



SYMPOSIUM

Long-term Field Study of Sea Kraits in New Caledonia: Fundamental Issues and Conservation

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Synopsis This short review focuses on the findings associated with a long-term field study on two species of sea kraits in New Caledonia. Since 2002, more than 30 sites in the lagoon have been sampled, and in most places mark-recapture was implemented. We collected detailed data on more than 14,000 marked individuals (>6000 recaptures) and used different techniques (stable isotopes, bio-logging, analyses of diet). The objective was fundamental: to examine how amphibious snakes cope with both terrestrial and aquatic environments. As access to abundant food is likely the main evolutionary driver for the return transition toward the sea in marine tetrapods, foraging ecology was an important part of the research and novel information was obtained on this subject. Rapidly however, field observations revealed the potential interest of sea kraits for conservation issues. Our results show that these snakes are useful bio-indicators of marine biodiversity; they also provide a useful signal to monitor levels of contamination by heavy metals in the lagoon, and more generally as a means of studying the functioning of reef ecosystems. Importantly, anecdotal observations (e.g., a krait drinking during rain) provided unsuspected physiological insights of general importance to fundamental problems and conservation. One of the lessons of this long-term study is that key results emerged in an unexpected way, but all were dependent on intensive field work.

Introduction

This short review focuses on the ecology of two species of sea snake (*Laticauda*) that occur in large numbers in the lagoon of New Caledonia. One aim of this report is to emphasize the virtue of detailed long-term field studies for both fundamental and applied ecology. The bottom-up approach adopted in this study highlights the fact that anecdotal, and often unexpected, field observations can provide inspiration for testing broader notions. Importantly, gathering a large data set through intensive field work is essential for adequate analyses and for assessing the validity of the conclusions at large geographic and temporal scales. Although restricted to the research undertaken in New Caledonia (Fig. 1), the results address various general topics (e.g., sexual selection, thermoregulation, eco-physiology, and management). In practice, this review is organized into three linked topics: (1) adaptation to marine life, (2) foraging ecology, and (3) conservation. The rationale

for this three-step approach is that although conservation programs can benefit from life-history studies (e.g., trophic relationships), the reverse is not necessarily true. For instance, it is not immediately obvious how fundamental knowledge on the evolutionary trade-offs faced by air-breathing predators that forage at sea can be used to derive actions for field management. However, as discussed later, incidental observations—e.g., a few kraits taking their breath during resting periods—can be used to identify potential implications for conservation. Below, each of the three topics is briefly presented and framed within a broader context; the results obtained on the two species of sea kraits studied in New Caledonia are then discussed.

Adaptation to marine life

Many species share their life between oceanic and terrestrial environments; this is the case for primarily marine organisms (e.g., mollusks, crustaceans) that

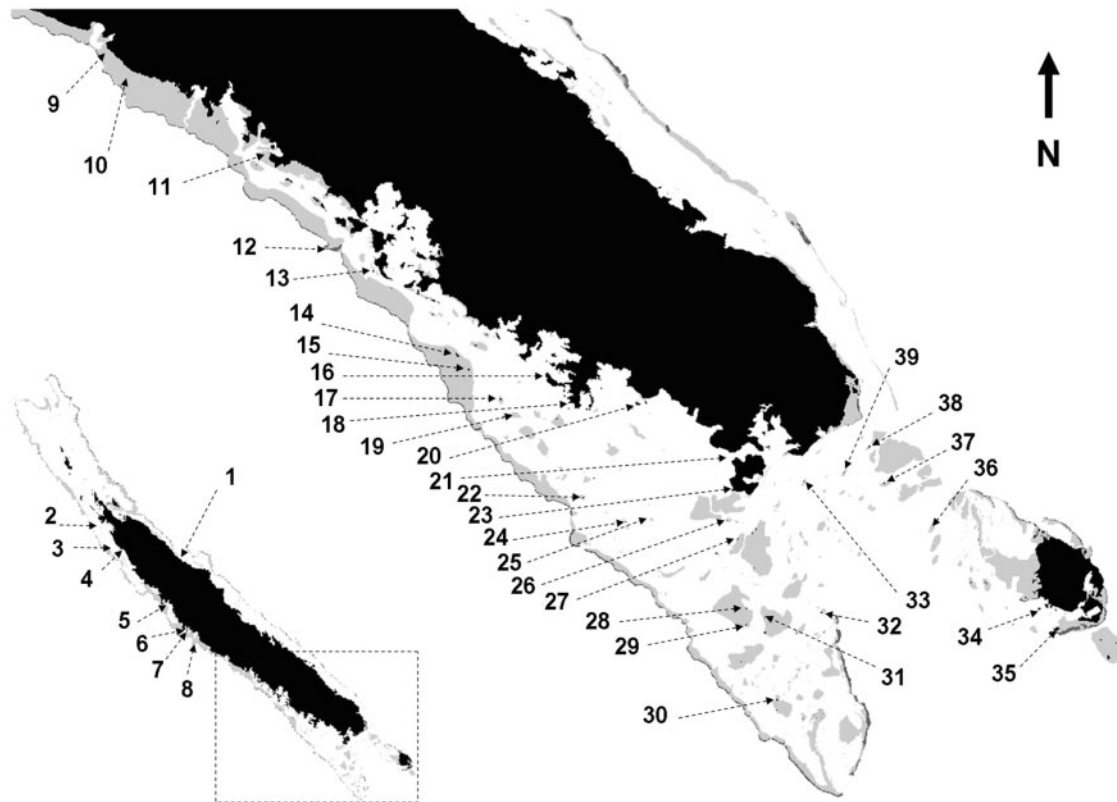


Fig. 1 Thirty-nine study sites (indicated by arrows associated with numbers) have been sampled for sea kraits in New Caledonia in the course of a long-term field study. One of the main study sites, Signal Island, is indicated by the number 17. The main igneous land is indicated in black; gray areas designate coral reefs. At this scale, most of the study sites are represented by a dot.

