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## TERRESTRIAL HABITATS INFLUENCE THE SPATIAL DISTRIBUTION AND ABUNDANCE OF AMPHIBIOUS SEA KRAITS

### IMPLICATION FOR CONSERVATION

Xavier Bonnet and François Brischoux

#### Introduction

Sea kraits are amphibious snakes that share their life between two worlds: the ocean, where they capture their prey, and land, where they return for performing many other vital activities (Heatwole 1999; Figure 3.1). Because sea kraits feed on relatively large, generally widely dispersed, and thus not easily accessible predatory fish (mostly moray eels and congers), long foraging trips alternate with digestive episodes lasting from days to weeks (Brischoux *et al.* 2007; Figure 3.2). Furthermore, the integument of sea snakes presents a large surface area to the environment, and this tends to constrain thermal and hydro-mineral balance (Lillywhite *et al.* 2008, 2009). Consequently, sea kraits experience prolonged physical, physiological, and behavioral shifts when they move between water and land. This amphibious lifestyle and the associated constraints have attracted substantial, albeit asymmetrical, scientific attention: Marine life-history traits of sea kraits are relatively well studied, whereas terrestrial aspects remain poorly documented. Information regarding the piscivorous diet and the morpho-functional adaptations to marine life of sea kraits has been reported in numerous publications and textbooks, whereas comparatively very few investigations have focused specifically on their terrestrial ecology. This bias seems paradoxical for colonial marine tetrapods that aggregate on narrow shorelines but forage over large oceanic areas, because it is more difficult to monitor animals



**FIGURE 3.1** An adult male Yellow Sea Krait (*Laticauda saintgironsi*) moving to the sea. The pictured individual exhibits a dark gray dorsal color pattern.

Source: Photograph by Xavier Bonnet.



**FIGURE 3.2** An adult female Yellow Sea Krait (*Laticauda saintgironsi*) regurgitating a freshly captured Moray Eel (*Gymnothorax eurostus*). This photograph illustrates the relative size of the prey; the left fang of the snake is visible.

Source: Photograph by Xavier Bonnet.

when they are at sea than when they are on land. Considering seabirds and pinnipeds, terrestrial research preceded marine investigations until technical development of telemetry enabled investigators to collect data on foraging or dispersing individuals (Ropert-Coudert and Wilson 2005).

In this chapter, we focus on the diversity of the terrestrial habits and habitat requirements of two species of sea kraits and the influence of microhabitat selection on their spatial distribution. The information we discuss is largely based on the results from a mark–recapture study in these species of sea kraits conducted at various sites in the very large lagoon of New Caledonia during the years 2002–2012 (Bonnet 2012). This relatively long-term monitoring and the large amount of data collected (>22,000 observations) offered us an opportunity to assess the relationships between terrestrial habitats, specific habitat requirements, and the spatial distribution of these snakes.

Sea kraits are very abundant in New Caledonia, where the lagoon stretches approximately 600 km along a north–south gradient. This large marine area of 24,000 km<sup>2</sup> is divided by an approximately 400-km mountain chain, whereas the distance from land to the barrier reef ranges from a few hundred meters to >60 km (Bonnet *et al.* 2015). Numerous colonies of sea kraits are distributed across this very wide range of geographical and climatic conditions. Most colonies are found on small coralline islets (Figure 3.3, inset), especially in the widest parts of the lagoon, but sea kraits also colonize shorelines of the mainland. Each site exhibits a singular physiognomy characterized by the total surface available to the snakes (sea kraits do not penetrate far inland), surrounding seafloor, exposure to dominant winds and currents, elevation, geological substrate, climate, vegetation, animal communities, and so on (Figure 3.3). The distribution of microhabitats (*e.g.*, beach rocks, sandy beaches, trees, and artificial constructions) is consequently heterogeneous among sites and also within each terrestrial site (see Figure 3.3). Due to the relatively small size and isolation of most islets, and due to the peculiar requirements of snakes, each rock, tree, log, or burrow may represent a potential refuge and thus creates critical fine-scale heterogeneity (Brischoux *et al.* 2009b; Lane and Shine 2011).

We begin with a short review of the activities of the sea kraits when they are on land. For each of these activities, we derive the associated essential eco-physiological requirements or constraints to examine the specific microhabitats selected by snakes and for what duration. Then, we examine the distribution of sea kraits over more than 30 sites in relation to available microhabitats to highlight the effects of variation in microhabitat and to recommend conservation strategies.



