Received: 25 August 2020 | Accepted: 15 January 2021

DOI: 10.1002/pan3.10190

RESEARCH ARTICLE

PEOPLE AND NATURE | BRITISH ECOLOGICAL SOCIETY

Peaceful coexistence between people and deadly wildlife: Why are recreational users of the ocean so rarely bitten by sea snakes?

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Funding information
PADI Foundation, Grant/Award Number: 28454

Handling Editor: Arjen Buijs

Abstract

1. Research on interactions between humans and deadly snakes has focused on situations that result in high rates of snakebite; but we can also learn from cases where snakes and people coexist peacefully. For example, coastal bays near Noumea, in the Pacific archipelago of New Caledonia, are used by thousands of tourists and snakes, but bites are rare.
2. Our long-term studies clarify reasons for this coexistence. Although 97% of snakes encountered in standardised snorkel surveys were a harmless species *Emydocephalus annulatus*, we recorded dangerously venomous taxa often enough (one snake per 8 hr snorkelling) that we would expect many risky human–snake interactions in these crowded bays. However, the risk is reduced by low overlap between humans and snakes in the timing of activity, both seasonally and on the diel cycle. Mate-searching male snakes, the group most likely to approach divers, enter the bays only in cooler months of the year when few beach users are present. Also, snakes tend to be active by night, whereas people are not.
3. Risk is further reduced by spatial divergence: bare-footed beach users stay in sandy areas rather than the adjacent coral-reef areas that are preferred by snakes. The response of snakes to disturbance is also important: most sea snakes are reluctant to bite even when harassed. Water currents frequently push sea snakes against hard objects, perhaps explaining why the snakes do not interpret brief contact with a human as an attack. The ability of snakes to flee is increased by uniformly high body temperature, and a complex three-dimensional aquatic environment.
4. Thus, the danger of snakebite for recreational users of these popular beaches is reduced by aspects of human and snake behaviour that (a) decrease encounter rates and (b) render snakes unlikely to bite even if contacted. The risk to snakes is also reduced because snakes are more difficult to detect and kill underwater than on land. As a result, thousands of snakes and people coexist harmoniously within these small bays.

KEYWORDS

Elapidae, human–wildlife conflict, Hydrophiinae, Laticaudinae, snakebite

1 | INTRODUCTION

The conflict between people and dangerous wildlife increases as human populations expand (Hill et al., 2017; Nyhus, 2016), exacerbated by the creation of resource hotspots (e.g. of garbage and rodents) that, in turn, attract predators (Soulsbury & White, 2016). Humans interact with a wide variety of dangerous taxa, but some of the most intense conflicts involve venomous snakes. More than 100,000 people die annually from snakebite (Gutiérrez et al., 2017), constituting a significant social and economic burden throughout developed and developing countries in subtropical and tropical regions of the world (Kasturiratne et al., 2008), so much so that the World Health Organisation has recently recognised snakebite envenomation as a priority neglected tropical disease (Williams et al., 2019). In response to perceived or actual threat, the killing of snakes by people may significantly impact snake populations globally (Fitzgerald & Painter, 2000). Most research on the management of snakebite focuses on incidences of venomous bites, and the development and administration of effective antivenom as a reactive measure. Documenting the ecology of venomous snakes in regions of high human interactions can provide significant insights into developing preventative measures to mitigate the risk (Murray et al., 2020).

Epidemiological research on the determinants of snakebite frequency in Asia has identified several factors that increase risk (e.g. Reid, 1968; Thomas & Scott, 1997). Unsurprisingly, conflict is most intense where high densities of people coincide with high abundances of deadly snakes, and during seasons and weather conditions that increase activity levels of both humans and snakes (Tomari, 1987). However, the behavioural responses of snakes to harassment are also important: bites are more common if the snakes involved are likely to retaliate rather than flee (e.g. Mirtschin et al., 2017). The severity of bites also depends upon human demography (children are more vulnerable than adults) and protective clothing (bare feet and legs allow fangs to penetrate deeply enough for venom transfer: e.g. Naik, 2017). Also, the incidence of bites may be higher if the local population has not been educated about ways to reduce risks of snakebite (Gutiérrez et al., 2017; Rodda et al., 1999).

At first sight, all of those risk factors apply to encounters between recreational users of the ocean and sea snakes. Marine snakes are abundant close to popular holiday sites; people in the water often wear little protective clothing; some species of sea snakes are reputed to be aggressive (e.g. Heatwole & Cogger, 1994); and most tourists do not know what snake species occur in the area, or how to reduce the risk of snakebite (e.g. White, 2017). Nonetheless, most bites from sea snakes are not to recreational users of the ocean. Instead, the main snakebite victims are fishermen who interact with sea snakes in nets or on lines (e.g. Fulde & Smith, 1984; Phillips, 2002; Thomas & Scott, 1997; Van Cao et al., 2014). Given that sea snakes are abundant in many sites where people swim, snorkel, dive and wade, why are recreational users of marine habitats so rarely bitten? Understanding situations where dangerous wildlife coexist peacefully with humans can provide important insight on how human-wildlife conflicts can be effectively managed (Carter et al., 2012).

Our long-term studies on sea snakes in the Pacific archipelago of New Caledonia offer a good example of coexistence between snakes and people. New Caledonia contains at least 15 species of marine elapids: three species of amphibious Laticaudines (sea kraits) and 12 species of ‘true’ (viviparous) Hydrophiines (Ineich & Laboute, 2002; Shine et al., 2019). Several of those species are common around the capital city of Noumea, in sites used by thousands of tourists annually (Borsa, 2008). For example, dense populations of Laticaudines inhabit small islands in this region (Brischoux & Bonnet, 2009), and more than 140 individuals of the Greater Sea Snake *Hydrophis major* were recorded within a single small bay next to Noumea in a 2-year period (Goiran & Shine, 2019). Nonetheless, there have been no confirmed reports of snakebite in this area during our study (Goiran & Shine, 2019). Records between 2000 and 2016 show seven confirmed cases of sea snake envenomation recorded in New Caledonia, with only two cases recorded in close proximity to the study site within that period (Maldonado, 2017).