live in the intertidal zone. This is also the case for amphibious tetrapods such as seals, sea birds, marine iguanas, sea turtles, and many sea snakes. Even if the precise origin of snakes is still debated (Tchernov et al. 2000; Vidal and Hedges 2004; Lee et al. 2007), palaeontology, morphology, and molecular phylogeny clearly suggest that the ancestors of these vertebrates were terrestrial (Ahlberg and Milner 1994). However, because much earlier ancestors originated from the marine environment (Long et al. 2006; Clack 2007; Coates et al. 2008), these secondarily marine tetrapods are representative of the evolutionary pathway followed by organisms that undertook a return transition toward the sea, a major transition in the history of life. These animals display a set of adaptations to marine life, such as well-developed salt glands, nostril valves, streamlined morphology, paddles (limbs and tail), and under-water vision derived from pre-existing organs previously adapted to terrestrial life (for major reviews on sea snakes see Dunson 1975; Heatwole 1999). Interestingly, compared to other terrestrial

phyla, the vertebrates (phylum Chordata) provide a great variety of clades that achieved this evolutionary transition; very few terrestrial invertebrates or terrestrial plants have returned to the sea (Vermeij and Dudley 2000). Furthermore, within vertebrates, the snake lineages exhibit a wide diversity of marine lifestyles, ranging from partly aquatic forms that live in brackish waters and that periodically come onto land, to truly pelagic species that spend their entire life in the ocean (Rasmussen et al. 2011). In snakes, the return transition to the sea evolved independently at least four times and is associated with a prolific, and sometimes very rapid, radiation (Lukoschek and Keogh 2006; Sanders et al. 2008). Currently, there are approximately 100 species of snakes that use the marine environment intensively or exclusively, and most of them evolved during the past 5–10 myr, the highly marine and diverse *Hydrophis* lineage being particularly recent (Sanders et al. 2010).

Compared to other secondarily marine tetrapods (seals, sea birds, sea turtles, marine iguanas) that

tend to be large and stockily built, sea snakes are characterized by a modest absolute body mass and an elongated shape. They consequently cope with an unfavorable mass:surface-area ratio in terms of regulating their hydro-mineral balance in the hyper-osmotic marine environment (Dunson 1978; Brischoux and Shine 2011; Fig. 2). The general biological flexibility of snakes, in terms of physiology, behavior, and reproductive mode, may have provided key advantages for dealing with marine environments and may (at least partly) underpin their biological diversity. For instance, snakes are low-energy specialists particularly tolerant to deviations in body temperature and in composition of the blood, whilst viviparity evolved in many genera (Shine 1985, 2003; Bickler and Buck 2007). These factors may have reduced the osmotic and respiratory complications and thus the corresponding physiological demands imposed by the hyper-osmotic and hypoxic characteristics of sea water, thereby facilitating the acquisition of independence from the terrestrial environment (Fig. 2). Viviparity was crucial in this respect because marine constraints are apparently insurmountable for amniotic embryos developing into independent eggs; all sea birds (a clade of reptiles) and sea turtles are oviparous and thus must reproduce on land. Uniquely, in comparison to other taxa, the whole “continuum” between terrestrial, amphibious, and truly marine species can be observed at the familial level in snakes (e.g., Elapidae: *Notechis*—*Laticauda*—*Pelamis*). These organisms are therefore well suited to examine within a relatively narrow phylogenetic context how air-breathing animals cope with locomotory, respiratory, and hydro-mineral limitations imposed by the marine environment.

Sea kraits are amphibious oviparous snakes that intensively use both terrestrial and oceanic habitats (Heatwole 1999). They are consequently situated somewhere on the evolutionary gradient between terrestrial and fully marine species. One of the first challenges for amphibious tetrapods is to locomote efficiently in two very different environments: in water and on land. Life-history theory predicts that various performances should be compromised in species that occupy an intermediate position, compared to species living wholly in the terrestrial (ancestral) or oceanic (novel) environment. This assumption found strong support through comparisons of the locomotory performances (swimming and crawling) measured in terrestrial, amphibious, and fully marine elapid snakes (Shine and Shetty 2001; Shine et al. 2003; Aubret et al. 2007). However, these investigations highlighted exceptions

to this trend, which stresses the need to consider the environment as well as life history. For instance, as expected, the hydrophiid *Emydocephalus annulatus* was particularly slow during terrestrial trials (this species can hardly move on land); however, it was also very slow in water contrary to the simplistic assumption that fully marine snakes should exhibit greater swimming performances than do amphibious or terrestrial species. This counter-intuitive result likely reflects the fact that *E. annulatus* feed on eggs (Voris 1966) and do not undertake long foraging trips; thus, swimming speed might be unimportant (Shine et al. 2003, 2004). This example illustrates the inevitable limitations associated with comparisons between species belonging to different lineages and exhibiting substantially different lifestyles. Indeed, the foraging mode of *E. annulatus* (viviparous) with frequent ingestion of small, spherical, and sessile prey (fish eggs) is extremely different from that of sea kraits (oviparous) that feed infrequently on large, potentially dangerous prey located during long and exhausting foraging trips (Shine et al. 2004; Brischoux et al. 2007a,b; Bonnet et al. 2010; Fig. 2). A means of circumventing such difficulties is to focus on sea kraits, notably because different species show different degrees of dependence on the marine environment. Further investigations are therefore less subjected to phylogenetic disparities. The *Laticauda colubrina* complex (including *L. saintgironsi*, *L. frontalis*) (see Heatwole et al. 2005) is more terrestrial than *L. laticauda*, which in turn is more terrestrial than *L. semifasciata*. Therefore, the trade off between alternative modes of locomotion should be visible at this fine phylogenetic scale. Sexual selection and fecundity selection represent additional forces that influence shape and composition of the body and locomotor performances. On an average, males tend to display larger musculature associated with greater muscular strength and better locomotor performances compared to females (Bonnet et al. 1998b). Overall, the sex/species cross comparison of sea kraits offers a straightforward means of assessing the influence of the evolutionary forces associated with adaptation to marine life and to sexual and fecundity selection.