**FIGURE 3.3** Habitats of sea kraits in New Caledonia. (a) Typical sandy beach at low tide on the western tip of Améree islet (reserve Merlet, fully protected area,  $22^{\circ}26'40''\text{S}$ – $167^{\circ}05'46''\text{E}$ ). Dense vegetation provides easy access to shelters for sea kraits. (b) Western shore of Signal islet (protected area,  $22^{\circ}17'48''\text{S}$ – $166^{\circ}17'34''\text{E}$ ), also at low tide. Blocks of limestone—deposited on the shore and used for lime production ages ago—offer snakes excellent shelters. (Inset) Améree Island is densely populated by sea kraits, especially *Laticauda saintgironsi*, which easily cross the narrow beaches. The habitat here is less favorable for *Laticauda laticaudata* due to the lack of abundant large rocks at the beach.

Source: Photographs by Xavier Bonnet.

## Why Do Sea Kraits Come on Land Periodically?

It is well known that sea kraits forage on the seafloor of coral reefs and then return to land for digestion or to lay their eggs (see Chapters 2 and 4, this volume). However, these two activities are not the only reasons why sea kraits utilize terrestrial habitats, and thus, they may not accurately account for the time and energy budgets of these amphibious snakes. In addition, the importance of the periods when snakes are secluded and resting is insufficiently recognized. Many crucial physiological or behavioral tasks do not require movement or displacements. For example, to optimize the digestion and assimilation of large prey, individuals should minimize their expenditure of energy during digestive periods and thus should remain motionless. When on land, breathing does not require locomotor movement and merely follows regular inspiration/expiration cycles (Bartlett *et al.* 1986) that are not interrupted by relatively long periods of apnea associated with diving and swimming (Cook *et al.* 2016; see Chapter 2, this volume). Thus, although not measured, it is likely that digestion is optimized on land but not at sea, particularly for tropical reptiles. Indeed, temperature rarely constrains digestive physiology in tropical reptiles (Shine and Madsen 1996). This reasoning may also apply to vitellogenesis, ecdysis, and resting. Significant displacements and elevated expenditures of energy are required during foraging, mating, and dispersal. Consequently, spending long periods while relatively motionless in appropriate terrestrial refuges is a well-suited strategy that optimizes energy budgets in air-breathing marine species. Here, we briefly discuss the main terrestrial activities of the sea kraits and attempt to provide a crude estimate of the relative importance of each of these activities.

### *Digestion*

Digestion is often associated with a strong behavioral shift to inactivity for several reasons (Brischoux *et al.* 2011). First, availability of assimilated energy is likely to be maximized if other competing activities are reduced. Second, rapid digestion often requires the selection of a precise thermal range that optimizes the digestive activity, and this involves selection of a specific microhabitat during the digestive process (Greenwald and Kanter 1979). Third, a digesting snake usually has a very large prey item (see Figure 3.2) in the stomach for several days following ingestion, and this impedes locomotion (Shine and Shetty 2001). The last two points are particularly true for sea kraits that need to return to land to digest and thus to select optimal thermal

conditions for digestion that may not be available at sea and also because the presence of a large prey in the stomach impedes efficient swimming (Webb 2004, Winne and Hopkins 2006). For these reasons, digestion is probably one of the more important and frequent requirements that sea kraits perform on land.

More than one-third of the snakes we captured on land were digesting (31.6%,  $n = 19,404$  observations), and this fraction reached almost 50% for some categories (e.g., *Laticauda saintgironsi* females; Table 3.1). Digestion is one of the terrestrial activities for which we found the largest numbers of snakes, with the proportions for other activities ranging between 2% and 47% (see Table 3.1). During the austral summer, most snakes were digesting while secluded beneath a shelter, probably because air and surface temperatures were high during the day (Brischoux *et al.* 2009a; Bonnet *et al.* 2009). On the other hand, many digesting individuals were found basking during the austral winter. Interestingly, the two species differ in this respect. During the winter, *Laticauda laticaudata* was still digesting under shelters, whereas *L. saintgironsi* was basking conspicuously during the day. This interspecific difference is perhaps related to differences in thermal ecology, sensitivity to transcutaneous evaporative loss of water (e.g., see Lillywhite *et al.* 2009), terrestrial tendencies (Bonnet *et al.* 2005), or a combination of these factors.

