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Fine scale site fidelity in sea kraits: implications for conservation

Francois Brischoux · Xavier Bonnet · David Pinaud

Abstract The shores of coral reef islands are major sites for biodiversity, but unfortunately they are also subject to strong anthropogenic disturbances. Indeed vast arrays of organisms live exclusively in these very narrow and well structured zones, many others depend on the rich and diverse micro-habitats for essential part of their life cycle (to reproduce, forage, etc.). Sea kraits are sea snakes that depend on the shore of coral islets; they forage at sea but digest, reproduce and rest on land. They have been killed in extremely large numbers in many places, causing local extinctions. In the current study we demonstrate through recapture and translocation studies that these snakes exhibit a strong and fine-scale fidelity for particular segments of the shore. Consequently, these specific areas should be under strong protection, as it the case for the breeding beaches used by marine mammals, birds or turtles.

Keywords Coral reef · Habitat · Philopatry · Sea snake · Shore · Tourism

Introduction

Coral reefs are the main oceanic hot spots for biodiversity (Roberts et al. 2002), but they face a deep ecological crisis (Rogers 1990; Hughes 1994; Guinotte et al. 2003; Pandolfi et al. 2003; Sheppard 2003; Bellwood et al. 2004). The causes of such calamity are diverse: global warming, over-fishing and marine pollution being among the main factors (Walker and Ormond 1982; Linden 1999; Hughes et al. 2003; Riegl 2003). Tourist activities

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represent another serious threat to coral reef areas. The negative impacts of tourism concentrate on the shorelines. Inevitably, massive human presence generates important pollution, excessive wildlife disturbances and over-fishing for leisure and for catering needs (Prior et al. 1995; Orams 2001). However, one of the most destructive effects of tourism on coralline islands is building and urbanisation, notably the construction of resorts, pools, pathways, marinas directly on or adjacent to the shoreline. Unfortunately, the shores of islands are important transition habitats between marine and terrestrial ecosystems for many species (Menge 1995; Kathiresan and Qasim 2005). Beside such role, the shores themselves contain diverse, fragile and spatially limited micro-habitats (i.e. sand banks, beach-rocks, mangroves) that shelter a vast array of highly specialized species (e.g. shorebirds, invertebrates, algae). Intertidal areas also play important functional roles by linking marine and terrestrial food webs (Polis and Hurd 1996). As a consequence, particular attention must be dedicated to understand how shore modifications could impact the species that heavily depend on these specific habitats (Castilla 1989; Hawkins and Roberts 1994; Chapman and Bulleri 2003).

Sea kraits (sea snakes) are highly dependent on the shores of coral reef islets (Heatwole 1999; Ineich and Laboute 2002). Indeed, they forage at sea but come back on land to digest, mate, lay their eggs and slough their skin (Heatwole 1999; Ineich and Laboute 2002; Brischoux and Bonnet 2009). These predators play a key role in the functioning of coral reef ecosystems; they notably feed on considerable quantities of fish (>40 species of anguilliform fish, mostly moray eels) that are predators themselves (Ineich et al. 2007; Brischoux and Bonnet 2008). Consequently, these snakes are considered as indicator species for reef status in many places of the western Pacific Ocean (Reed et al. 2002; Alcala 2004; Ineich et al. 2007; Brischoux and Bonnet 2008). Because sea kraits use terrestrial habitats for major biological functions, they might be very sensitive to shore perturbations; no data on this issue are available, however.

Experimental studies demonstrated that sea kraits exhibit a strong large-scale philopatry; they systematically return to their home islet when released more than 5 km away from the site of capture (Shetty and Shine 2002). This means that a complete destruction of the shore of a given island can potentially entail the disappearance of the associated snake populations (Shetty and Shine 2002). However, anthropogenic activities often damage natural habitats more progressively. Thus, more realistically sea krait vulnerability toward gradual modifications of the shore will depend on their degree of philopatry: the loss of terrestrial habitats would have less impact if the snakes use various pathways to move between the sea and land and shelter under a wide range of terrestrial sites. In such a case, the snakes could adapt to a partial (i.e. geographically limited) destruction of their terrestrial habitat by shifting rapidly toward non- or less-disturbed areas. Conversely, if sea kraits display a narrow and marked fidelity to particular spatially limited terrestrial sites, any shore modifications would strongly and immediately impact populations if the zones destroyed were those used by the snakes. The aim of this study was to assess the fine scale degree of philopatry exhibited by sea kraits with respect to shore areas.