As expected, we found that the most terrestrial species (*L. colubrina* and *L. saintgironsi*) surpassed the most aquatic species (*L. laticaudata*) in terms of crawling and climbing ability (Shine et al. 2003; Bonnet et al. 2005). In fact *L. laticaudata* is almost incapable of crossing steep cliffs and is thus restricted to the near-shore areas of relatively flat habitats when on land. This important result in terms of conservation and management of habitat is discussed



Fig. 2 This composite color plate illustrates several major topics. **(A)** An adult female *Laticauda saintgironsi* exhibits a flattened body shape during swimming. **(B)** The narrow diagonal black lines in the large blue stripes, used to mark a male *Laticauda laticaudata* are clearly visible several years after marking; this classical system permits individual identification. More than 14,000 snakes have been marked since 2002. **(C)** A moray eel (*Gymnothorax fimbriatus*), partly swallowed by a female *Laticauda colubrina*, that retaliated in an unsuccessful attempt to escape predation (Bonnet et al. 2010). **(D)** The sharp teeth of a moray eel (*Gymnothorax undulatus*), commonly found in the stomach of the sea kraits, are visible; many sea kraits show scars and wounds inflicted by their prey. **(E)** An adult female *L. saintgironsi* regurgitated a very large conger eel (*Conger* sp.) swallowed tail first. **(F)** A group of ticks (both sexes are visible) gorge themselves with the blood of a female *L. laticaudata*; they are all attached in an injury. **(G)** A male *L. saintgironsi* is drinking from a droplet on herbaceous vegetation (*Herbe à tricots*, *Sesuvium portulacastrum*). **(H)** Distended skin of a female *L. saintgironsi* with a prey in its stomach illustrates potential tradeoffs in skin permeability; sea kraits can cover part of their respiratory needs through cutaneous gaseous exchange through inter-scalar skin; however, dehydration when on land plus salt-overloading during foraging excursions in the sea pose serious physiological challenges. All pictures were taken in the field by X. B., except picture 3 that was taken by R. Lang.

in the third topic (conservation issues). Such difference in crawling and climbing performance was related to divergent relative muscular strengths. We also found the expected sex divergences in locomotor

performance: on average, males were stronger and swam, crawled, and climbed faster than did conspecific females (Shine et al. 2003; Bonnet et al. 2005). However, in contrast to our initial predictions, the

terrestrial species (*L. colubrina* and *L. saintgironsi*) exhibited better ability to swim compared to the most aquatic species (*L. laticaudata*).

The magnitude of such unexpected differences was less dramatic when derived from the inter-specific comparisons within *Laticauda*, rather than from the inter-generic comparisons between *Emydocephalus* and *Laticauda*; the problem nonetheless persisted. Various evidences accumulated in the course of our long-term field study suggesting that specific divergences in diet and foraging tactics are the main drivers for such results. *Laticauda laticaudata* exhibits a high degree of dependence on the marine environment, including pronounced skin permeability and significant risk of dehydration when on land (Lillywhite et al. 2008); this dependence markedly compromises terrestrial locomotion. On the other hand, *L. saintgironsi* is less dependent on the marine environment, less prone to dehydration on land (note that this species is nonetheless subject to dehydration at sea; see Lillywhite et al. 2008 for details), and retained excellent terrestrial locomotor abilities, surpassing most terrestrial snakes in rock-climbing performances for instance (unpublished data). However, to find and catch prey, *L. saintgironsi* must undertake long and physically demanding foraging trips in the ocean; in addition, this snake feeds on large powerful predatory fish (notably moray eels) that can move freely in the coral matrix; killing and subduing such fish requires substantial strength and agility (Bonnet et al. 2010; Fig. 2). In contrast, *L. laticaudata* prospects relatively shallow waters and feeds on smaller, sometimes defenseless, prey (such as gobies and snake fish) that are “trapped” in their burrow where they are particularly vulnerable. Selection should favor attributes that minimize expenditure of energy and maximize energy gains during foraging episodes. Thus, *L. saintgironsi* might be under strong selection to develop high physical performances at the cost of important energy expenditure and *L. laticaudata* may benefit from low-energy specialist features, such as slow cruising and swimming speeds. These assumptions are mirrored by the more developed locomotor musculature of *L. saintgironsi* compared to that of *L. laticaudata*; indeed, building up, maintaining, and activating locomotor muscles are demanding processes.

These hypotheses imply that the degree of adaptation to the marine environment does not necessarily correspond to a proportional loss of terrestrial performances mechanically linked to the improvement of swimming performances, but rather to alternative evolutionary trajectories depending upon

the equilibrium between the foraging tactics, the type of prey, and the overall energy budget. In addition, these hypotheses imply that maintaining elevated terrestrial locomotor performances is compatible with high performances in swimming in species that retained a marked terrestrial life style, whilst apparently highly aquatic species cannot maintain elevated terrestrial locomotor performances. In other words, terrestrial species can be proficient swimmers whereas aquatic species cannot be talented crawlers. Such asymmetry in a fundamental trade-off imposed by two extremely divergent habitats corresponds well with the fact that many terrestrial snakes evolved toward aquatic environments while the reverse has not been documented. Further studies are certainly required to test these speculative notions in a robust phylogenetic context (but see Caprette et al. 2004 for a controversial position).

Foraging ecology of the sea kraits

Access to abundant trophic resources may represent one of the main evolutionary forces that favored the return transition toward marine environments. Indeed, a brief survey of the life history of secondarily marine animals reveals a unique and systematic point of convergence across taxa: individuals primarily use the ocean to find their food (mostly prey). Amphibious species penetrate the water exclusively to forage; they provide a clear illustration of this concept. It is consequently important to investigate the foraging ecology of sea kraits to better understand the ecological and morphological adaptations in relation to the alternative use of aquatic and terrestrial habitats of these predators.

There is immense variation in the behaviors that predators use to capture their prey. Strong links exist between foraging tactics and attributes, such as activity patterns, habitat use, body shape, locomotor performance, metabolic rate, growth rate, age at maturation, and rate of reproduction (Boggs 1992). Extensive research covers the main biological aspects related to foraging ecology in marine birds and mammals (reviewed by Boyd et al. 2006). Unfortunately, comparable data are not available for sea snakes or, more generally, for predators from reef ecosystems. For instance, none of the recent major reviews (e.g., Sale 2006; Sheppard et al. 2009) provided a single profile of a foraging trip for any predator from a reef. More generally, current knowledge of the foraging ecology of marine tetrapods is strongly biased toward endothermic vertebrates. As endothermy involves massive physiological and ecological shifts compared to