### Ecdysis

Snakes periodically slough the epidermis of their skin (Figure 3.4), which permits growth, repairs injuries, and renews the permeability barrier, in addition to other possible functions. Each shedding cycle can be divided into several phases (Maderson 1965). During non-shedding periods (sometimes weeks or months), the epidermis is relatively quiescent. During the pre-shedding phase (2 or 3 weeks on average), cells proliferate from the stratum germinativum and form a new inner epidermal generation beneath the older outer epidermal generation of stratum corneum. During this phase, the epidermis is metabolically very active. Several days before the completion of this phase, a separating layer develops between the inner and outer epidermal generations, dulling the color of the skin and eyes (see Figure 3.4). This opacity degrades vision, impacts defensive behaviors, and can be associated with anorexia (Aubret and Bonnet 2005). Finally, the snake sheds the old outer generation of stratum corneum (“skin”) by employing specific movements of the body (ecdysis). Starting from the head, the old “skin” is generally removed

**Table 3.1 Summary of the Numbers of Observations of Sea Kraits Recorded During Their Main Activities<sup>a</sup>**

Activity	Species	Sex	<i>N</i> (%)	Additional Information
Digestion	Ls	F	1,314 (49.2)	Individuals found with prey item and/or highly digested material in the stomach
		M	2,303 (34.4)	
	Ll	F	811 (39.5)	
		M	2,374 (29.6)	
Sloughing skin	Ls	F	329 (11.7)	Individuals presenting at least one of the following characteristics: opaque eyes, milky skin, and sloughing
		M	651 (9.2)	
	Ll	F	262 (13.6)	
		M	750 (11.8)	
Recovering	Ls	F	114 (4.1)	Individuals presenting recent, sometimes severe, wound(s)
		M	160 (2.3)	
	Ll	F	92 (4.8)	
		M	269 (4.3)	
Resting	Ls	F	509 (41.2)	Individuals observed motionless in a refuge, without any material in the stomach, not wounded, and not (pre)shedding
		M	1,209 (43.1)	
	Ll	F	479 (37.0)	
		M	1,282 (34.3)	
Reproduction	Ls	F	224 (18.2)	Males observed courting ( <i>e.g.</i> , male jerking on a female), or mating, or gravid females ( <i>e.g.</i> , follicles or developed eggs in the abdomen)
		M	62 (13.1)	
	Ll	F	202 (19.5)	
		M	53 (3.2)	

<sup>a</sup>Sample sizes (*N*) indicate the number of individuals observed performing a given activity for each category of species and sex. Proportions (%) were calculated based on the total number of observations for which all the relevant information was available (*e.g.*, 2,671 female Ls and 6,703 male Ls were palpated to assess their digestive status). Variations in sample size occur due to incomplete information (*e.g.*, a snake observed with opaque eyes might not have been palpated). Several individuals were observed performing more than one activity (*e.g.*, recovering from a wound and digesting), which explains why the sum of percentages does not equal 1.

F, female; Ll, *Laticauda laticaudata*; Ls, *Laticauda saintgironsi*; M, male.



**FIGURE 3.4** A male Yellow Sea Krait (*Laticauda saintgironsi*) in the pre-shedding phase with shaded color pattern, sheltering in a log. A shed skin from another Yellow Sea Krait is visible on the left. The inset photographs feature a pre-shedding sea krait with opaque eyes (left) and another in the process of shedding (right).

*Source:* Photographs by Xavier Bonnet.

whole (see Figure 3.4). This process is facilitated if the snake can anchor the old “skin” onto a rough substrate.

Terrestrial refuges offer the potential of precise thermoregulation needed to meet the increasing metabolic demands of ecdysis (Gibson *et al.* 1989). Shelters also reduce the risks of predation (while opacity of the eyes obscures vision) and provide humid conditions that are essential for reducing evaporative loss of water during shedding. Because foraging and possibly transcutaneous exchanges of gases are also impeded during pre-shedding, immobility is profitable and more accessible on land than at sea. The removal of “old skin” is physically easier and can be performed unseen on land. It is thus expected that amphibious snakes should preferably come on land during the pre-shedding and shedding phases of ecdysis. We used visible indicators of pre-shedding (*e.g.*, opacity of the eye and whitish belly) and ecdysis to examine the extent to which sea kraits come on land to shed. It is likely that we misclassified some pre-shedding snakes into the non-shedding category when no obvious signs were visible.