Answering the questions above is essential to better appreciate the potential impact of shore modifications on sea kraits. Indeed these snakes have been killed in huge numbers in various places, generating dramatic population declines or local extinctions (Bacolod 1984, 1990). It is important to describe and assess the value of different terrestrial habitats to first efficiently protect healthy populations, and secondly to propose conservation plans to restore other populations. For instance, if sea kraits exhibit strong fine-scale site fidelity for narrow particular terrestrial habitats, the protection of such zones becomes a priority. To

assess the possible fine scale terrestrial fidelity of two sea kraits species, we employed two complementary techniques:

(1) We analysed the results from a translocation experiment by moving a number of snakes between two opposite shores of the island. This procedure enabled us to assess site fidelity at a medium geographic scale (i.e. >500 m).
(2) We analysed series of recaptures with precise location within and between years to assess fine scale site fidelity (i.e. 10 m) over long time periods.

Materials and methods

Study species

Two species of sea kraits occur in New Caledonia: *Laticauda saintgironsi* (the yellow sea krait, endemic to the area, Cogger and Heatwole 2006) and *L. laticaudata* (the blue sea krait) widely distributed in the western Pacific Ocean (Ineich and Laboute 2002; Saint Girons 1964). Sea kraits spend half of their time foraging at sea, and come onshore for all their other activities (Heatwole 1999; Ineich and Laboute 2002). When on land, they shelter within the roots of large trees, cavities, crevices, burrows, under logs and rocks, and spend very little time in the open (Bonnet and Brischoux 2008). However, the yellow sea kraits (*L. saintgironsi*) can undertake relatively long trips on land; these snakes are regularly observed hundreds of meters inland, sometimes more than 40 m above the sea level. By contrast, blue sea krait (*L. laticaudata*) do not move easily on land, cannot readily cross obstacles such as small cliffs, and this species is almost always observed in a narrow habitat swath at a short distance from the water limit (Bonnet et al. 2005).

Study site

Signal Island is a 10-ha, flat and rectangular islet (22°17′45 S; 166°17′34 E, Fig. 1). The proximity (15 km) from the main city, Nouméa, generates an important flow of tourists, essentially during weekends and summer holidays. A large pontoon, two camp-sites (with several shelters, fire places), and a terrestrial pathway have been constructed to accommodate and canalise the tourists (Fig. 1). This islet, classified as a natural reserve, shelters large populations of both yellow and blue sea kraits (Ineich et al. 2007; Brischoux and Bonnet 2008).

Survey procedures

Since the beginning of the study in 2002, one to five persons walked along the shores of Signal Island and surveyed a 20 m wide area (including the intertidal area). Each survey lasted 30 min to 1 h. Over 168 days of fieldwork, the total searching effort represented more than 400 h (see Bonnet and Brischoux 2008 for details). Sea kraits were easily located (owing to their banded colour pattern). We concentrated our searching effort to the activity periods of both species (notably sunrise and sunset), and reduced searching during the hottest phases of the day when the snakes remained sheltered (Bonnet and Brischoux 2008). At capture, the species and the sex were recorded; individuals were permanently marked by scale clipping, and the snakes were measured (snout vent length-SVL, ±1 cm) and weighed (±1 g) (Brischoux and Bonnet 2009).
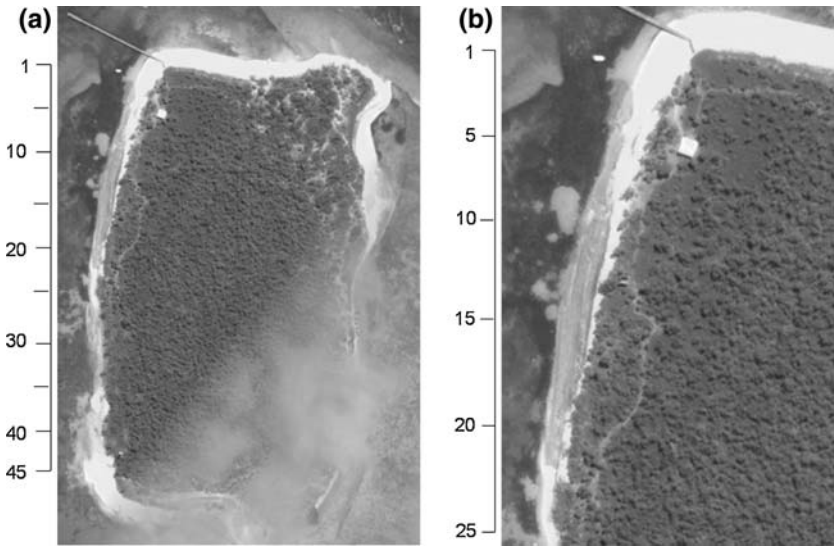
Fig. 1 Pictures of Signal islet (22°17′45 S; 166°17′34 E, modified from GoogleEarth). The *scale* represents the 45 capture areas of 10 m long. **a** General view of Signal islet showing the four different shores. **b** Detailed view of the west shore. Note that beach-rocks (areas 5–20, *light grey*) and sandy beaches (*white*) are clearly visible. On both pictures, the pontoon, the camp site and the terrestrial pathway are discernible