ectothermy (Pough 1980; Bonnet et al. 1998a; Brischox et al. 2008), information on marine reptiles is strongly needed. Major information on the diet of sea snakes, including different species of sea kraits, has been collected through pioneer studies (Voris 1972; Voris and Voris 1983). This research shows that sea kraits are the only known predators that specialize on anguilliform fish (Voris and Voris 1983; Heatwole 1999; Reed et al. 2002; Ineich et al. 2007). More recently, studies performed in Fiji and Vanuatu on *L. colubrina* and *L. frontalis* suggested that differences in mean body size of adults and in the degree of sexual dimorphism (in body size and relative head size) were influenced by divergent feeding ecologies (Shine et al. 2002). However, basic information about frequency of feeding, foraging habitat, or quantification of the trophic relationships between major predators (including sea kraits) and their prey in coral reef ecosystems remain undocumented. Logistical difficulties preclude direct continuous visual monitoring of many marine predators; this is notably the case for sea kraits that undertake long foraging trips (days to weeks) and usually escape observation before any foraging event can be recorded, thereby preventing quantitative analyses based on adequate sample sizes. Alternative methods have been developed: marine mammals, sea birds, and a few pelagic fish have been successfully monitored in the course of their foraging trips in the open oceans through the use of bio-logging techniques (Ropert-Coudert and Wilson 2005; Graham et al. 2006; Brunnschweiler et al. 2009). This approach has been successfully tested only recently on sea kraits in New Caledonia (Brischox et al. 2007b, 2008, 2010). In addition to the long-term data, the use of bio-logging and of new simple techniques contributed to describing different aspects of the foraging ecology of sea kraits. This research was notably carried out by F. Brischox in the course of his PhD thesis on two closely related species, *L. saintgironsi* and *L. laticaudata*. We emphasize that attempts were made not to kill or cause detectable damage to the kraits, for instance prey items were obtained via regurgitation (not dissection) and blood samples were taken via intra-cardiac punctures. Prior to the research in New Caledonia, it was assumed that the two species (*L. saintgironsi* and *L. laticaudata*) greatly overlapped in their general ecology, and this included their supposedly very similar diet and reproductive ecology (Saint Girons 1964; Ineich and Laboute 2002). Our data rather suggest strong divergences and reveal important specific characteristics.

Until recently anguilliform fish were considered as poorly diversified and rare in the lagoon of New

Caledonia (Kulbicki 1997). Based on large sample sizes, our analyses revealed that sea kraits are abundant top predators and that they have a large and diverse diet of anguilliform fish (approximately 50 species) (Ineich et al. 2007; Brischox et al. 2007a; Brischox and Bonnet 2008). Several species routinely found in the stomach of sea kraits have been rarely observed; one species was known by a single specimen collected >6000 km away in Taiwan (Séret et al. 2008). Therefore, sea kraits' sampling of eels significantly modified the understanding of the lagoon's biodiversity by adding a complex and rich guild of predators, notably composed of moray eels, congers, and sea kraits; these animals should now be considered as important predators that play a role in the functioning of reef ecosystems (Ineich et al. 2007; Brischox and Bonnet 2008).

Sea kraits swallow their prey whole, many prey items are intact, and most of the remains are identifiable and measurable at least in diameter. This allows an assessment of the relationship between sizes of predator and prey, a key relationship in a gape-limited predator. The slope of this relationship was higher in *L. saintgironsi* that feeds on relatively stockier prey compared to *L. laticaudata*, suggesting a divergence in the foraging strategy of these two species (Brischox et al. 2007a). These results were reinforced by the significant divergence of their respective diets, and by the contrasted ontogenic shifts in the selection of prey from birth to adulthood exhibited by the two species (Brischox et al. 2009a, 2011). The (very) limited data available in the literature on the ecology of the anguilliform fish consumed by the sea kraits suggested that the prey of *L. saintgironsi* live on hard bottoms (coral matrix, rocky areas), whereas prey of *L. laticaudata* are typical inhabitants of soft bottoms (sandy, muddy substrates). The prey are relatively large considering the dimensions of the kraits' jaws and are swallowed headfirst or tailfirst (they very rarely swallowed folded prey). This is the first time such data have been systematically collected. The prey captured by *L. saintgironsi* were swallowed headfirst 50% of the time, but 80% of the time for *L. laticaudata* (Brischox et al. 2007a). These proportions were expected considering that *L. laticaudata* forages for fish usually retreated in burrows dug into the soft bottom with the head directed toward the exit (ambush position): the snake must enter the refuge to kill and capture the prey, often resulting in a head-to-head encounter. By contrast, *L. saintgironsi* explores crevices and cavities in the hard coral bottom where the size of the refuge does not necessarily match the size of the fish; consequently, the snake is free to swallow

the killed prey beginning either at the tail or at the head (anguilliform fish are smooth); such events have been observed and photographed (Bonnet et al. 2010; Fig. 2). Consequently, two different sources of information, diet and direction of swallowing, converge to suggest a divergence in foraging ecology. A third source of information based on stable isotopes reinforced these conclusions.

Analyses of stable carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) isotopes are effective and powerful techniques capable of assessing key processes (e.g., sources of carbon, predator/prey relationships, habitats) in the global functioning of marine ecosystems (Peterson and Fry 1987; Michener and Schell 1994; Hobson and Wassenaar 1999). Our data of $\delta^{13}\text{C}$ values reveal a clear spatial segregation of the respective prey taken by each species of sea krait (from hard versus soft bottoms) (Brischoux et al. 2011). This provided an additional support for the conclusion that the marine habitats exploited by these top predators are clearly divergent. Our data of $\delta^{15}\text{N}$ values suggested an unsuspected high complexity of the trophic webs involving secondary prey systems (sea kraits and anguilliform fish) in both soft (*L. laticaudata*) and hard (*L. saintgironsi*) habitats (Brischoux et al. 2011). The degree of complexity (i.e., number of trophic levels) is apparently as important as those documented for other top predators (fish) of the lagoon and their prey. This indicates that there are an equivalent number of trophic levels “compacted” within the few meters of the coral matrix and/or soft-bottom habitat of the sea kraits, compared to the tens of meters of water-column foraging habitat above. Although other top predatory fish (e.g., skates) forage in the corals and on soft bottoms as well, the importance and complexity of the trophic relationships and therefore species diversity revealed by the sea kraits have been neglected.

Overall, contrary to previous assumptions, the two species of sea kraits that prospect the lagoon of New Caledonia exhibit marked differences in their foraging ecology: prey species, relative prey size, fishing tactics, and foraging habitat are all different. In addition, these previously overlooked communities play major roles in the functioning of reef ecosystems. Gathering information on the patterns of foraging trips, searching effort, and foraging success, rather than merely describing diet and performing stable isotope analyses, was technically more challenging. We combined simple, initially anecdotal, information with bio-logging.