On average, 12.3% of the snakes on land were observed in the process of ecdysis ( $n = 18,161$  observations). Most of these observations correspond to

pre-shedding snakes (58.2%)—an expected result because pre-shedding lasts longer compared to shedding. Many shed skins, either compacted (if shedding occurred between rocks) or stretched (if shedding occurred in the vegetation), were observed in places where refuges are abundant, but never on open, flat surfaces such as sandy beaches. During summer rainfalls following droughts, many snakes leave their shelter to drink fresh water from temporary puddles (Bonnet and Brischoux 2008). The proportion of pre-shedding snakes was greater during these observations, reinforcing the notion that well-buffered refuges are intensively utilized by sea kraits for shedding. We also observed many pre-shedding and digesting snakes that were sheltered in partly emerged shipwrecks. The skin of these snakes showed a marked red coloration, suggesting they had spent long periods in contact with rusted materials. Only 4% of the snakes were observed simultaneously with a prey in the stomach and in the process of ecdysis, but this reached 8.6% for snakes with well-digested food items (very soft palpation) ( $n = 13,053$  observations). These observations suggest that foraging and ecdysis tend to be temporally distinct. Clearly, ecdysis represents a major reason for sea kraits to come onto land, and during the pre-shedding period they are usually found quiescent within well-buffered shelters.

### *Recovery from Injuries*

During the course of the population survey, we observed many snakes with wounds or significant scars indicated by a marked change in the color of the tegument (Brischoux and Bonnet 2009). In many cases, such wounds were inflicted by fish, as revealed by the typical V-shape cuts caused by the teeth rows of anguilliform fish (Figure 3.5; Bonnet *et al.* 2010). We do not know how much time is necessary for individuals to recover from recent injuries, but the recovery time correlates with the severity of injury and is likely influenced by the general condition of the snake. We can broadly estimate that at least 1 week is necessary. Because swimming ability, osmotic balance, immunity, and possibly cutaneous respiration might be compromised by injury, sea kraits must shelter under well-buffered terrestrial refuges during the recovery period.

Our data suggest that injury and recovery are relatively frequent in sea kraits. We observed 635 cases in which at least one recent wound was visible (4.5%,  $n = 17,925$  observations; see Table 3.1). Detailed information was available on 358 occasions. Although in 49.5% of the cases the skin was superficially damaged, in 14.4% of the cases the underlying tissues were also



**FIGURE 3.5** A Yellow Sea Krait (*Laticauda saintgironsi*) with deep cuts (top) likely inflicted by a retaliating prey (Moray Eel or Conger). The cuts were sewn (bottom), and the snake recovered as indicated by recaptures.

*Source:* Photographs by Xavier Bonnet.

visible (see Figure 3.5). In severe wounds, muscles and/or the body cavity were exposed, and in the most extreme cases substantial portions of the skin and underlying tissues were missing. Snakes did not always recover from these deep wounds (*e.g.*, some wounded individuals were found dead), but most sea kraits exhibit scars, suggesting that recovery on land is generally successful providing that the snake can reach a refuge.

Overall, terrestrial episodes are essential for sea kraits recovering from wounds (and possibly from diseases). During these episodes, movements are likely to be minimized, thereby limiting accumulation of sand in the wounds and/or encounters with ticks that selectively target damaged skin.

### *Resting*

Resting enables individuals to recover from exhausting activities. It also permits individuals to optimize their time budget through the selection of the best time windows for engaging in energetically demanding or risky activities. Resting is thus an essential function in many animal species, but it has received little scientific attention. Theoretically, assessing resting is easy in snakes because the main activities are chronologically delimited. For example, foraging is generally separated from digestion, and in many instances, snakes do not engage simultaneously in multiple tasks or activities. Thus, the “resting status” can be relatively easily distinguished from other functions. Table 3.1 illustrates that the sums of the proportions for each activity per species or sex category are usually lower than 1, suggesting there is limited overlap among activities.

Here, we considered that a snake observed to be motionless within a terrestrial refuge, without any obvious prey item in the stomach, without wounds, without any obvious signs of pre-shedding, and not involved in reproduction (*e.g.*, developing eggs in females and mating season in males) was truly a resting individual. Although arbitrary, this procedure limited the risk of mixing resting with other activities when individuals, although motionless in their refuge, achieve other functions. Indeed, an apparently resting female may well be involved in the extremely demanding process of vitellogenesis (Bonnet *et al.* 1994; Van Dyke and Beaupre 2011). In practice, results were very similar whether reproduction was factored out or not, and therefore our data include reproductive individuals.

