SYMPOSIUM

Habitat Selection by Sea Kraits (Laticauda spp.) at Coastal Sites of Orchid Island, Taiwan

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Synopsis  Three species of amphibious sea kraits (Laticauda spp.) spend variable time at sea and require fresh water for water balance. Both the rate of cutaneous evaporative water loss and the extent of terrestriality are known to differ among them. Laticauda semifasciata has the greatest rate of water loss and the least extent of terrestriality, whereas L. colubrina exhibits the reverse and L. laticaudata is intermediate. These sea kraits tend to be more abundant at places where there are sources of fresh water, but other factors also influence their distribution. To further clarify the habitat requirements, we investigated the abundance of each species of sea krait at six different habitats and the availability of each type of habitat on Orchid Island, Taiwan. The six habitats were high coral reef without fresh water (HR) and with fresh water (HRF); low coral reef without fresh water (LR) and with fresh water (LRF); sand or gravel coast, which has no coral reef, without fresh water (NR) and with fresh water (NRF). The extent of safety judged from the relative availability of retreat sites, from high to low, was HR, LR, and NR among these habitats. More than 75% of individuals counted for each species were found in HRF. We found no sea kraits in NRF and NR. The most available habitat was LR, but no L. laticaudata or L. semifasciata were found in this habitat. We found 3.3% and 16.7% of L. colubrina in LR and HR, respectively. For L. colubrina, the second abundant habitat was HR, whereas for L. laticaudata and L. semifasciata, the second abundant habitat was LRF. We conclude that both safety (availability of retreat sites) and fresh water are important to the habitat selection of sea kraits. Compared with other species, L. colubrina is characterized by a greater extent of terrestrial habit and possibly greater variety of access to sources of fresh water.

Introduction

The activity of animals and the habitats they utilize are related to complex interactions between physiological requirements, available resources, species interactions, and the attributes of the environment. Habitat selection involves the use of an animal’s environment for activity as well as for selection of sites to retreat when resting or inactive, and both components have consequences for fitness. Safety, or avoidance of predators, is considered to be a very critical factor that determines how a reptile chooses its retreat sites or microhabitats (Downes and Shine 1998; Theodoratus and Chiszar 2000; Stapley 2003). However, an ideal retreat site not only provides safety but also fulfills needs related to thermoregulation, digestion, conservation of water, and other physiological requirements (e.g., Huey et al. 1989; Shah et al. 2004).

Water balance is a critically important physiological requirement for marine reptiles, and salinity is a major abiotic factor that limits the colonization of marine environments by reptiles (Dunson and Mazzotti 1989). It was formerly believed that marine reptiles maintain water balance by drinking sea water (Schmidt-Nielsen and Fange 1958; Shuttleworth and Hildebrandt 1999). However, investigations of marine file snakes (Lillywhite and Ellis 1994) and sea kraits (Guinea 1991; Bonnet and Brischoux 2008; Lillywhite et al. 2008) demonstrated a dependence on fresh water. Additionally, the abundance of sea kraits is correlated with availability of freshwater both in space and in time.
Brischoux et al. 2007). Nevertheless, the distribution of sea kraits is heterogeneous, and they are not necessarily present at locations having a source of fresh water. For example, we have not seen sea kraits at the mouths of rivers during more than 20 years of field experience with species in Taiwan (unpublished observations, MCT, HBL). Although sea kraits might occasionally occur as waifs in these areas, it seems likely they are not present in large numbers due to the lack of physical habitat that might provide retreat sites and safety at estuaries.

Here, we examine quantitatively the abundance of sea kraits in different habitats, and we test the hypothesis that sea kraits select habitats that provide both safe retreats and sources of fresh water.

**Materials and methods**

**Sea krait species**

Three species of sea kraits are commonly seen at Orchid Island (= Lanyu), Taiwan, each spending variable periods on land to reproduce, digest, and rest within retreats such as rock or coral crevices (Lillywhite et al. 2008). *Laticauda colubrina* is the most terrestrial species and can be found hiding among rocks or crevices near the shoreline, while sojourning to sea for variable periods to forage, as does its closely related species, *L. saintgironsi* (Brischoux et al. 2007). *Laticauda semifasciata* is the most aquatic species and spends nearly all of its time at sea except for terrestrial sojourns to oviposit. The third species, *L. laticaudata*, is intermediate to the other species in terms of its aquatic versus terrestrial tendencies. Individuals of all three species can be found active among rocks and in the intertidal zone during the early hours of dark following sunset.