We observed that digestion is not uniform: the progression of digestion is clearly delimited. The fish is

degraded at one end as it progresses into the digestive gut, such that the end farthest into the digestive tract may be nearly completely digested while the rest of the animal is intact and identifiable. Prey obtained by forced regurgitation can be intact, almost entirely dissolved, or at any intermediate stage between these extremes. Because the size and mass of the remains of most prey can be reconstructed using allometric equations, we were able to quantify the degree of digestion of the regurgitated prey (proportion of the prey digested) (Brischoux et al. 2007c). The duration of this digestive process was estimated using individuals captured with a full stomach that were kept in small enclosures until the end of digestion (Brischoux et al. 2008). The routine swimming speed of the sea kraits was also measured. Individuals that had just returned from a successful foraging trip were forced to regurgitate their meal and the proportion of prey digested at sea was measured. The duration and the distance of the return foraging trip (from the capture of the prey to the home islet) could therefore be estimated (Brischoux et al. 2007a). In one of the main study sites (Signal Islet, $22^{\circ} 17' 45''$ S; $166^{\circ} 17' 34''$ E) one-third of the regurgitated prey were almost intact and were thus recently captured (<1 day) in the surrounding flat reef close to the home islet. The remaining prey were at a further stage of digestion and therefore captured at greater distance (~ 2 – 5 days), and thus from a much wider area (estimated surface area ranging from 615 – 1660 km^2 for *L. laticaudata* to 1380 – 4500 km^2 for *L. saintgironsi*). Interestingly, the lack of intermediate durations (very few return trips of 0.5 – 1 day long) suggested a clear geographic demarcation between close versus remote foraging areas. On an average, *L. saintgironsi* must forage over longer distances (a proxy of foraging effort) compared to *L. laticaudata*. Different patterns were obtained at other study sites (X. Bonnet, F. Brischoux, and T. Fauvel, unpublished data) revealing an important geographic flexibility in the foraging zones used by the sea kraits, possibly influenced by habitat type and prey availability, or by relative distances between the home islet and productive areas for foraging.

In a pioneer study we fitted sea kraits with time depth recorders (Brischoux et al. 2007b, 2008). The foraging profiles revealed that to find their prey the sea kraits can dive and intensively explore the bottom of the lagoon over long periods of time (weeks), accumulating hundreds of dives without obvious resting periods. They also revealed long episodes of submersion (2 h) during which the krait remained on the bottom separated by very short surface episodes (<1 min) that correspond to breathing

events. In one female *L. saintgironsi* we recorded a set of depths of 80 m, indicating an exploration of the drop-off of the barrier reef situated >8 km from her home islet. Direct observation of sea kraits prospecting the bottom of the lagoon support these bio-logging data: divers observed sea kraits visiting the drop-off areas, 50–100 m deep, and several individuals that explored the coral matrix continuously over several hours (likely over longer times as observation stopped after 1–3 h) were observed to have a very low hunting success (less than one prey located for more than 100 crevices explored). Sea kraits appear to be extremely enduring animals that must deploy considerable effort to find and capture their prey. It should be noted that bio-logging data and estimates of the duration of foraging trips based on the degree of digestion of the prey led to similar conclusions: sea kraits undertake long trips during which they forage actively and intensively to find their food. It is currently assumed that compared to endothermic predators, the low metabolic requirements of ectothermic predators is associated with low feeding rates and moderate foraging effort (e.g., low number of attempts to capture prey per unit time); this pattern has been widely documented for snakes (Secor and Diamond 2000). Our data suggest that the foraging mode of sea kraits (and perhaps other marine snakes) differs considerably from the patterns reported for other snakes; sea kraits display prolonged episodes (weeks) of continuous and intensive prospecting of their habitat in search of prey (hundreds of foraging dives) with little or no resting phase. This extremely active foraging mode, instead of the classic ambush foraging of snakes, means that the association between foraging mode and metabolic requirements is weaker than previously assumed. The examination of the diving profiles triggered further comparative analyses between endothermic and ectothermic marine tetrapods. Our analyses challenged the paradigm stipulating that body mass is a major determinant of maximal duration of dive (a major parameter of dive performances) (Halsey et al. 2006); we did not find the expected effect of body mass in ectotherms (Brischoux et al. 2008).

At all the sites visited, we observed typical V-shaped injuries on many snakes (Bonnet et al. 2010). The proportion of recently wounded snakes was sometimes near 10%, and roughly 30% of the snakes had scars (the proportions were similar for both species). Some snakes exhibited very deep cuts. Many anguilliform fish possess sharp teeth; individuals can retaliate when attacked by sea kraits and are capable of inflicting dangerous bites. The

first high cost for the snakes is represented by long recovery periods, usually weeks, during which the snakes cannot forage, for example, but there are additional costs. On several occasions the wounds were infected (possibly portending the death of the snake), and on many instances large numbers of ticks (*Amblyomma laticaudae*, *A. nitidum*) (Fig. 2) (Rageau 1960; Clark and Oakley 2011) were attached to the damaged tissues (perhaps intact skin is not easily accessible to these parasites?). We do not know the impact of this, sometimes massive, parasitism (occasionally more than 50 ticks), but the quantity of blood removed might be substantial in individuals already exposed to physiological complications. Perhaps diseases are transmitted as well. These data suggest the existence of a strong trade-off between the benefit of feeding on large prey instead of multiple small ones (thereby minimizing foraging costs) versus the risk of injury risk that increases with prey size. Because diet, foraging effort, hunting tactic, and efficiency of venom (see Heatwole and Powell 1998 for the evolution of resistance of eels to the venom of sea kraits) can be affected by such a trade-off, the relationship between snake size and prey size might not be a simple consequence of the constraints imposed by the size of kraits' jaws.

Together, the results presented above suggest that capturing fish is more difficult for sea kraits than previously assumed. Not only must they often deploy an intensive effort to find prey, but in addition, despite their potent venom, they must engage in a dangerous fight to subdue the fish and, finally, they must come back to their home islet to digest it, sometimes facing massive attacks by ticks that target the wounds inflicted by the prey. The information we collected on the foraging ecology of sea kraits provided a strong basis for the conservation of both species of sea kraits and for their use as bio-indicators of the ecosystems.