Our data suggest that a significant proportion of individuals (38.3%,  $n = 9,073$  observations; see Table 3.1) were observed while resting on land. This proportion is likely overestimated because snakes recovering from a disease,

with invisible internal wounds, during a non-obvious part of pre-shedding, or at the end of a digestive episode might have been wrongly counted as resting. Despite such potential imprecisions, however, it is noteworthy that sea kraits frequently come on land to rest, and this activity concerns a proportion of individuals similar to the cohort of digestive snakes.

The definition of resting we adopted here is not applicable to all species of snakes. For example, Turtle-headed Sea Snakes forage almost continuously, at least during daytime (Shine *et al.* 2004), and thus do not follow the sequential lifestyle for this major trait. Similarly, the notion that to be resting an animal must not be engaged in any other function (*e.g.*, reproduction) is questionable. Nonetheless, our data clearly suggest that snakes spend considerable amounts of time resting and that in most cases they are not performing any other obvious physiological task. We emphasize that resting is a neglected, albeit important, behavior that deserves further investigation.

### *Reproduction*

Sea kraits are oviparous, and thus gravid females are constrained to find suitable terrestrial nesting sites to lay their eggs. Gravid female sea kraits sometimes undertake long migrations to communal coastal oviposition sites, which is a classical observation for terrestrial species. Supposedly, specific sites offer appropriate conditions for incubation that are unavailable in remote offshore sandy islets (Bonnet *et al.* 2014). True sea snakes are viviparous and thus do not face these constraints. Discussing the respective advantages of oviparity versus viviparity is beyond the scope of this chapter (*e.g.*, see Shine 2014). However, there are several potential benefits associated with oviparity in sea kraits.

Copulation may be facilitated on land because the intromission of the hemipenis requires intimate contact between the partners and a position that appears much less stable under water (for pictures, see Heatwole 1999; Ineich and Dune 2013). Furthermore, we can hypothesize that it might be easier for a male to follow pheromonal trails deposited by reproductive females on land rather than those possibly dispersed and transported by sea currents (courtship appears highly visual in water; Shine 2005). Mating concentrates individuals in prescribed places such as small coralline islets, where rates of encounter increase; sexual selection is enhanced by the density of snakes because many males compete to access copulation and females can be choosy. Differential access to females may involve variable searching effort, ability to detect sheltered females, and jerking effort that can last for hours.

The more terrestrial sea kraits (*L. saintgiroisi*) form mating balls (Figure 3.6; see also Table 3.1) that are typically observed in near-shore vegetation. Gravid females with one to five males, curled and jerking, are routinely observed under large trees, or in the cavity of fallen trees, and within the dense herbaceous vegetation close to the shore (see Figure 3.6; see also Chapter 4, this volume). Mating is frequently observed during the day. On the other hand, the more aquatic species (*L. laticaudata*) tends to mate in, or very close to, the intertidal zone, in the open on wet substrates, or in refuges very close to the water (e.g., logs, beach rocks, rocky jetties, or sea walls), and especially at night. Thus, mating of each species differs in time and specific microhabitats, respectively distributed from the intertidal zone to the vegetation above the berm of the shore.

Although females appear highly selective in choosing oviposition sites, current information is indirect. Gravid females with large eggs in the abdomen have been intercepted moving from the sea to large rock formations, piles of large boulders, natural crevices, or burrows of seabirds. Female *L. saintgiroisi* are able to climb steep cliffs to reach deep crevices that are well exposed to the sun. Finally, neonates were observed near these rocky sites and are absent from remote offshore sandy islets, generating a marked spatial age



**FIGURE 3.6** A mating ball of Yellow Sea Kraits (*Laticauda saintgiroisi*). A female (not visible) is covered by males. In this species, mating balls are often observed in the vegetation just above the berm of the shore.

*Source:* Photograph by Xavier Bonnet.

structure of the population where the lagoon is large (Bonnet *et al.* 2015). In *L. saintgironsi*, nurseries are associated with very thick herbaceous vegetation situated just above the shore bank (Figure 3.7), where neonates spend the first weeks or months of life before dispersing across the lagoon (Bonnet *et al.* 2014). Another species of sea krait, *Laticauda semifasciata*, oviposits eggs inside tidal caves that have an opening to the sea (Tu *et al.* 1990; see Chapter 4, this volume).

