraits was already obvious during the first stages of the destruction of the islet (observations by XB and II); strongly suggesting that the snakes have been actively killed in huge numbers to “clean” the area.

Last, on one of the surveyed islet (Konduyo, Fig. 5), one of us (FB) failed to detect any sea krait. It was very surprising: the configuration of the islet apparently offered the same kind of environment than what is found on the other islets that accommodate high snake densities (e.g., Signal islet). We later learn that this islet has been inhabited during 25 years until recent years. We acknowledge that it is hard to know if a sea krait population existed before the presence of the humans but the total absence of snakes on that kind of islet led to some interrogations.

Hopefully, those cases are still limited, and most of the time the cohabitation of sea kraits and human is peaceful. Some of our study sites (Signal and Amédée islets for instance) support both high population density of sea snakes and a high human pressure with nearly hundreds of people visiting these < 8 ha islets each week. Inevitably, most of the snakes have been closely approached by humans without being killed or injured. Although we still find regularly snakes crushed under rocks after the week-ends, obviously maliciously killed by human visitors, the mortality rate remains low and do not seem to impact the snake populations. It is likely that a promotion in favour of the snakes could improve the situation. Many peoples and tourists are attracted by the sea kraits, perhaps thanks to their beautiful colour patterns. An effort of scientific vulgarisation about their natural history and ecology has been undertaken and should be developed.

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REFERENCES

- BAUER A. M. & DEVANEY D. 1987. — Convergence and mimicry in sea snakes and other New Caledonian reef flat organisms, in VAN GELDER J. J., STRIJBOSH H. & BERGERS P. J. M. (eds), *Proceedings of the 4th Ordinary general meeting of the societates europaea herpetologica*. Catholic University of Nijmegen, Nijmegen: 43-48.
- BONNET X., NAULLEAU G. & MAUGET R. 1994. — The influence of body condition on 17- β estradiol levels in relation to vitellogenesis in female *Vipera aspis* (Reptilia, Viperidae). *General and Comparative Endocrinology* 93: 424-437.
- BONNET X., INEICH I. & SHINE R. 2005. — Terrestrial locomotion in sea snakes: the effects of sex and species on cliff-climbing ability in sea kraits (*Serpentes, Elapidae, Laticauda*). *Biological Journal of the Linnean Society* 85: 433-441.
- BONNET X. & BRISCHOUX F. 2008. — Thirsty sea snakes forsake their shelter during rainfall. *Austral Ecology* 33: 911-921.
- COGGER H. & HEATWOLE H. 2006. — *Laticauda frontalis* (De Vis, 1905) and *Laticauda* n. sp. Nov. from Vanuatu and New Caledonia (Serpentes: Elapidae: Laticaudinae), a new lineage of sea kraits. *Records of the Australian Museum* 58: 245-256.
- GREER A. E. 1997. — *The biology and evolution of australian snakes*. Surrey Beatty and sons Pty Ltd, Chipping Norton, NSW, Australia, xii + 358 p.
- GUINEA M. L. 1986. — *Aspects of the biology of the common Fijian sea snake Laticauda colubrina* (Schneider). Unpublished Master's Thesis, The University of the South Pacific, Suva, Fiji.
- HEATWOLE H. 1999. — *Sea Snakes*. Australian Natural History Series. University of New South Wales, Sydney, 148 p.
- INEICH I. & LABOUTE P. 2002. — *Sea snakes of New Caledonia*. IRD et Muséum national d’Histoire naturelle, Collection Faune et flore tropicales, Paris, 302 p.
- INEICH I., BONNET X., BRISCHOUX F., KULBICKI M., SÉRET B. & SHINE R. 2007. — Anguilliform fishes and sea kraits: neglected predators in coral-reef ecosystems. *Marine Biology* 151: 793-802.
- LEACH J. A. (1928). — Notes made during a holiday trip to New Caledonia. *Emu* 28: 20-42.
- LORIOUX S., BONNET X., BRISCHOUX F. & DE CRIGNIS M. 2008. — Is melanism adaptive in sea kraits? *Amphibia-Reptilia* 29: 1-5.
- RANCUREL P. & INTÈS A. 1982. — Le requin tigre, *Galeocerdo cuvieri* Lacépède, des eaux neo-calédoniennes – examen des contenus stomacaux. *Tethys* 10 (3): 195-199.
- REED R. N., R. SHINE, S. SHETTY & H. COGGER. 2002. — Sea kraits (*Squamata: Laticauda* spp.) as a useful bioassay for assessing local diversity of eels (*Muraenidae, Congridae*) in the western Pacific Ocean. *Copeia*:1098-1101.
- SAINT GIRONIS H. 1964. — Notes sur l’écologie et la structure des populations des Laticaudinae (Serpentes: Hydrophiidae) en Nouvelle-Calédonie. *La Terre et la Vie* 111: 185-214.
- SHETTY S. & SHINE R. 2002a. — Sexual divergence in diets and morphology in Fijian sea snakes, *Laticauda colubrina* (Laticaudidae). *Austral Ecology* 27:77-84.
- SHETTY S. & SHINE R. 2002b. — Activity patterns of yellow-lipped sea kraits (*Laticauda colubrina*) on a Fijian island. *Copeia*:77-85.
- SHETTY S. & SHINE R. 2002c. — The mating system of yellow-lipped sea kraits (*Laticauda colubrina*, Laticaudinae). *Herpetologica* 58:170-180.
- SHETTY S. & SHINE R. 2002d. — Philopatry and homing behavior of sea snakes (*Laticauda colubrina*) from two adjacent islands in Fiji. *Conservation Biology* 16:1422-1426.
- SHINE R. & SHETTY S. 2001a. — The influence of natural selection and sexual selection on the tails of sea-snakes (*Laticauda colubrina*). *Biological Journal of the Linnean Society* 74:121-129.
- SHINE R. & SHETTY S. 2001b. — Moving in two worlds: aquatic and terrestrial locomotion in sea snakes (*Laticauda colubrina*, Laticaudidae). *Journal of Evolutionary Biology* 14:338-346.
- SHINE R., REED R. N., SHETTY S. & COGGER H. G. 2002a. — Relationships Between Sexual Dimorphism And Niche Partitioning Within A Clade Of Sea-Snakes (Laticaudinae). *Oecologia* 133:45-53.
- SHINE R., REED R. N., SHETTY S., LEMASTER M. & MASON R. T. 2002b. — Reproductive isolating mechanisms between two sympatric sibling species of sea-snakes. *Evolution* 56:1655-1662.
- SHINE R., BONNET X. & COGGER H. G. 2003a. — Antipredator tactics of amphibious sea-snakes (Serpentes, Laticaudidae). *Ethology* 109:533-542.
- SHINE R., COGGER H. G., REED R. N., SHETTY S. & BONNET X. 2003b. — Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). *Journal of Zoology (London)* 259:261-268.