We suggest that conflict between snakes and people in this area is reduced by several factors, involving snake behaviour as well as human behaviours. The end result of those factors is that snakes and people tend to be active at different places and at different times; and also, snakes are likely to flee rather than retaliate. To explore these ideas, we assembled data from published literature, and from our own surveys of snake and human behaviours in the bays near Noumea.

2 | MATERIALS AND METHODS

2.1 | Study site

We worked primarily in two small adjacent bays (Baie des Citrons and Anse Vata: see Figure 1a) that contain the main tourist beaches for the city of Noumea, in New Caledonia (22°16′S, 166°26′E). The bays attract many local residents (Noumea is home to 100,000 people, and these two bays are popular sites for recreation) and a vast number of tourists. Cruise ships arrive on most days during warmer months (e.g. http://crew-center.com/noumea-new-caledonia-cruise-ship-schedule-2019), and each ship contains thousands of people. Many of those people spend the day at the Noumea beaches (see Figure 1b,c). The most popular aquatic recreational activities are walking, swimming, snorkelling, wind-surfing and kite-surfing. Most recreational users of the bays wear swimwear only (see below) and, based on our conversations with them, are unaware of the presence of venomous snakes.

2.2 | Study species, relative abundance and encounter rates

During standardised surveys in January each year over a 17-year period, we recorded seven species of sea snakes in Baie des Citrons and Anse Vata (we have also found an eighth species,

FIGURE 1 (a) Map of study site in Noumea where telemetered snakes were tracked using an array of fixed acoustic receivers across four main habitats (colours of points represent predominant habitats), and locations of two popular beaches where human activity was surveyed (red areas). Two photographs of the two popular beaches: (b) Baie des Citrons and (c) Anse Vata during a typical day time survey. Both beaches have shallow sandy and fringing reef habitats, which are typically frequented by holiday-makers. Photographs by V. Udyawer

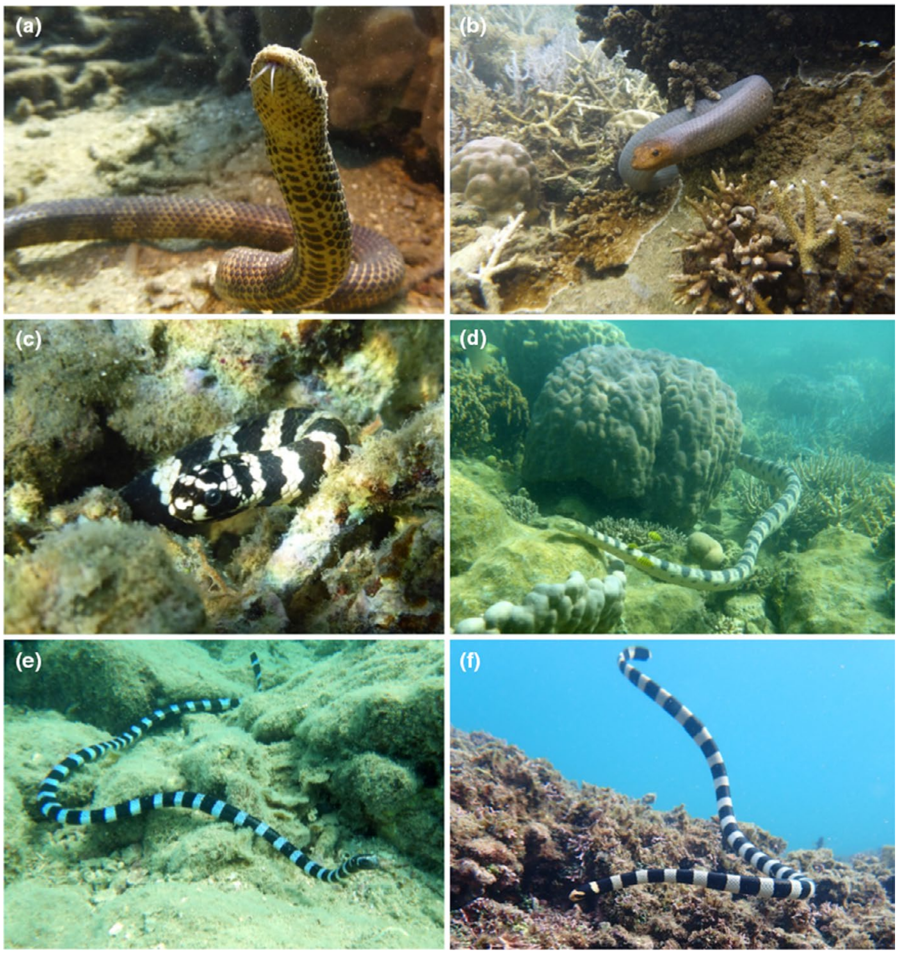

FIGURE 2 Snake species commonly recorded in the Baie des Citrons. (a) Reef Shallows Sea Snake, *Aipysurus duboisii*; (b) Olive Sea Snake, *Aipysurus laevis*; (c) Turtle-headed Sea Snake, *Emydocephalus annulatus*; (d) Greater Sea Snake, *Hydrophis major*; (e) Blue-banded Sea Krait, *Laticauda laticaudata;* (f) Yellow-banded Sea Krait *Laticauda saintgironsi*. Photographs by C. Goiran

Hydrophis coggeri, but not during our surveys; Figure 2). Table 1 provides the information on relative abundance of these taxa at these beaches, with a brief assessment of snakebite risk for each species based on encounter likelihood, propensity to bite and toxicity. We used survey data collected over the 17-year period to estimate relative abundance and encounter rates of commonly observed species of sea snakes within Baie des Citrons and Anse Vata.