Mating can be observed in remote, offshore and coastal colonies. However, oviposition appears to be more restricted, and coastal igneous sites attract gravid females and accommodate nurseries. Overall, the specific requirements of reproduction (*i.e.*, acquisition of resources, mating, oviposition, and early survival of juveniles) are associated with a variety of terrestrial refuges with sharp differences among the species of sea kraits. Broadly, complex shorelines are more likely to offer the density and diversity of refuges required for the reproduction of sea kraits. Therefore, cleaning sandy beaches, removing logs and leaves, and clearing thick vegetation to accommodate tourists are highly detrimental.

## Costs and Benefits of an Amphibious Lifestyle

Performing major activities on land is advantageous for sea kraits, providing that suitable and easily accessible shelters are available. Digestion, ecdysis, healing of injuries, resting, and mating are likely facilitated and optimized on land. The expenditure of energy is minimized in motionless individuals, hydromineral balance is easier to maintain out of the hyperosmotic seawater, precise thermoregulation is possible, and the risks of predation are likely to be minimal on land compared with water. These advantages may explain why the largest colonies of snakes are usually observed in amphibious species, such as natricines or homalospids (Brooks *et al.* 2007; Ajtić *et al.* 2013).

A piscivorous diet, however, imposes periodic shifts between oceanic foraging grounds and terrestrial sites, and living in two worlds likely involves costs or limitations (Shine and Shetty 2001; Brischoux *et al.* 2008). Species that divide their life cycle across two highly contrasted habitats are limited by the availability of microhabitats that often need to be geographically close, or even contiguous. Clearly, to be very selective for microhabitats over two different environments reduces the potential geographic range, and thus distribution, of these species. Such a high level of specialization may also affect the persistence of populations insofar as disturbances affecting only one of the two environments are likely to be detrimental to survival.



**FIGURE 3.7** Juvenile Yellow Sea Kraits (*Laticauda saintgironsi*)  $\leq 6$  months old aggregate in the thick herbaceous vegetation just above the berm of the shore. All the pictured snakes were found in a coastal nursery, deeply sheltered in the vegetation; they were measured, marked, and released at the place of capture.

*Source:* Photographs by Xavier Bonnet.

Another set of costs induced by amphibious lifestyle relates to trade-offs that can occur for a variety of physiological and morphofunctional aspects of the life of amphibious species. Indeed, physical and chemical properties of these environments are so contrasted that they often involve antagonistic selective pressures on major phenotypic traits; thus, being optimized for life in one environment (*e.g.*, land) inevitably compromises performances in the other (*e.g.*, water). Intensive studies of amphibious snakes have identified that such trade-offs affect such key life history traits as thermoregulation (Aubret and Michniewicz 2010), locomotion (Shine *et al.* 2003; Wang *et al.* 2013), or osmoregulation (Lillywhite *et al.* 2008, 2009). Finally, living in two worlds includes being in contact with two different sets of predators and thus may involve increased risk of predation. For example, amphibious snakes might be susceptible to predation by carnivorous mammals and birds on land but also by fish in the water (Ineich and Laboute 2002). Interestingly, the same issue may apply to susceptibility to parasites and epibionts that can colonize amphibious snakes (Figure 3.8; Pfaller *et al.* 2012). However, in the case of sea kraits, survival of parasites from one habitat may be jeopardized in the other. Ticks (*Amblyomma nitidum*) can be found dead on snakes returning from foraging trips at sea (François Brischoux and Xavier Bonnet, personal observations), whereas barnacles do not survive for long periods on land. The



**FIGURE 3.8** Ticks (*Amblyomma nitidum*) attached to a Blue Sea Krait. The ticks selected a damaged part of the skin. The gray ticks (three large and one small) are female; the small orange tick is a male.

*Source:* Photograph by Xavier Bonnet.

“sanitary” consequences of amphibious lifestyle, and especially the susceptibility to both airborne and waterborne diseases, have yet to be investigated.

