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**ARTICLE**

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THE TERRESTRIAL LIFE OF SEA KRAITS: INSIGHTS FROM A LONG-TERM STUDY ON TWO LATICAUDA SPECIES (REPTILIA: SQUAMATA: ELAPIDAE) IN THE ANDAMAN ISLANDS, INDIA

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Abstract: Sea kraits forage in water and return to land to digest their prey, mate, slough, and lay their eggs. The temporal terrestrial patterns in encounter rate and behaviour of two species of sea kraits Laticauda colubrina and L. laticaudata were studied over four years at the New Wandoor beach in the southern Andaman Islands. The encounter rate of L. colubrina was found to be 20 times higher than L. laticauda, and sea kraits were observed to prefer the natural refuge that the microhabitat of uprooted trees provide. Additionally, nesting observations are presented that emphasize the need to promote the conservation of these crucial terrestrial habitats.

Keywords: Andaman Islands, encounter rate, habitat use, India, Laticauda colubrina, Laticauda laticaudata, nesting behaviour, sea snake, terrestrial pattern.

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Author Contribution: TK and EY conceived the idea; TK and ZT collected the data; NPM performed the analysis; ZT and NPM led the writing, all authors contributed to the writing.

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INTRODUCTION

Sea snakes of the genus *Laticauda*, most commonly known as banded sea snakes or sea kraits, are amphibious in nature (Shine 2003; Heatwole et al. 2005). They rely entirely on aquatic prey and display adaptations to marine life such as a flattened paddle-like tail, salt-excreting glands, and enlarged lungs (Heatwole 1999; Shine & Shetty 2001; Brischoux & Shine 2011). Unlike the other lineages of marine snakes, however, sea kraits retain an oviparous mode of reproduction and hence must return to land to lay their eggs. They also mate, digest their prey, and slough their skins on land (Heatwole 1999; Greer 1997). They possess large ventral scales that help them move efficiently on land (Bonnet et al. 2005; Shine & Shetty 2001). Acquiring fresh water is crucial for sea kraits (Lillywhite et al. 2008; Kidera et al. 2013) and a combination of availability of fresh water on land and low salinity at sea may determine the sea kraits’ geographic distributions and indicate their environmental tolerances (Brischoux et al. 2012, 2013). Sea snakes may also act as indicators of climate change effects (Lillywhite et al. 2008, 2014), thus heightening the interest in their ecology, behaviour, and conservation (Brischoux et al. 2009a; Bonnet 2012; Elles et al. 2013).

Sea kraits are widely distributed in the tropical and subtropical coastal waters of the eastern Indian Ocean, southeastern Asia, and archipelagoes of the western Pacific Ocean (Heatwole et al. 2005). Of the eight *Laticauda* spp., Yellow-lipped Sea Krait *L. colubrina* and Blue-lipped Sea Krait *L. laticaudata* have the largest range, extending throughout the southeastern Asian islands and seas. Comparatively, the distribution of *L. laticaudata* is fragmented with a smaller extent of occurrence than *L. colubrina* (Gherghel et al. 2016). *Laticauda colubrina* grow to an average total length of 100cm with females growing larger than males, whereas *L. laticaudata* grow to an average length of 80cm (Shetty 2000). While *L. colubrina* are considered to be more terrestrial, *L. laticaudata* are considered to be intermediate, using both terrestrial and aquatic phases equally (Heatwole 1999; Greer 1997; Bonnet 2012). Juveniles of both species rarely venture far from water but stay close to its edge, whereas adults move inland (Shetty & Shine 2002a,b). Mate-searching males move about much more actively on land than do females (Shine & Shetty 2001).

In the Andaman Islands, *L. colubrina* and *L. laticaudata* are known to occur throughout the archipelago (Bhaskar 1996; Shetty & Sivasundar 1997, 1998). On South Reef Island off North Andaman, the relative abundance of *L. colubrina* with respect to *L. laticaudata* was found to be 200:1 (Bhaskar 1996). Preliminary studies on the behaviour of sea kraits, conducted in the late 1990s at South Reef Island (Bhaskar 1996; Shetty & Prasad 1996), show that sea kraits restrict their terrestrial activities between 1800 and 0400 hr. During the day, they take shelter in the cool microclimatic conditions provided by the crevices of live and dead trees (Shetty & Prasad 1996). Terrestrial activities such as digesting of prey and sloughing have been encountered with one record of copulation (Bhaskar 1996; Shetty & Prasad 1996). The reproductive behaviour of these two species in the archipelago is not well known, with no nesting observations apart from one record of egg laying in captivity (Bhaskar 1996; Shetty & Prasad 1996). In addition, sea kraits are known to exhibit positive phototaxis on land at night, making them extremely vulnerable to anthropogenic activities (Bhaskar 1996). Therefore, there is a necessity for a contemporary study to observe the terrestrial behaviour of sea kraits, specifically of reproduction and habitat use.