2.3 | Field methods

2.3.1 | Movements and residency of sea snakes

For three of the study snake species (all potentially deadly to humans; Heatwole, 1999), we implanted acoustic transmitters to track movements within the bays (4 *Aipysurus duboisii*, 2 *A. laevis* and 16 *Hydrophis major*). Signals from those transmitters were detected by an array of 18 acoustic receiver stations (Figure 1a), and the movements of these individuals were monitored continuously between January 2017 and November 2018. Snakes were collected by hand as we snorkelled through the study site during daylight hours and were held in captivity for <15 days before transmitters (V9P-2H, Innovasea Ltd., 3g) were implanted in the peritoneal cavity under general anaesthesia in veterinarian care (see Udyawer et al., 2020 for details of surgery methods). The animals were then released at their points of capture after a 24-hr period of post-surgery recovery and appeared to be unaffected by the transmitter implantation. Behaviour and recovery of individuals post-surgery were also monitored in the field when tagged individuals were encountered during subsequent field surveys.

2.3.2 | Occurrence of species within the bays

For one of the focal taxa (*H. major*), we also work with a citizen science group (the Fantastic Grandmothers; FGM) who look for snakes almost every day, and who photograph the snakes' tails for individual identification (see Goiran & Shine, 2019 for details of this ongoing monitoring programme). That study recorded 140 individual *H. major* within the bays over a 25-month period, although most snakes were seen only once or twice (M = 277 sightings in total). Subsequent to publication of that paper, the FGM have increased the total number of individuals recorded to 275 (as of December 2020; unpubl. data).

2.3.3 | Human behaviour

On 5 days in January 2019, 4 days in October 2019 and 4 days in January 2020, we walked along the beachfront of both bays at hourly intervals (daylight hours only during good weather) to record numbers of people in areas where the substrate was dominated by sand versus by fringing coral reef (see Figure 1). These months represented seasonal periods where we expect high human–snake interactions, when numbers of recreational users are high (December–February) and when snake movements are at their peak during the winter mating season (August–October). The numbers of people in each ~200 m section of that transect were scored, as were their locations (in water vs. on the beach), and on some surveys we also estimated age groups (children < ~10 years old, vs. older people) and clothing (barefoot or not) as a function of activity (walking, swimming, snorkelling, etc.) and substrate type (sand vs. coral). Our surveys encompassed the entire diel period of human use of the water, with no people recorded in the

TABLE 1 Sea snakes encountered during snorkelling surveys in two shallow bays near Noumea over the course of 17 consecutive January fieldtrips (total = 999 person-hours in the water over that period; M = 58.8 person-hours per year). The counts include all records of snakes seen, so include multiple observations of some individual animals. Species-specific likelihood of encounters, propensity to strike and toxicity are summarised to assess a brief risk of snakebite and envenomation

Common name	Scientific name	Number encountered	Likelihood of encounters with beachgoers	Propensity to bite	Toxicity (LD_{50} dose; mg/kg)[a]	Risk of snakebite and envenomation
Turtle-headed Sea Snake	*Emydocephalus annulatus*	3,992	High	Low	25[1]	Very Low
Reef Shallows Sea Snake	*Aipysurus duboisii*	45	Low	Low	0.032[1]	Low
Yellow-banded Sea Krait	*Laticauda saintgironsi*	44	High	Low	0.45[b][2]	Low
Greater Sea Snake	*Hydrophis major*	27	High	Medium	0.194[3]	High
Olive Sea Snake	*Aipysurus laevis*	9	Low	Medium	0.069[1]	Low
Blue-banded Sea Krait	*Laticauda laticaudata*	5	High	Low	0.179[2]	Low
Dragonhead	*Hydrophis peronii*	3	Low	Low	0.062[1]	Low

[a]All LD_{50} values were sourced from literature and standardised to measures from laboratory testing on mice from sub-cutaneous injection. Lower values indicate higher toxicity. [1]Ineich and Laboute (2002); [2]Russell and Saunders (1967); [3]Broad et al. (1979).

[b]LD_{50} values based on studies of closely related *Laticauda colubrine*.

water at night during occasional nocturnal surveys on foot (as above) nor during 24 nocturnal observations (hourly, 18:00 hr–06:00 hr over two nights) from a hotel balcony overlooking one of the bays (to verify the absence of people in the water).

2.4 | Analysis methods

2.4.1 | Spatial and temporal overlap between sea snakes and people

We have quantitative data on this topic only for the two telemetered species (*A. duboisii* and *H. major*) that were frequently recorded by listening stations adjacent to the beaches for which we quantified human presence. For the other species, we rely upon published reports, our experience during fieldwork and information from colleagues.

We assessed the spatial overlap between telemetered snakes and beachgoers during daylight hours and at night. Numbers of residency events of each telemetered snake were summarised for each acoustic receiver for the entire period of the study using the VTrack r package (Campbell et al., 2012). Residence events for each snake at each receiver were estimated as the time an individual was continuously detected within the detection range of the receiver. The residence event ended if the snake moved to another receiver within the array or was not detected on the full array for more than 30 min. Receivers nearest to the coast (and hence, in close proximity to beachgoers) were classified as 'shallow', whereas those further offshore were classified as 'deep' receivers. Mean numbers of residence events for each of the two species of sea snake at shallow receivers were plotted against mean numbers of beachgoers in the water during day and night to assess the potential spatial overlap between snakes and people. Temporal overlap between snake presence and use of beaches by people was assessed by comparing the mean numbers of residence events for each species of sea snake on shallow receivers with the mean numbers of beachgoers in the water for every hour during day and night periods in regions where snake–human presence overlapped. We used a Wilcoxon rank-sum test to assess if there was a significant difference in the distribution of residence events of snakes at shallow receivers and observations of beachgoers in the water for each hour of the diel periods ($\alpha = 0.05$).

2.4.2 | Use of habitats by snakes and people

To further understand fine-scale spatial overlap and encounter rates between snakes and humans, we assessed how both snakes and people were using habitats within the two bays in Noumea. For the two telemetered species of snakes for which we have large sample sizes, we estimated the proportion of time individuals spent in coral-reef-dominated sites to those where the substrate consisted primarily of sand. Proportion of times at each of the predominant habitats (Figure 1a) were estimated using the calculated duration of residence events for within the study site. We used a chi-squared test to compare the mean residency periods of both species of sea snakes within coral-reef and sand-dominated habitats. Similarly, we characterised the habitats used and use of protective clothing used by swimmers within the two bays in Noumea using survey data. We conducted chi-square contingency-table tests to compare the mean numbers of people walking versus swimming on the reef versus sandy beach areas.