Although sea kraits have been observed on the whole perimeter of the island, the west shore concentrates most of the observations and is the only one to shelter the blue sea kraits. Broadly, the 450-m west shore composed by flat beach rocks (80%) and small sandy beaches (20%, Fig. 1) provided excellent habitat for both species of sea kraits; while the North, East and South shores were visited only by smaller numbers of *L. saintgironsi* (Bonnet et al. 2009). Therefore, we devoted most of the searching effort to this section of the island, but we nonetheless surveyed regularly the three other shores ($N = 30$ surveys). For simplicity, hereafter we refer to the "west shore" versus the "three other shores" (North, East and South, Fig. 1) to describe the system at a broad scale. Since 2002, the shore of capture and recaptures of each snake was systematically recorded.

In 2004, the west shore was divided in 45 areas of 10 m long, visualized using flagging tape marks (Fig. 1). Consequently, for each snake, we recorded the exact area of capture with a precision of at least 10-m. Because we captured more than 2,500 snakes and accumulated an equivalent number of recaptures, since 2004 we obtained large sample sizes of precise locations for many individuals.

Translocation experiment

In 2004, we performed a translocation experiment at a medium spatial scale. More than 270 snakes (179 *L. laticaudata* and 98 *L. saintgironsi*) captured on the west shore of Signal Islet were released on the east shore less than 24 h after capture. On 14 different occasions (field work days from February 22 to March 14 2004), between 7 and 33 snakes have been released on the east shore. Translocated snakes were randomly selected and this sample included both already marked and newly identified snakes, and mixed different age classes and both sexes. Because the aim of this experiment was to assess the ability of translocated snakes to come back on the shore of capture (west shore), we did not rely on a specific

re-sampling design. We rather relied on a direct comparison of recapture rates between undisturbed and translocated snakes recaptured on the west shore during classical patrols (see "Results").

Fine scale recaptures

From 2004 to 2007, to test if the successive recaptures of a given individual concentrated in a particular area versus occurred randomly along the west shore, the mean observed distance between each successive recaptures was compared to a calculated random mean distance. Random mean distances between recaptures were generated according to the null hypothesis: for each individual we considered n 10 m-shore segments visited by the snake (corresponding to the total number n of recaptures). Then, n recapture locations were randomly re-sampled with replacement. Importantly, the re-sampling procedure was adjusted to the distribution along the shore of the total pool of captures + recaptures for the considered species. This design allowed taking into account the marked preference for particular 10 m-segments of each species between the 45 10-m segments available (unpublished). That is, snakes tended to use particular zones of the west shore, and the species diverged for such preferences (Bonnet et al. 2009). The mean simulated distance between successive recaptures for each individual was compared to the observed mean. Because we used only one value per individual (mean of all the distances between captures for a given snake), each individual contributed only once and with the same weight in the analyses; irrespectively of the number of recaptures. Therefore, our analyses do not include pseudo-replicates.