In this context, a long-term study was carried out to investigate the temporal patterns in abundance and behaviour of two species of sea kraits *L. colubrina* and *L. laticaudata* in the Andaman Islands. The relative abundance of sea kraits was primarily investigated with respect to ambient climatic and tidal conditions, along with the sea kraits’ behaviour and substrate use. In addition, incidental natural history observations were documented.

METHODS

The study was carried out at the New Wandoor beach, located between 11.594°N & 92.607°E and 11.600°N & 92.608°E, in the southwestern corner of the South Andaman Island (Fig. 1a,b). The study area lies adjacent to the Mahatma Gandhi Marine National Park and Lohabarrack Crocodile Sanctuary and is lined with fringing reefs (Raghuraman & Raghunathan 2013). The islands are significantly influenced by the southwestern and northeastern monsoons from May to December, receiving up to 3,500mm of rainfall annually (Andrews & Vasumati 2002). The site experiences high anthropogenic activity as it is within the boundaries of Wandoor Village that is used for tourism and a part of the location lies in front of the Sea Princess Hotel, a tourist resort.

The study was conducted as a volunteer program to introduce groups of laypersons to conservation-related experiential learning and all groups were led and monitored by the Andaman Nicobar Environment Team (ANET) staff. As part of the ANET volunteering program,
Figure 1a. Study area map showing the Andaman Islands. Inset top - the location of Andaman & Nicobar Islands in India, inset bottom - the location of the study area at the New Wandoor Beach, South Andaman Island.

Figure 1b. Transect sampled at the New Wandoor Beach for the study.
27 surveyors participated in the overall monitoring and walked one transect of 680m parallel to the sea 181 times between 2012 and 2016. The transect lies within the intertidal region, consisting of a sandy shoreline with rocky outcrops at the start and a small estuarine inlet at the end. *Ipomea pes-caprae*, a pantropical salt tolerant creeper (Devall 1992), lines the supratidal zone. During the 2004 tsunami, many littoral trees (e.g., Sea Mohwa *Manilkara littoralis*) were uprooted in the region; in the study area, there were 19 such uprooted trees that were sparsely distributed on the beach.

The transect was walked between 1830 and 2130 hr as sea kraits are known to restrict their terrestrial activities between 1800 and 0400 hr with a peak in activity between 1800 and 2300 hr (Bhaskar 1996). An average of two people wearing headlamps actively searched for sea kraits on the intertidal area, scanning from the sea up to the sandy vegetation (*Ipomea* sp.) lining the supra-tidal zone. At the start of each transect, the time, moon phase, weather conditions (clear, cloudy, or rainy), and ambient climatic variables (sand temperature & humidity, atmospheric temperature & humidity) were recorded using a pocket weather meter (Kestrel 3000).

Upon encountering a sea krait, the following data were recorded: i) species — *L. colubrina* or *L. laticaudata*, ii) activity when sighted — moving, resting, mating, or dead, iii) behaviour/condition — sloughing, gravid, and cluster size, and iv) substrate — *Ipomea* sp., sand, or wood. The microclimatic factors of the sea kraits were not recorded to avoid disturbing them and all participants were instructed not to handle any specimens as part of the study. In addition to these parameters, natural history observations were recorded ad libitum.

**Analyses**

Since the same transect of a fixed distance was walked by the surveyors on all occasions, the number of encounters of individuals reported are as such and not as a time-constrained encounter rate. Further analyses of data on *L. laticaudata* were not performed as the number of encounters was low. The influence of microclimatic variables and moon phase on the number of encounters of *L. colubrina* was tested using univariate linear regressions. A one way-ANOVA was performed to evaluate the differences between tide categories based on time to the nearest high tide (0–2 h, 2–4 h, >4h) coupled with the direction of the tide (Shetty & Shine 2002a) on the number of encounters in the case of *L. colubrina*. Additionally, effect sizes-η² in percentage for one-way ANOVA (Zar 2010) are reported.