## The Spatial Distribution of Terrestrial Habitats and Sea Kraits

In a previous study based on the description of the shores of 10 islets, we highlighted that the proportion of peculiar structures, namely beach rocks with crevices or not attached to the substrate situated in the intertidal zone, was strongly linked to the proportion of *L. laticaudata* captured at a given site (Figures 3.9 and 3.10; Bonnet *et al.* 2009). Interestingly, the study also showed that *L. saintgironsi* was also dependent, but to a lesser extent, on such specific microhabitats (Bonnet *et al.* 2009; see also Chapter 4, this volume).

For the current chapter, we have conducted a similar analysis by extending our initial sample to a total of 32 islets. It is noteworthy that adding new sites allowed us to increase the breadth of the lagoon’s characteristics surrounding each site. Most notably, we have now added sites that are situated in wider and more open parts of the lagoon, as well as sites that are in very narrow parts (for a map, see Bonnet *et al.* 2015). These sites encompass a set of variables



**FIGURE 3.9** Blue Sea Kraits sheltering under beach rocks. Several beach rocks were lifted to expose the snakes.

*Source:* Photograph by Xavier Bonnet.

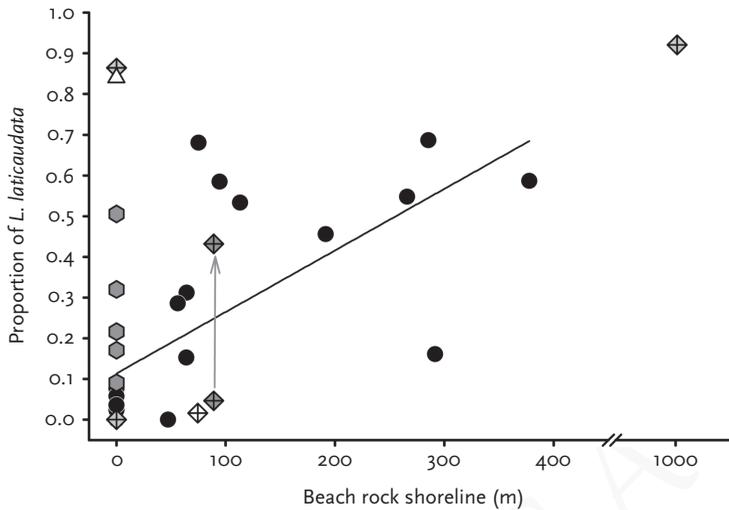


**FIGURE 3.10** An adult male Blue Sea Krait taking a breath. Individuals shelter under the well-buffered beach rocks situated in the intertidal zone. At high tide, they must partly leave their refuge to reach the water's surface. Two air bubbles (one per nostril) expelled just before surfacing can be seen at the right of the snake.

*Source:* Photograph by Xavier Bonnet.

including climate (*e.g.*, rainfall), distance to the mainland or to the open ocean, and width of lagoon. Examination of the data (Figure 3.11) compared with Figure 5 from Bonnet *et al.* (2009) suggests that the strong trend we previously detected (*i.e.*, *L. laticaudata* being dependent on the availability of beach rocks) was challenged by increased sample size (*i.e.*, many sites without beach rocks actually sheltered a significant proportion of *L. laticaudata*; Figure 3.12). However, a precise examination of the peculiarities of the shores at each site reveals that small-scale habitat heterogeneity almost always robustly explains the presence of datum “outliers” (for explanations and details, see legend to Figure 3.11). Interestingly, addition of new sites highlighted the complexity of the selection of terrestrial microhabitats by these two species of sea kraits and emphasized its importance.

Large colonies of sea kraits were systematically observed at sites provided with abundant refuges near the shore—beach rocks, crevices, boulders, large trees, or thick vegetation. The most prosperous colonies were generally found in protected areas, either natural reserves or remote islets. However, in some of the larger colonies, population structure suggests that they could not function independently from other colonies. For example, one islet was only populated by thousands of adults with no local productions of recruits,