3 | RESULTS

3.1 | Relative abundance and encounter rates of snake species

Of 4,111 snakes that we recorded over a 17-year period of January surveys, 3,992 (97%) were Turtle-headed Sea Snakes *Emydocephalus annulatus* (Table 1). The next most common taxa were the Reef Shallows Sea Snake *Aipysurus duboisii* and the Yellow-banded Sea Krait *Laticauda saintgironsi*, then the Greater Sea Snake *Hydrophis major* (Table 1). Many individual snakes were re-sighted on several occasions, but we include these repeated sightings because snakebite risk likely is affected more by the number of encounters rather than the numbers of individual snakes involved. Average rates of encounter (snakes per snorkeler per hour) averaged 5.50 overall (5.35 for *E. annulatus*, 0.15 for the other species combined).

3.2 | Spatial and temporal overlap between sea snakes and people

We obtained 37,422 detections from 14 *H. major*, and 13,619 records from 4 *A. duboisii*, but only 15 records from one of two telemetered *A. laevis*. Estimation of residence events resulted in a total of 6,118 residency events for the tracked *H. major*, 3,456 residence events for *A. duboisii* and a single residence event for *A. laevis*. The spatial patterns in residency between the two species for which sufficient data were available revealed interspecific differences in spatial ecology. Residency of all four *A. duboisii* monitored was restricted to shallow habitats within Baie des Citrons, whereas *H. major* moved more actively throughout shallow and deeper habitats (Figure 3). The use of beaches by people was high in Baie des Citrons during daytime, overlapping with residency patterns of *A. duboisii*.

Both telemetered species (*A. duboisii* and *H. major*) were active throughout the diel cycle, but the more nocturnal residency pattern observed in *A. duboisii* significantly reduced overlap with the numbers of people using shallow regions of Baie des Citrons ($W = 130.5$, $p < 0.01$; Figure 4a). The more widespread movements of *H. major* meant that their residency at shallow receivers was less frequent, but was most common during the day and hence exhibited high temporal overlap with beach users ($W = 305.2$, $p = 0.07$; Figure 4b). Of the other species, *Emydocephalus annulatus* is mainly

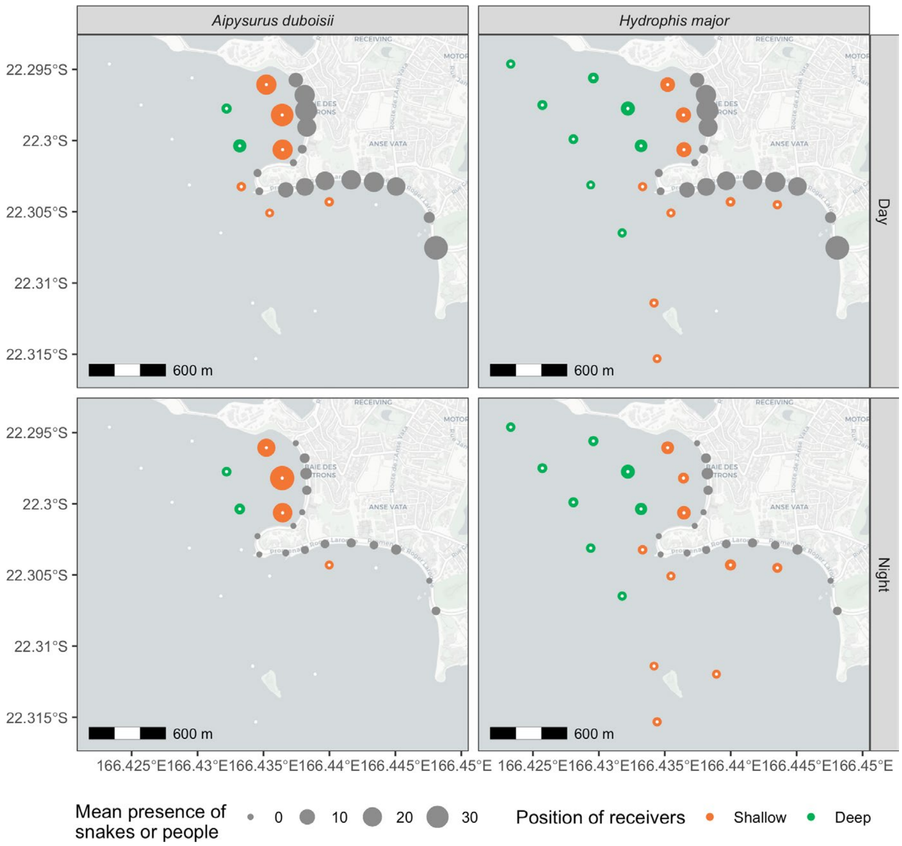

FIGURE 3 Bubble plot highlighting spatial overlap between recreational users of the Noumea bays, and two species of acoustically tracked sea snakes in the same bays. Size of points represent mean numbers of human beach-users recorded across all sites (grey circles), and mean numbers of residence events measured for telemetered *Aipysurus duboisii* ($n = 4$ snakes; left-hand panels) and *Hydrophis major* ($n = 14$ snakes; right-hand panels). Colour of points for snake residency represent shallow (orange) and deep-water (green) receivers