   Overall, during the study (2002–2007) we collected broad scale data since 2002 (the shore of capture–recapture was recorded), performed a translocation experiment in 2004, and collected fine scale location observations since 2004. Because we gathered large sample sizes, and obtained clear-cut results based on high recapture rates (see below), the analyses were straightforward.
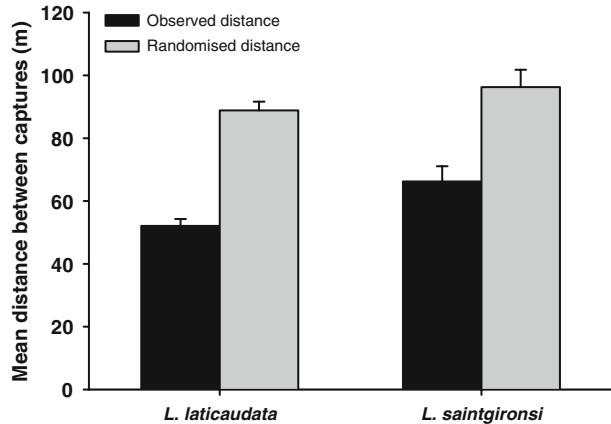
Results

Translocations

We recaptured 47% of the translocated *L. saintgironsi* and 76% of the translocated *L. laticaudata*. These values accord well with the respective recapture rates obtained for each species on the west shore, independently from the translocation experiment: 52% in *L. saintgironsi* (comparing translocated versus not-translocated snakes, $\chi^2 = 0.02$, $P = 0.9$) and 77% in *L. laticaudata* ($\chi^2 = 0.02$, $P = 0.9$). The elapsed time between translocation and further recaptures ranged from 1 day to 3 years. Such time delay did not differ when comparing translocated (mean calculated on 50 randomly selected snakes: 259.91 ± 39.16 days between captures) versus not translocated snakes (mean calculated on 50 randomly selected snakes: 297.54 ± 51.36 days between captures; t-test, $t = -0.58$, $P = 0.56$). Taken together, these results suggest that the snakes returned to the shore of capture. If the snakes had used the other shores (e.g. decided to settle in the novel site of release, moved to another islet, or have been lost due to the translocation), then the probability to recapture them in the initial shore would have been lower.

   We cannot exclude the possibility that the snakes, translocated or not, visited all the four shores of Signal Island, but concentrated on the west shore and simply rarely visited the

Fig. 2 Mean observed distance (*black bars*) and mean simulated distance (*grey bars*) between captures for *L. laticaudata* and *L. saintgironsi*. Observed distances were significantly lower than simulated distances for both species. Observed distance were significantly lower in *L. laticaudata* compared to *L. saintgironsi*. Means are presented ± standard error

three other shores. In such a case, our translocation experiment would have been useless. To explore this possibility, we used the data of the snakes captured and marked in the three other shores (34 *L. saintgironsi* but no *L. laticaudata*). None of the snakes captured in the three other shores have been observed in the west shore at any time; and none of the 1,407 *L. saintgironsi* captured in the west shore were recaptured in any of the three other shores. Given the very large number of snakes marked in the west shore, because recaptures probabilities were all greater than 50%, and because the study was conducted over 168 days of fieldwork (5 years), these results strongly suggest that the snakes exhibited a strong fidelity to a given shore. At least in terms of terrestrial habitat use, the snakes from the west shore are distinct from the snakes that use the other shores. If not, we would have almost certainly recaptured several snakes initially captured and marked on the three other shores on the west shore, and some of the very numerous snakes that originated from the west shore would have been observed on one of the three other shores.

Fine scale fidelity

We gathered precise data on recapture areas for 404 *L. laticaudata* (mean 3.15 recapture areas per individuals, max = 11) and 174 *L. saintgironsi* (mean 2.47 recapture areas per individuals, max = 6). Observed mean distances were significantly smaller than randomly generated mean distances (paired *t*-test, $t = -10.45$, $P < 0.0001$, for *L. laticaudata*, and $t = -4.09$, $P < 0.0001$, for *L. saintgironsi*, Fig. 2). Restricting analyses to individuals with more than two observations to increase the power of the analysis led to similar results (paired *t*-test, $t = -9.55$, $P < 0.0001$, for *L. laticaudata*, and $t = -3.16$, $P < 0.001$, for *L. saintgironsi*).

   Interestingly, the observed mean distances between recaptures were significantly lower in *L. laticaudata* (*t*-test, $t = -3.05$, $P < 0.01$; Fig. 2), suggesting a species-specific divergence in the degree of philopatry.