Conservation issues

Coral reefs cover <0.1% of the oceans but they contain most of the marine biodiversity (Myers et al. 2000; Roberts et al. 2002; Bellwood et al. 2004). These ecosystems also provide a huge variety of goods to 500 million people, with 30 million of these depending almost entirely on fishing; coral reefs also sustain 10% of the world's commercial fishing (Wilkinson 2006). Unfortunately, coral reefs face a deep crisis (Wilkinson 2006). More than 20% of the world's coral reefs have been destroyed during past decades, and >50% of the remaining reefs are under risk of imminent collapse (Reefs at Risk

Revisited 2011). In 2008, more than 1.5 million hectares of the lagoons of New Caledonia were added to the UNESCO World Heritage List. Covering 23,000 km², the lagoon of New Caledonia forms the second most extensive continuous coral reef system in the world and is one of the world's main biodiversity hot spots currently considered as healthy. As restoring highly degraded reefs over large geographic scales might well be an insurmountable task, it is of prime importance to study and protect the marine ecosystems of New Caledonia.

Until recently, anthropogenic pressures have been limited in New Caledonia as both the population size (250,000 people) and the annual tourist flow (100,000) remained relatively modest. New Caledonia is a rapidly developing area, however, as the annual growth rate of the population is estimated at 1.9%. The growing demand for ore, notably nickel, resulted in the construction of factories and the opening of new mines. Nickel extraction requires total clearing of forests, huge consumption of water and energy, and generates massive deposits of sediment that threaten coral reefs. The recently established nickel factory (Vale Inco) in the Bay of Prony (southwestern lagoon) will discharge more than 10 million cubic meter of effluents per year. Considering these serious threats we analyzed our long-term data collected over a wide geographic scale (more than 30 sites spread throughout the lagoon) to examine whether habitat factors such as proximity of urbanized area and protection status influence such parameters as foraging effort, foraging success and/or the levels of contaminants in the sea kraits and in their prey. Moreover, one of our goals was to assess whether sea kraits could be useful bio-indicators of the reef ecosystems of New Caledonia.

An efficient practical approach to monitor complex ecosystems involves studying the trophic relationships among species. Top predators are situated at the apex of trophic webs, they integrate the functioning of the underlying levels, and thus are often considered as useful bio-indicators (Burger 2006; Sergio et al. 2008). Like other animals, they are sensitive to alterations in their habitat that affect breeding areas and the availability of refuges. Furthermore, top predators play a key regulatory role for secondary consumers and enhance the number of trophic links between organisms, thereby strengthening the resilience of whole ecosystems (Carr et al. 2002). However, there are limitations to using top predators to monitor ecosystems (Durant et al. 2009; Grémillet and Charmantier 2010). To be effective, bio-indicators must fulfill a number of

criteria. Disregarding important mathematical properties desired to limit bias in comparative analyses (van Strien et al. 2012), several criteria that are immediately useful in terms of monitoring and management can be proposed: (1) the populations of the candidate organism(s) should cover large geographic areas, (2) the focal trophic relationships must be adequately documented, and (3) the cost/efficiency ratio for data collection (this also involves the quality of the signal eventually used to monitor the system) must be as low as possible.

A number of species of top predators (mainly birds and mammals) have been used to monitor oceanic areas (Boyd et al. 2006; Grémillet and Charmantier 2010). However these animals prospect large areas and are unsuitable to accurately survey coral reefs. For example, seabirds forage both within and out of the lagoon, sometimes in remote pelagic zones. Seabirds are inaccessible for long periods of the year during which they are at sea and do not return to the colony; they feed on vagrant prey and their feeding ecology is poorly documented in New Caledonia. Monitoring seabirds would provide a time-constrained, unclear depiction of the New Caledonian reef ecosystem. Identical complications apply to marine mammals: dolphins, whales, and dugongs. Other top predators cannot easily be used as surrogates. For instance, sharks are logistically difficult to monitor and their trophic ecology is not well characterized. By contrast, sea kraits boast numerous advantages. They are highly phylopatric top predators, specialized on sedentary carnivorous anguilliform fish (Reed et al. 2002; Shetty and Shine 2002a; Ineich et al. 2007). Large populations of sea kraits are sustained by large assemblages of anguilliform fish (approximately 50 species) (Brischoux et al. 2007a; Ineich et al. 2007; Brischoux and Bonnet 2008), that in turn, feed on supposedly abundant secondary prey (such as invertebrates and fish), thereby encompassing important elements of the reef's biodiversity. Anguilliform fish are sedentary, they remain sheltered most of the time in the coral matrix and in the burrows they excavate in the soft bottoms. Sea kraits feed all year and prospect almost exclusively around their home islet. The two species of sea kraits that were studied provide complementary information: *L. laticaudata* prey on soft-bottom-dependent species whilst *L. saintgironsi* prey on species inhabiting hard reefs. This segregation provides a powerful means of discriminating between two major lagoon habitats. Sea kraits are abundant on and around most islets, they are easy to catch, manipulate, and measure. Forced regurgitation is also a routine technique. Our network of sampling

sites extends over a vast area, covering most of the New Caledonian Lagoon. It includes marine habitats classified under different protection statuses: integral biological reserves, special marine reserves (permanent and temporary), and unprotected areas. The gradient of distances of islets from the main contaminant sources (urbanized zones, marinas, and nickel industries) provides another pivotal element for comparisons among sites. Finally, there is no equivalent to the long-term mark-recapture study of sea kraits in New Caledonia; only infrequent (usually short-term), broad counting of sea birds, sea mammals, marine turtles, fish, mollusks are available. To our knowledge there is no concurrent system likely to provide equivalent spatial information over such an extended time.