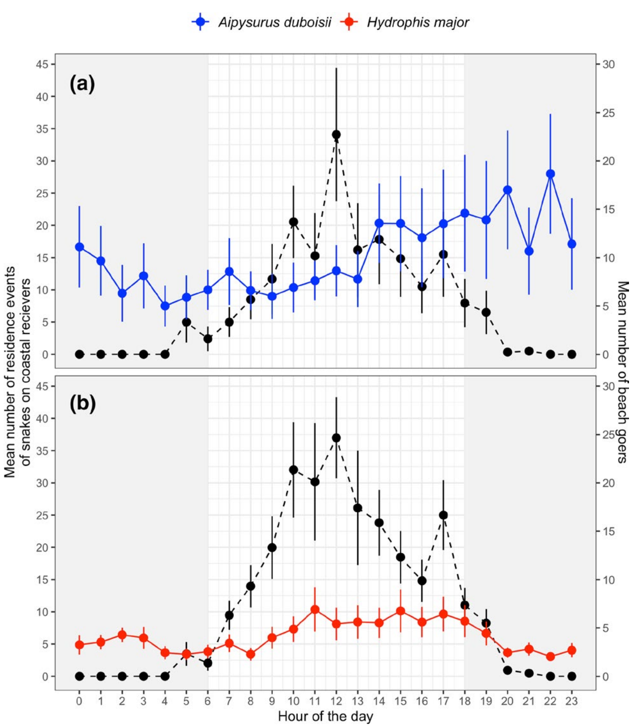

FIGURE 4 Temporal overlap between the hourly numbers of residency events of two species of acoustically tracked sea snakes (a: *Aipysurus duboisii*, b: *Hydrophis major*) and mean hourly numbers of human beach-goers (black points) in areas with high spatial overlap between residency by snakes and people in shallow areas of the same bays

diurnal (e.g. rarely seen during nocturnal dives at our study sites: C. Goiran, pers. obs.), whereas *Laticauda* spp. move between the ocean and the land mostly from dusk to dawn (e.g. Shetty & Shine, 2002; Shine, et al., 2003; Shine, et al., 2003) but forage actively at sea at all hours of the day and night (Cook et al., 2016). Information on the other species is more fragmentary but Burns and Heatwole (1998) reported that radio-tracked *Aipysurus laevis* foraged both by day and by night. Unfortunately, we did not obtain enough telemetry information for *A. laevis* for more detailed analysis.

3.3 | Use of habitat by snakes

Within a mosaic of habitat types, *E. annulatus* was recorded more often in sites characterised by coral than would be expected by chance (Goiran et al., 2020). In keeping with that preference, we rarely saw *E. annulatus* in sandy areas between adjacent coral patches, even though the snakes would have been highly visible in such sites. The telemetric records of *A. duboisii* reveal extensive movements in shallow water, with a significant preference for coral-line fringing reef and shallow sandy substrates rather than deeper habitats ($\chi^2 = 138.4$, 3 *df*, $p < 0.01$; Figure 5). In contrast, *Hydrophis major* often used deeper sandy habitats but primarily utilised fringing reefs when in shallow waters within Baie des Citrons ($\chi^2 = 76.29$, 3 *df*, $p < 0.01$; Figure 5). All of the other species in our study area except for *L. laticaudata* and *H. coggeri* were invariably most often sighted over coralline rather than sandy substrates.

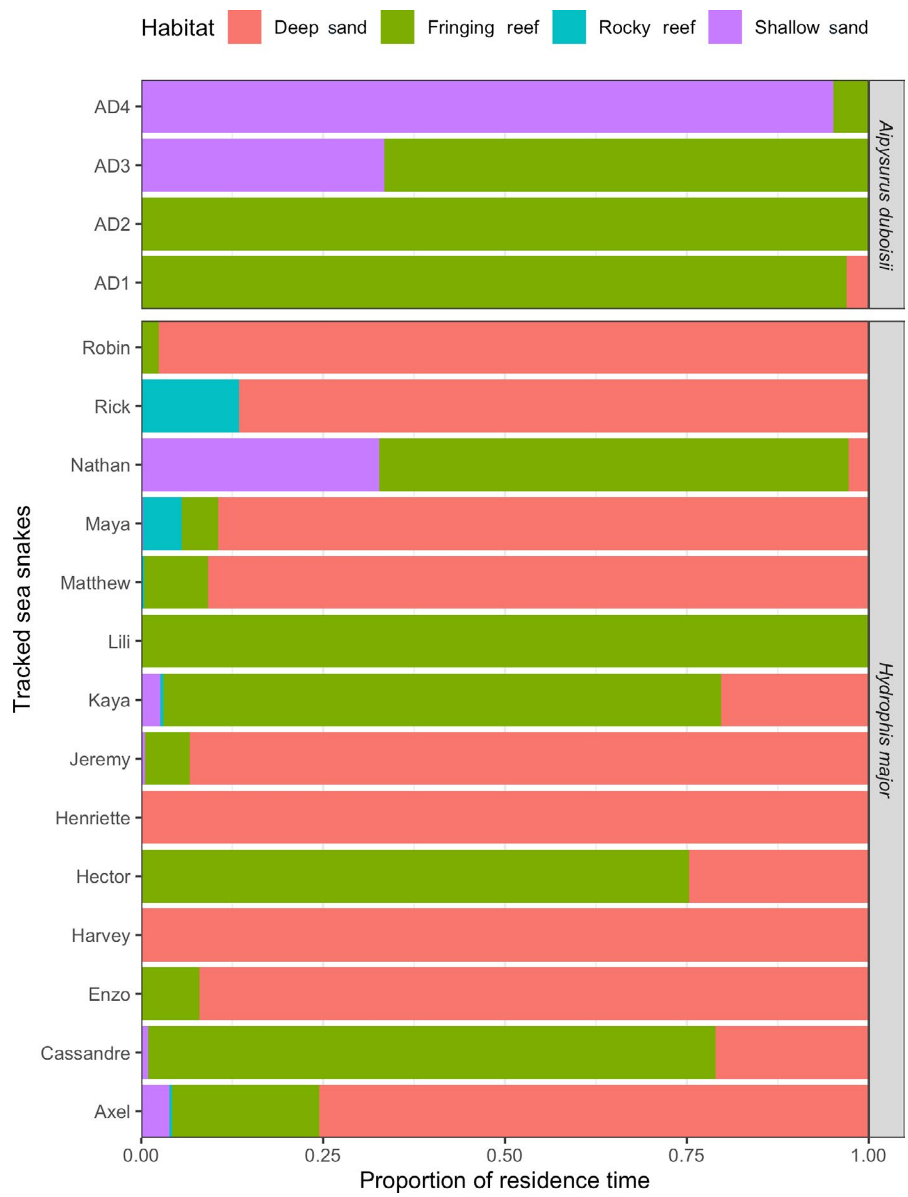

FIGURE 5 Use of habitats by two species of telemetered sea snakes *Aipysurus duboisii* and *Hydrophis major* close to populated beaches of Noumea. Figure 1a indicates the spatial distribution of habitat types within this study site