**FIGURE 3.11** Relationship between the dimension of the beach rock formation along the shoreline measured in 32 sea krait colonies (X axis) and the proportion of *Laticauda laticaudata* relative to *Laticauda saintgironsi* (Y axis, recaptures excluded). The former species cannot penetrate far inland and thus must shelter in the intertidal zone or very near the shore, whereas *L. saintgironsi* can use a greater diversity of terrestrial habitats. A positive relationship is observed among typical coralline islets (black circles,  $n = 22$  sites); the lack of beach rocks precludes the occupancy of the site by *L. laticaudata*. The gray hexagons ( $n = 5$  sites) also indicate coralline islets spread out in the lagoon, but sandy beaches represent the only type of shore. The presence of *L. laticaudata* (up to 50% of the snakes) is thus counterintuitive at these sites. However, almost all individuals (*L. laticaudata* + *L. saintgironsi*) were found curled and well sheltered among the roots of large trees very close to the tidal limit (see Figure 3.12). Crossed diamonds ( $n = 4$  sites) indicate mainland coastal colonies where partly submerged boulders are abundant (artificial jetties and walls were considered as beach rock). The two symbols connected by a gray arrow represent a single site—a coastal nursery for *L. saintgironsi*; when neonates (all *L. saintgironsi*) are excluded from calculations, the proportion of *L. laticaudata* increases. The white diamond indicates a wreck on the barrier reef (>30 km offshore). Although many artificial shelters are available, the barrier reef is mostly visited by *L. saintgironsi* (Brischoux *et al.* 2007). Finally, the white triangle indicates a very peculiar microhabitat in an igneous islet without beach rock; an accumulation of dead coral at the base of a cliff offers a wet, hot, and very well-protected refuge for a colony of *L. laticaudata*. Many snakes were found deeply sheltered there. Overall, roots of large trees, artificial buildings made of large rocks and/or with cavities (walls, jetties, wharfs, and terraces), dead coral, and likely various other materials that offer wet and well-buffered terrestrial conditions are used as alternative refuges to beach rocks.



**FIGURE 3.12** Several Yellow Sea Kraits (*Laticauda saintgironsi*) sheltering in hot and wet interstices in roots in the sandy berm of the shore.

Source: Photograph by Xavier Bonnet.

and thus there was obligatory reliance on recruits coming from other sites (Bonnet *et al.* 2014). Overall, our large sample size (numerous sites spread over a large distance within the lagoon and characterized by a specific physiognomy) highlights the fact that despite their marked philopatry (Shetty and Shine 2002; Brischoux *et al.* 2009a), sea kraits are generally unlikely to perform their entire life cycle at a single site because their terrestrial requirements are so variable between different activities. Indeed, there are only four sites for which we have unequivocal evidence that at least one of the two neo-Caledonian species of sea krait can perform its entire life cycle and where populations are stable without immigration (*i.e.*, <20% of all surveyed islets).

Such large-scale functioning of populations associated with a high diversity of the characteristics of the islets may, at least partly, explain why the populations of sea kraits in New Caledonia are still dynamic and flourishing, whereas closely related species tend to decrease in other areas where anthropogenic activities (*e.g.*, tourism) have homogenized the terrestrial environments (shores of islands and islets) available to sea kraits. Indeed, sea kraits can optimize activities through the selection of foraging and terrestrial microhabitats (see also Chapter 7, this volume).

## Conclusion

Sea kraits divide their life between the ocean and terrestrial habitats, notably small islets spread throughout coral reef archipelagos of the Indian and Western Pacific Oceans. They broadly spend half of their life on land, where they achieve vital activities such as digestion, resting, mating, egg-laying, ecdysis, and drinking fresh water. Well-buffered shelters easily accessible from the sea are essential. Precisely, our results show that the distribution and abundance of sea kraits are strongly influenced by terrestrial microhabitats, notably refugia such as rock boulders and roots of large trees that offer thermally stable and moist conditions (Liu *et al.* 2012; Brischoux *et al.* 2013; see also Chapter 4, this volume). The characteristics of terrestrial sites selected by sea kraits (distance to the ocean, substrate, vegetation, etc.) determine a range of conditions and microhabitats and consequently create fine-scale heterogeneity that appears critical to sea kraits. Overall population viability of sea kraits heavily relies on the availability of such terrestrial microhabitats. Conservation efforts should focus on the maintenance, restoration, and/or creation of artificial terrestrial microhabitats. However, large-scale population functioning revealed that most colonies are interdependent. For example, in the remote sandy islets that contain large numbers of reproductive individuals, females migrate to lay their eggs in coastal nurseries; later, juveniles disperse and supply recruitment throughout the lagoon. In practice, protecting sea kraits requires protecting a wide diversity of partly connected sites that are respectively best suited for different activities (*e.g.*, mating, oviposition, or resting), and thus maintaining fine-scale habitat heterogeneity. Preserving a dense network of terrestrial refuges (including artificial constructions) is essential for maintaining connectivity among sites and thus to promote the global functioning of colonies.

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