We recently demonstrated that sea kraits are useful bio-indicators of the biodiversity of anguilliform fish on coral reefs (Brischoux et al. 2009b). This assertion was previously proposed for the related species *L. colubrina* (Reed et al. 2002). Our analyses based on krait prey diversity showed that relatively small sample sizes ($N < 50$ prey items; hence moderate sampling effort) were sufficient to characterize the anguilliform fish assemblage of the targeted sites (Brischoux et al. 2009b). We also found significant differences in fish assemblages between sites, in addition to differences in sea-krait populations, providing a reference for the biodiversity of top predators. Our research recently revealed 15 fish species not previously observed in New Caledonia, along with a species (*Cirrimaxilla formosa*, Muraenidae) only known from its haplotype (Ineich et al. 2007; Séret et al. 2008). Overall, sampling of sea kraits is an efficient means of surveying biodiversity of the reef and of monitoring assemblages of otherwise inaccessible communities of anguilliform fish. Sea kraits forage on fish that are themselves predators, they swallow their prey whole (hence many prey items are intact), thereby offering access to secondary prey: notably we found crustaceans (shrimps, crabs), fish, annelids, and mollusks. An ongoing study (collaboration with M. Briand and Prof. Y. Letourneur, University of New Caledonia) focusing on these additional trophic levels will likely reinforce the usefulness of sea kraits as pertinent bio-indicators of the New Caledonian marine biodiversity. As sea kraits occur across vast areas of the Indo-Pacific oceans, the value of these snakes as bio-indicators of specific animal assemblages on reefs may well apply to many marine ecosystems other than those from New Caledonia.

In collaboration with Prof. Paco Bustamante (LIENSs—UMR 7266, University of La Rochelle,

France), we assayed the levels of 13 different heavy metals in the prey of sea kraits (Bonnet and Fauvel 2011). The New Caledonian Lagoon is subject to increasing levels of pollution generated by growing urbanization and rapidly developing mining activities (Peters et al. 1997; Bustamante et al. 2000; Hédouin et al. 2010). Anthropogenic pollution creates concentration gradients from the point source along the shore (Pernice et al. 2009). Species that depend on specific and localized habitats (benthic organisms) are impacted in a progressive manner: from a significant negative impact of pollution in the vicinity of the contaminant source, to an absence of impact in well-protected zones. As sea kraits are phylopatric, and as they forage on sedentary prey, the established network of sampling sites provided a nice opportunity to assess this important issue. We found strong positive correlations between levels of heavy metals (e.g., nickel [Ni] and cobalt [Co]; $r = 0.70$, $N = 50$, $P < 0.001$), with 10% of the samples exceeding nickel levels of $5 \mu\text{g/g}$. These findings strongly imply that anguilliform fish were contaminated by heavy metals in the sampled areas, possibly linked to mining activity that typically releases large quantities of effluents contaminated by Ni and Co into the sea, followed by bio-accumulation of these metals in the tissues of benthic organisms (Hédouin et al. 2010). We acknowledge that the biological significance, potential ecological impact, and exact sources of the heavy metal concentrations measured in these fish are currently unknown; however, we stress that our data show that the sampling system of sea kraits is operational, and that we can monitor possible long-term accumulation of heavy metals in the anguilliform fish (and likely in the yet-untested sea kraits) over a wide and precise spatial scale. Further studies are needed to thoroughly assess the anthropogenic effects of urban development and mining on animal assemblages in one of the planet's few remaining relatively intact reef ecosystems.

During field work, anecdotal observations of snakes' behavior highlighted further eco-physiological issues with possible applications to conservation. For example, over 140 days of monitoring at one study site (Signal Island), we recorded the behavior of almost 7000 snakes under different environmental conditions of temperature, wind, and precipitation. During the summer drought, sea kraits spent the majority of their day sheltered under rocks or within burrows, likely avoiding overheating and dehydration. They selected periods of the day when the air was cooler, notably at dusk, to move to the sea for foraging excursions. However, during a heavy daytime downpour, a vast number of kraits left

their refuge to drink freshwater (Bonnet and Brischox 2008). Each species exhibited a particular drinking pattern (mostly from ephemeral puddles for *L. Laticaudata*, versus from running water and droplets attached to the vegetation for *L. saintgironsi*) (Fig. 2), and they emerged from different shelters (beach rocks for *L. laticaudata* versus burrows and large boulders for *L. saintgironsi*). This phenomenon suggests that sea kraits depend on freshwater more than previously assumed (they must drink freshwater episodically to survive), and that access to freshwater is influenced by habitats that catch rain, notably the vegetation and/or rocky substrate on sandy islands (Guinea 1991). These habitat features are particularly important, as the combination of drizzling and the presence of near-shore herbaceous vegetation (the leaves catch droplets) provides the main source of freshwater for kraits during the hot dry, and thus critical, season. Note that local people call these herbaceous zones “sea-krait grass” (“l’herbe à tricots”). Unfortunately, tourists represent a serious threat to this critical and fragile habitat. Indeed, the vegetation of some highly frequented islets has been cleared, and is regularly mowed on others, including natural reserves (e.g., Ilot Larégnère, Ilot Maître). Protecting these habitats should be an important management practice for authorities. Independent studies of three other species of sea kraits examined the relationships between water balance and the availability of freshwater, both in captivity and in the field, and came to similar conclusions: freshwater is essential and its availability influences both distribution and inter-annual variation in kraits’ activity (Lillywhite et al. 2008; Lillywhite and Tu 2011). It is therefore clear that changes in patterns of natural precipitation due to global climatic changes represent an important factor for the conservation of sea kraits. Long-term field studies provide the unique opportunity to scrutinize and quantify the impact of climatic changes on the distribution and persistence of sea krait populations.

Like terrestrial species, sea snakes are in strong decline (Heatwole 1997; Reading et al. 2010; Rasmussen et al. 2011). Possible actions may involve protection of areas dedicated to sea kraits (like protected beaches for turtles, seals, and birds), restoration, and improvement of specific habitats, including provision of freshwater by artificial means. Indeed, repeated observations show that leaks from artificial freshwater reservoirs are particularly attractive for sea kraits on sandy islets. Improvement in habitat quality and access to freshwater may allow sea kraits to better cope with rapid environmental changes. The implications of anecdotal field observations during this

study reinforce the notion that accurate knowledge about the specific terrestrial requirements of sea kraits is crucial for successful conservation.