Discussion

The importance of protecting the shores of islets used by sea kraits is supported by convergent evidences from different spatial levels. At a broad scale (i.e. between islets), both a marked philopatry and clear homing capacities have been documented in sea kraits

from Fiji (*L. colubrina*, Shetty and Shine 2002). In this study, we showed that beside a strong fidelity to a particular islet, sea kraits display a strong philopatry toward a particular shore, and more precisely to a small area of the shore itself: over a 450 m long beach, each individual tended to be repeatedly re-captured within a narrow 60 m area. Such fidelity suggests that sea kraits know precisely where to return on land, and thus are able to recognise their terrestrial environment, to follow a precise pathway and shelter under familiar beach rocks, roots of large trees, crevices, bird burrows or logs (Brischoux and Bonnet 2009; Bonnet et al. 2009). Indeed, sea kraits often undertake long foraging trips and travel great distance at sea (Brischoux et al. 2007). For instance we recaptured snakes from Signal Island more than 80 km away (unpublished data). Their ability to return to their home islet and to use particular narrow zones of the shore reveals a well-developed knowledge of both their marine and terrestrial environments. Focusing on terrestrial habitat, strong selective advantages likely enabled the development of the senses and behaviours associated with fine navigation ability: despite the tide, fluctuating weather, changes in the currents, the snakes were able to follow a precise route. Familiarity with certain segments of the shore may first increase the probability to reach a safe and buffered shelter on land (Bonnet et al. 2009). It may also reduce significantly the transit time between the sea and the terrestrial shelter. Such decrease in the transit time might be important to reduce the snake exposure to predators, but also might allow the snakes to rapidly reach the thermal optimum for digestion, sloughing and reproduction, and to avoid overheating or overcooling, and finally to collect freshwater efficiently during rainfall (Bonnet and Brischoux 2008). All the aspects raised above can have strong impact on the survival and energy budget of ectotherms (Seigel and Collins 2003).

The proportion of individuals from a given islet that disperses on other islets is modest: less than 50 snakes among a total of >7,000 marked individuals on 12 islets have been recaptured on more than one islet (unpublished). Thus, despite its important biological meaning, dispersal does not represent a significant factor in our calculations. The four shores of signal islet were not evenly surveyed generating a bias notably by increasing the probability to not observe the putative translocated snakes that would have used effectively the three other shores (i.e. the shore of translocation plus the adjacent ones). Nonetheless, in such a case, the recapture probability would have markedly decreased (i.e. there are four different shores on signal islet, all of a comparable size, so the recapture probability should have been divided by four). However, we did not detect any effect of translocation on the recapture probability.

Interestingly, the degree of philopatry was different between the two sea krait species. This result accords well with other field observations: *L. saintgironsi* tends to use the shores as a transition habitat between the marine foraging grounds and the various terrestrial shelters situated just above the shore bank, notably large rocks and puffin burrows (Bonnet et al. 2009). By contrast, *L. laticaudata* use intensively the beach-rocks situated within the intertidal area (Bonnet et al. 2009). To provide suitable shelter, intertidal beach-rocks must be of minimal size, thereby buffering thermal fluctuations, and must not be submerged by more than 40 cm of water at high tide to allow aerial breathing; consequently they tend to be localised in precise intertidal areas (Bonnet et al. 2009). As expected, the blue sea krait exhibited narrower terrestrial site fidelity compared to the yellow sea krait.

What is the applicability of our results in terms of conservation? Our main conclusion is that specific segments of the shore are essential for sea kraits. Because we cannot experimentally degrade the most favourable habitats to examine population consequences, we rely on the impact of tourism on other islets situated in the same areas: the southwest

lagoon of New Caledonia. In 2003, one of us (XB) directly observed and pictured the destruction of the shore of a coral islet comparable to Signal Island (Maitre islet; 7.5 ha, 22°20′00 S; 166°24′37 E). Despite its classification as a natural reserve, the construction of pools, resorts, restaurants, resulted in a severe transformation of the west shore including high coverage by concrete (see Google Earth). Concomitant to these modifications and constructions, the sea krait populations disappeared.

Marine mammals, sea birds or marine turtles benefit from the protection of their terrestrial breeding sites. Our results strongly argue for the creation of equivalent areas for sea snakes. For instance, the west shore of Signal Island is one of the specific sites that should receive such protection and where human activity should be strictly limited. Tourist numbers should be limited or canalised, and any project to increase the island's carrying capacity should be carefully examined in the light of our results.

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