**RESULTS**

**Encounter rate**

Eight-hundred-and-five individuals of *L. colubrina* and 39 individuals of *L. laticaudata* were encountered during the surveys. The number of encounters of *L. colubrina* per transect was $4.45 \pm 0.21$ and that of *L. laticaudata* was $0.22 \pm 0.04$. The average encounter rate for *L. colubrina* ranged from 2.93 in October to 7.6 in August, whereas for *L. laticaudata* it ranged from 0 in June to 0.55 in May (Fig. 2). The number of encounters for *L. colubrina* had a statistically significant correlation with atmospheric temperature ($R^2 = 0.072$, $\beta = 0.387$, SE = 0.018, p < 0.001), sand temperature ($R^2 = 0.066$, $\beta = 0.368$, SE = 0.108, p < 0.001), atmospheric humidity ($R^2 = 0.024$, $\beta = -0.099$, SE = 0.046, p = 0.032), and sand humidity ($R^2 = 0.022$, $\beta = -0.096$, SE = 0.046, p = 0.039). These relationships, however, had poor model fit values. The phase of moon did not influence the number of encounters in the case of *L. colubrina* ($R^2 = 0.01$, $\beta = 0.04$, SE = 0.03, p = 0.185). Tide categories based on time to high tide did not correlate with the number of encounters for *L. colubrina* ($F = 1.68$, p = 0.14, $\eta^2 = 4.86$).

**Behaviour**

Sloughing of *L. colubrina* was encountered on six separate occasions, more frequently in August to December; sloughing of *L. laticaudata*, however, was not observed (Table 1). Gravid females of *L. colubrina* were observed throughout the year on 37 separate occasions, with the maximum number of observations in April, whereas only one gravid female of *L. laticaudata* was observed, in February (Table 1). Clusters of two to four individuals were observed on 19 separate occasions for *L. colubrina* and once for *L. laticaudata* (Table 1).

The most utilized terrestrial substrate of the sea kraits was found to be uprooted *Manilkara littoralis* while...
resting (Image 1), followed by sand (Table 2). Eighty per cent of the sea kraits encountered on sand were moving (Table 2). Five dead sea kraits were recorded during the study, out of which one was found on *Ipomea* sp., whereas the other four were found on sand (Table 2).

**Natural history observations**

Some of the sea kraits living in the crevices and hollows of the uprooted trees were seen to be sharing their space with hermit crabs, unperturbed by them. Sea kraits displayed signs of disturbance when tourists photographed them using a flash. The snakes, however, were not aggressive but only changed their direction of movement. During the sampling period, only two aggressive snakes were encountered even though the surveyors were at a distance of more than 5m away. Out of the two snakes, one was injured and struggling on the dry section of the sandy beach.

On 02 December 2015, a gravid *L. colubrina* was recorded to be resting in the hollow of an uprooted tree with an egg partially covered by the snake’s coiled form (Image 2). The individual was photographed and no further disturbance was caused. The next day, the egg was observed to be fully exposed, outside the snake’s coiled form (Image 3). The egg was creamy-beige speckled with small dark spots, oviducal, approximately 7cm long, and appeared soft-shelled. The following day, the hollow was empty with no signs of the sea krait or the egg. The hollow was located 9.6m from the water’s edge at low tide at an elevation of 0.8m from the ground. Due to its low location, the hollow would have received an influx of water during high tide.

On 04 December 2015, courtship behaviour was observed. A female *L. colubrina* was observed to be moving from the waterline towards the beach. Once
on the trunk and root of the uprooted tree, the sea krait disappeared into a crevice. A conspecific male was observed following the path the female had taken. The male was seen to be repeatedly tongue-flicking while following the path. Once near the crevice, it circled the area and entered another crevice, close to where the female had entered.