In addition to the mark-recapture study during which the exact location of several hundred snakes was systematically recorded (precision ± 10 m) we translocated sea kraits from Signal Island. Individual relocations during recaptures and the translocation experiment showed that kraits exhibit a strong and fine-scale fidelity for particular areas of the shore (Shetty and Shine 2002a; Brischox et al. 2009c). When on land, sea kraits select precise microhabitats for shelter; they usually return to the localized zone of beach-rocks, boulders, or burrows from whence they were captured before translocation. Despite translocating more than 300 sea kraits, and repeatedly precisely relocating more than 500 sea kraits, we almost never captured any sea krait on a different beach than the one of original capture. Recaptures across all study sites nonetheless revealed that dispersion and juvenile recruitment can occur over large geographic scales; almost all settled sea kraits from a given colony, however, exhibit a marked fidelity to a particular home site between foraging trips. Considering the strong dependence of sea kraits on specific terrestrial habitats, it was not surprising to observe a nonrandom distribution along beaches; the kraits concentrated in areas with abundant refuges. Seabird burrows, thick vegetation, large tree roots, and rock complexes offered the most suitable habitats. However, a systematic counting of the snakes along the shore revealed that some beach rocks were heavily used by the snakes whilst others tended to be avoided (Bonnet et al. 2009). To explore why the sea kraits were so selective in their choice of refuges we recorded ambient, substrate, and refuge temperatures; we used sea krait models to estimate variations in body temperature, and we examined kraits’ movements. During hot and sunny periods the snakes avoided dry beach rocks. Indeed, such refuges rapidly accumulate heat, explaining the selection of large humid beach rocks, cooled down by the sea at high tide and by evaporation at low tide. However, focusing on such humid shelters was insufficient to accurately describe the nonrandom distribution of the snakes: some humid, large rocks were neglected by the snakes whereas others sheltered many individuals. The answer to this question arose from a fortuitous observation: to breathe at high tide without leaving their shelter, sea kraits must stretch their body to reach the surface. The most suitable refuges allowing breathing are those submerged by <30 cm of water at high tide. Taking into account breathing and thermal requirements, it was possible

to accurately determine the spatial distribution of the refuges intensively used by the sea kraits. *Laticauda laticaudata*, a species prone to dehydration and with limited terrestrial mobility, was far more dependent on these particular humid beach rocks than was *L. saintgironsi*, a species capable of traveling long distances on land. The distribution and abundance of *L. laticaudata* across the New Caledonian lagoon is strongly influenced by the availability of humid beach rocks situated in a very narrow zone of the shore, and/or of large tree cavities near the shore (Bonnet et al. 2009). Our data militate for a strong protection of this poorly represented, albeit important, overlooked habitat. Artificial constructions such as wharf-consolidating stone stacks offer suitable terrestrial habitat for *L. laticaudata*, and to a lesser extent for *L. saintgironsi*, notably on those islets where sandy beaches predominate. During the maintenance of a wharf in 2010 (Phare Amédé Natural Reserve), local authorities followed our recommendations and carefully replaced the key-stones under the wharf in the intertidal zone after completion of the works. Later, our surveys (2011) confirmed that the sea kraits were still using this artificial microhabitat (including marked kraits previously captured under the wharf), providing encouragement to restore or create suitable habitat using a simple technique. These practical results show that the protection of each sea krait species requires specific actions; these actions are in accordance with the more fundamental issues raised above and suggesting that *L. laticaudata* and *L. saintgironsi* have followed divergent evolutionary routes during return transition to the sea.

This present short review is based on different results derived from a long-term and intensive field study of sea kraits; it reveals strong links between fundamental issues and conservation. However, it is equally obvious that many major questions were not addressed. Although our large data set permits demographic analyses in order to estimate survival, dispersal, and recruitment, none were presented here. Information about reproductive traits (age and size at maturity, fecundity, and reproductive frequency), although essential, is also absent (but see Brischox and Bonnet 2009). These data are essential for population viability analyses (PVA), and thus are of prime importance for conservation. There are three main reasons why such important issues were omitted. First, several manuscripts are under review (e.g., examining demography), precluding the presentation of the main outcomes. Second, we are currently performing analyses (e.g., regarding genetic or geographic variations of contaminant levels) and we do

not yet know the main conclusions. Third, despite our willingness to encompass a variety of topics, we were only able to deal with a limited number of (often narrow) questions. It is nonetheless possible to provide several broad extensions to this review.

The mean body condition of the sea kraits from each of the sites was correlated with the distance from urbanized zones: the lowest body conditions were near the most exposed area (in the vicinity of Nouméa, the main urbanized zone), the highest body conditions were in the fully protected reserve, and all intermediate values fit within the gradient between these two extremes. This result suggests that sea kraits can provide a useful index to probe and to monitor the overall quality of selected sites. Our PVA and large-scale recapture analyses clearly revealed that despite the high site fidelity exhibited by most individuals, the persistence of most populations heavily depends on dispersal of juveniles across a complex network of sites. Consequently, it is necessary to protect the whole lagoon and not a subset of isolated sites; this is a key consideration for successful establishment of new protected marine areas. Genetic analyses performed by Lane et al. (2008) and Lane and Shine (2011) showed complex sex divergent dispersal patterns, either female-biased or male-biased, in different areas of the lagoon of New Caledonia, reinforcing the notion of important interconnectivity between populations. Finally, our observations refute several published (and thus cited) observations about life-history traits of the New CaledoniaN sea kraits (Saint Girons 1964; Ineich and Laboute 2002). For instance it is not true that most prey are swallowed head first (80%), that the main prey item is *Echnida nebulosa* (we never found a single specimen in the stomach of the sea kraits), that the time elapsed between capture of prey and digestion is $\sim 1.5\text{--}2.5$ months (see also Shetty and Shine 2002b), that clutch size varies between 4 and 20 eggs with a mean of 6.5 (the real value is far below, about 3 on an average and often less), that reef birds are predators of the sea kraits (zero records), and that mating generally occurs in water (always observed on land). All these refuted facts may appear superficial and anecdotal; however, it is essential to redress incorrect information, as such errors can generate highly biased general conclusions. For example, running PVA by implementing the incorrect 6.5 fecundity in the calculations would lead to the wrong result, i.e., that most populations can persist without requiring a strong component of juveniles' immigration. This would seriously impede the establishment of efficient conservation plans.

Conclusions

Long-term detailed field studies are essential for framing superficially disparate information into a coherent context. For example, our data revealed strong links between locomotor performances, breathing behaviors, foraging patterns, and terrestrial microhabitats of *L. laticaudata* and *L. saintgironsi*, essential knowledge for an understanding of the evolutionary pathways followed by each species and for the development of appropriate conservation actions. Unfortunately, long-term field studies are seldom implemented, partly due to logistical difficulties, but also because it is far easier to publish results based on the modeling of already gathered (or artificially generated) data. We nonetheless hope that our field work will allow better protection of sea kraits, notably in New Caledonia where they are traditional emblematic species in the Kanak culture.

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