3.4 | Use of habitat by people

Our hourly counts show that people were in the water only during daylight hours, with peaks during the middle of the day and the afternoon (Figure 4). Most people were seen in sandy-substrate areas rather than in reef-substrate areas (18 vs. 531: vs. null of equal numbers, $\chi^2 = 541.03$, 1 *df*, $p < 0.0001$; see Figure 6). Most beach users in Noumea are passengers in cruise boats that spend a single day moored in Noumea as part of a longer trip. We have no data on the proportion of people on each boat that spend the day (or part of it) at our study sites, but the beaches are one of the most popular destinations for these day trippers (see Figure 1). During our surveys, people in reef areas were generally swimming (usually, snorkelling) or in windsurfers, and thus were not in direct contact with the substrate. In contrast, many people in sandy areas were walking. Thus, a higher proportion of people were in contact with the substrate in sandy sites than in coral-reef sites (28.1% vs. 0%; $\chi^2 = 12.18$, 1 *df*, $p < 0.003$: see Figure 6).

3.5 | Protective clothing

Almost all recreational users of reef-associated sites wore protective footwear (typically, boots and/or fins: cumulative total 99%), whereas people in sandy sites usually had bare feet (89%; comparing the two substrate types in this respect, $\chi^2 = 76.33$, 1 *df*, $p < 0.0001$; see Figure 6). Overall, children were less likely to have protective footwear than were adults (11% vs. 36%).

3.6 | Responses of snakes to people

We rarely saw free-ranging snakes perform any behaviours that could be construed as aggressive or retaliatory. One exception occurred in January 2019, when two FGM snorkellers encountered a snake *Hydrophis peronii* as it was feeding. After the fish escaped, the snake approached the snorkelers and repeatedly struck towards the

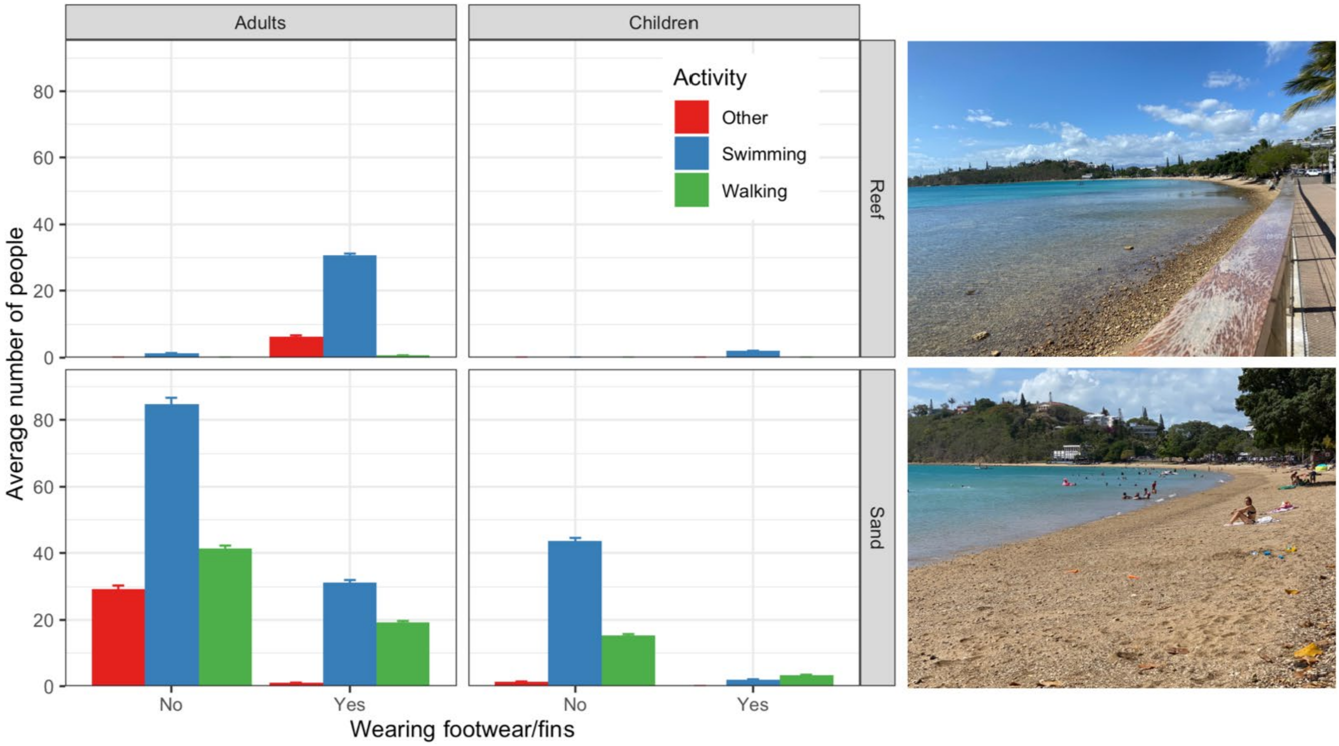

FIGURE 6 Relationships between substrate type (coral reef vs. sand) and the numbers, activities and protective footwear of recreational users of the area. Histograms show mean values, with associated standard errors. Other activities observed include kitesurfing, windsurfing and other water sport. Photographs on the right highlight typical habitat types at Baie des Citrons and show differences in beach use by people. The top photograph, taken from the southern end of the bay, shows coral reef in shallow water in the foreground. The bottom photograph, taken in the middle part of the sandy area, shows holiday-makers using the area. Photographs by Terri Shine, with permission

fins of one of them (see Video S1 for footage of this encounter). We have also recorded many instances of snakes approaching snorkelers (but not attacking them), especially during the winter mating season when male snakes search for reproductive females (see Shine, 2005, and Videos S2 and S3). Male sea snakes find it difficult to identify females based on visual cues alone, so it is common for male snakes to approach people, tongue-flick them then move away (Shine, 2005, and see Video S2 and S3).