DISCUSSION

This study provides long-term data on the number of encounters, habitat use, and behaviour of sea kraits. The encounters of *L. colubrina* was found to be 20 times higher than that of *L. laticaudata*, similar to the findings on South Reef Island (Bhaskar 1996). This rarity in abundance likely contributes to the fragmented distribution of *L. laticaudata*. Both the rate of cutaneous evaporative water loss and the extent of terrestrial dependence are known to differ among the sea krait species with *L. colubrina* having relatively higher dehydration rates in seawater (Brischoux et al. 2012), lower rate of cutaneous evaporative water loss, and higher dependence on the terrestrial habitat, and with *L. laticaudata* showing intermediate levels of water loss and terrestrial dependence (Liu et al. 2012). *Laticauda laticaudata* are known to utilize shelters almost exclusively under mobile beach rocks, which are both easily accessible from the sea and regularly submerged at high tide (Bonnet et al. 2009). In contrast, *L. colubrina* frequently travel long distances overland, with males moving significantly further from the beach than females (Bonnet et al. 2005; Shine & Shetty 2001). The availability of both shelter and fresh water are important to the habitat selection of sea kraits; while *L. laticaudata* requires a source of fresh water, *L. colubrina* is characterized by a greater preference for the terrestrial habitat and possibly greater opportunities for access to a freshwater source (Liu et al. 2012). The difference in the number of encounters between the two sea kraits is likely due to the varying degree of dependence on terrestrial habitats or site selection (Bonnet et al. 2005) and naturally low densities of *L. laticaudata* (Bhaskar 1996). Avoidance of *L. colubrina* by *L. laticaudata* and vulnerability of *L. laticaudata* to anthropogenic disturbance, however, cannot be ruled out. Relatively high numbers of sea kraits were encountered between April and September. Although the mean abundance of sea kraits has been observed to be three-fold higher in the wet season compared to the dry season due to the dependence on availability of fresh water (Bonnet et al. 2009; Lillywhite & Tu 2012), the results from this study could be skewed due to the low sampling size during these monsoon months.

Ambient abiotic factors such as atmospheric temperature & humidity and sand temperature & humidity were found to significantly correlate with the number of encounters of *L. colubrina*; however, these relationships were not biologically meaningful given the poor model fit values. Neither lunar nor tidal phases were found to influence the number of encounters. Moreover, these results do not match the findings of studies that show nocturnal high tides to influence encounters with sea kraits (Girons 1964; Heatwole & Guinea 1993). Sea kraits of different age and sex classes, however, use terrestrial habitats differently and thus vary in their temporal and spatial distribution (Shetty & Shine 2002a).
The results from this study could be attributed to the influence of moon phase and tide on all the individuals of the species collectively. As the microclimatic conditions of the sea krait sites were not recorded in order to avoid disturbing them, comments on the sea kraits' microclimatic distribution cannot be made.

The use of substrates by sea kraits was studied where a majority of the individuals were encountered on wood where they were predominantly resting, followed by sand where they were moving (Table 2). Sea kraits are known to use natural refuges on beaches, which are both easily accessible from the sea and regularly submerged at high tide (Bonnet et al. 2009). Moreover, the spatial arrangement of terrestrial coastline microhabitats, especially refugia, plays a key role in the distribution of different sea krait species (Bonnet et al. 2009). In the current study area, sea kraits utilized the gradual slopes of the sandy beach to move from the sea to refugia in the form of uprooted trees dispersed along the intertidal zone. The protection of such refugia can lead to the conservation of these species (Webb et al. 2000; Berryman et al. 2006; Bonnet et al. 2009).

Clustering of sea snakes was observed to increase from January to May; unconfirmed reports of mass aggregations (ca. 200 individuals) on Rutland Island were recorded and are pending validation. The sea kraits' resting behaviour on wood and clustering could possibly be explained by 1) thermoregulation (Shetty & Shine 2002a) and kleptothermy (Brischoux et al. 2009b), 2) sharing of resources to increase body temperature, or 3) mating behaviour (Parrish & Edelstein-Keshet 1999; Gregory 2004).

Previous observations on the mating behaviour of sea kraits describe the male locating the female through vomeronasal system not only allows male snakes to locate receptive females by following scent trails but also facilitates pheromonally mediated mate choice (Shine 2003). A sophisticated vomeronasal system not only allows male snakes to locate receptive females by following scent trails but also facilitates pheromonally mediated mate choice (Shine 2003). This corresponds with the description stated in this paper of an instance where a male followed a female by regularly visiting the same location (Table 2). Sea kraits describe the male locating the female through vomeronasal system not only allows male snakes to locate receptive females by following scent trails but also facilitates pheromonally mediated mate choice (Shine 2003).

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