In contrast to that tolerance underwater, snakes often attempt to bite us while we are handling them on land post-capture, for mark–recapture and telemetry studies. This is true for all the species we have handled except for the *Laticauda* species, both *L. laticaudata* and *L. saintgironsi* (see Shine, Bonnet, et al., 2003; Shine, Shine, et al., 2003). Sea kraits often refrain from retaliating even when handled (Heatwole, 1999; Shine, Bonnet, et al., 2003; Shine, Shine, et al., 2003). Nonetheless, on rare occasions (<1 in 100), laticaudine snakes have been observed attempting to bite the handler. We know of three bites from *L. saintgironsi* (one juvenile, two adult males) to biologists, all after prolonged handling (X. Bonnet & H. Cogger, pers. comm.).

4 | DISCUSSION

Although it is difficult to explain why something does not happen, our data identify two major mechanisms that reduce the risk of snakebite in the bays of Noumea: factors that decrease the probability of an encounter between a person and a deadly snake, and factors that decrease the likelihood of retaliation by a snake when such an encounter occurs.

At first sight, the reason why snakebite is rare in the Noumea bays appears to be absurdly simple: 97% of the snakes encountered during daylight hours in midsummer are of a species (*Emydocephalus annulatus*) that is incapable of biting people (Table 1). But although the other (deadly) species comprised only 3% of our sample, they nonetheless are relatively common in absolute terms. A person snorkelling in these bays is likely to encounter one dangerous snake per 8 hr in midsummer. There are hundreds of beach users in the water each day during this period (see Figure 1b,c). Thus, simple mathematics would predict hundreds (perhaps thousands) of close encounters between these snakes and recreational users of the ocean each year. So, the question remains: why do not these large deadly snakes bite recreational users of the ocean? Our studies suggest two reasons for that situation: relatively low overlap between snakes and people in times and places of activity, and a reluctance for snakes to retaliate even if humans approach closely.

First, rates of encounter between snakes and people are reduced by divergences in time and space (Figures 3 and 4). By far the riskiest form of encounter would involve a person treading on a snake—but people are rarely active at night, when the larger sea snakes are most active. Most beach users also avoid deep water, and walkers in shallow water shun coral-reef substrates to avoid lacerating their feet (Figure 6). The small number of people who venture into reef habitats tend to stay on the water surface (snorkelling) and/or to use protective footwear, thereby reducing the risk of envenomation (Figure 6). This divergence in the use of habitat is likely widespread in marine systems, because laticaudine and hydrophiine snakes are strongly associated with coral-reef habitats overall (e.g. Heatwole, 1999). However, one hydrophiine species (*Hydrophis platurus*) is pelagic, and others are collected over muddy or sandy substrates (but typically, in water too deep for people to wade: e.g. Crowe-Riddell et al., 2019; Heatwole, 1999).

The overlap between peak activity for snakes and beach users is also low on a seasonal basis. The month when we conducted our snake surveys (January) is the most popular time for cruise ships to visit Noumea (over the period 2017–2019, 75 of 490 boats arrived in January, versus 20 or less per month in the winter months of June, July and August: http://crew-center.com/noumea-new-caledonia-cruise-ship-schedule-2019). The rate of encounter with *E. annulatus* is similar year-round (e.g. 5.45 snakes per person per hour in July 2011, from our surveys) but larger species of snakes are seen more frequently in months when water temperatures are lower. For example, Goiran and Shine (2019) recorded >40 *H. major* per month in September, October and November, compared to an average of six snakes per month in January through March. Almost all of the snakes seen in the colder months are adult males, engaged in mate-searching, whereas females outnumber males in summer (December through March: Goiran & Shine, 2019). That sex-ratio shift affects the risk of snakebite because mate-searching male *H. major* commonly approach humans in the water (checking for potential mates: Shine, 2005; see Videos S2 and S3), whereas females and juveniles ignore swimmers. Hence, the subgroup of snakes most likely to interact closely with people—adult males in search of mates—are unlikely to be encountered by beach users visiting the bays of Noumea. A similar seasonal pattern was identified in recorded snakebite incidences in New Caledonia between 2000 and 2016, with five confirmed cases during the peak tourist season in summer and two in the winter months (Maldonado, 2017).

Even when people and dangerous snakes are in the bays at the same time, the likelihood of life-threatening bites is reduced by features of the marine habitat and of the snakes' behaviour. The importance of specific factors differs among snake species—for example, some taxa are harmless, some are reluctant to bite, others are active when people are not, and yet others use habitats that are rarely exploited by recreational bathers. That divergence in habitats may occur at different spatial scales—for example, *Aipysurus laevis* and *Hydrophis peronii* at our study sites rarely venture into water shallow enough to encourage recreational use, whereas *Hydrophis major* enter shallow water but are found primarily over coralline substrates that are avoided by beach users walking on the substrate.

The response of a snake to close approach by a person depends upon a range of factors relating to the environment and to the snake itself. An extensive literature supports Clifford Pope's classic summary from the early 1900s that 'snakes are first cowards, then bluffers and last of all warriors' (e.g. Shine et al., 2000). That is, snakes evade people if they are able to do so. The marine environment facilitates escape, for at least three reasons. First, the snake can flee in three dimensions rather than two, as on land. Second, potential refuges are common in complex coral-reef systems (as opposed to an open field, for example). Third, high water temperatures mean that snakes are warm, and thus capable of sustained locomotion (Heatwole et al., 2012; Shine, Bonnet, et al., 2003; Shine, Shine, et al., 2003). One of the most common scenarios for retaliation in terrestrial snakes is 'hypothermal aggression', whereby a snake that is too cold to flee relies instead on retaliation (e.g. Shine et al., 2000). That situation is unlikely to arise within coral-reef habitats, especially in midsummer when tourist numbers are at their peak.

In short, snakes are most likely to bite in defence if they cannot escape, either because of a lack of refuges or to impaired mobility of the snake itself (e.g. due to low body temperature). Neither of these factors apply in tropical coral-reef systems, decreasing the probability that a snake will react to a human's approach with a defensive bite. Interspecific differences in 'aggressiveness' are difficult to quantify, but our experience with terrestrial elapids as well as sea snakes suggests that most (but not all: Heatwole, 1999) sea snakes are more placid than their terrestrial counterparts. One reason for that tolerance may be that marine snakes are frequently buffered by current and wave action, or by the movement of objects (e.g. seaweed, coral fragments). Perhaps for this reason, sea snakes tend to have thicker skin (more resistant to abrasion) than do terrestrial snakes (Shine et al., 2019). As a result of frequent and unpredictable contact with hard objects, the snakes may not interpret firm contact (e.g. from being stepped-upon by a human) as aggression. The snake does not attempt to bite unless the harassment continues.

The likelihood of conflict is also reduced by responses of humans to the aquatic environment. Thus, for example, many snakebites occur when people try to kill snakes (Pinheiro et al., 2016). That attempt usually involves hitting the snake (e.g. with a stick or a rock) or shooting with a firearm, methods that cannot be adopted in even moderately deep water. Thus, even if the person sees the snake (less likely in the water than on land), he/she is unlikely to try to kill it. The only cases we know of direct killing of snakes in New Caledonia involve snakes encountered on land—either hydrophiines that have washed up on the beach (*Aipysurus duboisii*—R. Shine, pers. obs.; or laticaudines found during their terrestrial activities—e.g. Saint Girons, 1964).

Why, then, are sea snakes responsible for so many human deaths worldwide? The victims are primarily fishermen, who capture snakes in nets or on baited lines (e.g. Alirol et al., 2010; Reid, 1961). Most records of sea snake envenomation have occurred in southeast Asia where barefoot fisherman working in muddy estuarine waters are bitten when either treading on snakes or trying to extract them from nets without using safety equipment (Reid, 1961). In this situation, the snake has no way to escape, is likely injured and resorts to retaliation. Official records of sea snake bites and envenomation may underestimate actual incidences due to the lack of access to medical facilities, and stigmas and superstitions surrounding sea snake bites in parts of Asia (Alirol et al., 2010). Interestingly, most recorded bites come from a single species, *Hydrophis schistosa*, that may be more willing to bite than are many other marine snakes (Heatwole, 1999), although other species like *H. cyanocinctus* and *H. curtus* also recorded to inflict dangerous bites (Warrell, 1994). In such situations, the best option to reduce the incidence of fatal snakebite may be education programmes for fishermen so that they can adopt safer practices when handling snakes (Lalloo et al., 1995).

4.1 | Recommendations and conclusions

A pro-active means to mitigate snakebite risks can be to magnify pre-existing differences in habitat use between people and snakes (terrestrial as well as marine species) to reduce the risk of encounters that are likely to be fatal to both participants. For example, the current study highlights spatial and temporal divergence between the use of the coastal habitats of Noumea by beach users and by dangerously venomous sea snakes. Exploiting the mismatch in where (i.e. coral-reef habitats vs. sandy beaches) and when (i.e. tourist season vs. sea snake mating season) sea snakes and humans are most likely to come into contact may provide an effective mitigation strategy. We can restrict human access to critical areas of habitat that house high densities of venomous snakes or other dangerous animals. Additionally, campaigns to educate the public and foster interest about sea snakes occurring within a region, their movement behaviours and to remove preconceived stigma associated with snakes may provide an effective mitigation strategy to reduce snakebite risk. Similarly, education about safe handling and first aid practices for fishers who frequently encounter sea snakes may mitigate ongoing snakebite risks (Udyawer et al., 2018). In the system where we work, discouraging people from walking on coral has obvious benefits not just for snakes and people, but for the physically fragile corals and the other life forms that they support (Leujak & Ormond, 2008).

Appropriately, most of the published literature on human–wildlife conflict examines situations where such conflict is intense (e.g., Hill et al., 2017; Nyhus, 2016). To gain a broader understanding of that issue, however, we also need to explore situations where people coexist with wildlife, despite the presence of factors (e.g. high densities of people plus dangerous animals) that might be expected to create risky encounters between people and animals. If we can identify the characteristics of situations where conflicts are minimal, compared to those where conflicts are intense, we will be better placed to develop new ways to mitigate problematic interactions, and achieve the goal of harmonious coexistence between humans and potentially dangerous animals.

ACKNOWLEDGEMENTS

We thank the members of the Fantastic Grandmothers (FGM) citizen scientist group (Geneviève Briançon, Aline Guémas, Sylvie Hebert, Cathy Le Bouteiller, Monique Mazière, Marilyn Sarocchi and Monique Zannier), Marine Marziac, Fabien Srauy and Rafael Valente for providing invaluable field and laboratory assistance. We also thank staff at the Aquarium des Lagons including O. Chateau, R. Farman, J. Dubosc, H. Gossuin, S. Govan, X. Neyrat, V. Robineau, M. Baussan, S. Bourget and T. Brasseur for facilitating the field instrumentation and our access to aquaria facilities. We thank Dr Jean-Christophe Vivier and staff at Sainte Marie veterinary clinic for assistance with surgeries for this study, and LabEx Corail for Acoustic Telemetry funding. Our research on sea snakes has been funded by the Australian Research Council, Labex Corail and The PADI Foundation. Research was conducted using methods approved by the Charles Darwin University animal ethics committee A18029 and collection permits from New Caledonia Province Sud 3252-2017/ARR/DENV. Valuable comments on an earlier version of this manuscript were provided by Harvey Lillywhite and an anonymous reviewer.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas, designed the methodology and collected the data; V.U. and R.S. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Processed telemetry data and beach survey data can be accessed through the Dryad Digital Repository https://doi.org/10.5061/dryad.z8w9ghxbd (Udyawer et al., 2021).

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How to cite this article: Udyawer V, Goiran C, Shine R. Peaceful coexistence between people and deadly wildlife: Why are recreational users of the ocean so rarely bitten by sea snakes? *People Nat*. 2021;3:335–346. https://doi.org/10.1002/pan3.10190