**Habitat categories**

The extent of safety was classified into three categories according to the physical structure of shore line where these snakes travel between aquatic and terrestrial environments and often seek retreat (Shetty and Shine 2002a; Brischoux et al. 2007) (Fig. 1). When the shore is composed of mainly dead coral reef or igneous rock and most of these structures remain above sea water during high tide, it provides the most safety for sea kraits because there are numerous crevices in which they can retreat without submersion. These sites are not affected by the tide. Insofar as this habitat normally has dead reef that extends high above the sea level, we named it high reef (HR). On the other hand, coral reef that is mostly submerged under water during high tide was designated as low reef (LR). The retreat sites at LR experience tidal flooding, and they provide fewer retreats because fewer crevices are available in this type of habitat, which is tidally flooded. The habitat with the least extent of sites for retreat is the open shore which has no reef (NR) and is composed of gravel or sand. Retreat sites and safety are entirely absent at NR habitat (Fig. 1).

Our designation of habitats is categorical and not quantitative. We justify this procedure because (1) the physical differences are qualitatively distinct and obvious (Fig. 1 and consideration of tides), and (2) it is not possible to measure the labyrinth of possible retreats that are present beneath the coral and rock surfaces. Moreover, little is known about the natural history and behavior of sea kraits with respect to selection of retreats. We do know that sea kraits are found at HR and LR habitats where they can be found secluded within crevices and crannies. Out of the possible spaces available, however, we do not know which ones are more or less likely to be selected by the snakes.

The presence of fresh water at the three habitats was assisted by knowledge of local springs and river outflows. At the location of mixture between fresh water and seawater, there were differences in temperature and refractive properties that blurred the water so that it lacked the clarity of the surrounding sea-water. We confirmed the presence of fresh water by measuring the salinity using an Atago S/Mill Refractometer. Salinity measurements ranged from 0 ppt to 30 ppt in gradients that were consistent with the topography of the inlets and locations of fresh water, whereas the water at strictly seawater sites measured 32 ppt (Lillywhite et al. 2008). We also measured the salinity of sea water at locations every 10 m apart. The three habitat categories were further classified according to whether fresh water was present (HRF, LRF, NRF; water salinity variably < 32 ppt) or absent (HR, LR, NR; water salinity ≥ 32 ppt). We confirmed the presence of a freshwater source by measuring water near the source, which typically had values near 0 ppt.

**Habitat availability and sea krait abundance**

We sampled the availability of habitat and counted the abundance of three species of sea kraits within each habitat during July to September 2009. We selected three transects that included the six habitat categories, each one being 1 km in length of shoreline (Fig. 2). During high tide, we measured the distance of each habitat type by walking along each transect.
using a Global Positioning System (GPS, Garmin Edge 705) and following the coastline. According to the topography and salinity, we determined the type of habitat every 10 m. We used Shp Trans V2.2 (http://gis.ascc.net/ISTIS/tools.html) to change the lat/lon coordinates system to TWD97 system. We defined the area of each habitat by a 1-m extension from the walking line, measured toward shoreline. The area of each habitat was calculated using aerial photographs, which were opened by ArcMap 9.1. After we determined the availability of each type of habitat, we counted the number of each *Laticauda* species during 2–4 h in each transect once per month. Due to tidal variation, the areas in which snakes were counted paralleled closely, but did not correspond precisely to, the areas measured from photographs.

To further determine the abundance of sea kraits within each habitat, we counted the number of each *Laticauda* species twice per month at 22 additional sites of shoreline at Orchid Island (Fig. 2). We counted the number of each species for 15–30 min at night along 100 m of shoreline, the time depending on the nature of the terrain. In these counts, there was no representation of the NR habitat. Considering all sampling sites, each habitat category was represented by five sampling sites, except for NR.

**Statistical analysis**

We used the non-parametric Kruskal–Wallis Test to analyze the differences in the five habitat types, and Mann–Whitney U tests for post hoc analysis. We used Spearman’s correlation to analyze the relationship between the area of each habitat type and the numbers of each sea krait species that were found therein. All analyses and figures were conducted using SPSS 18.0 and SigmaPlot 10.0.

**Results**

Data from the 3-km long transects enabled us to rank habitats according to availability. The total area of each habitat was $LR = 43,112.9 \text{ m}^2$, $HRF = 32,989.7 \text{ m}^2$, $LRF = 15,711.5 \text{ m}^2$, $HR = 12,276.1 \text{ m}^2$, $NR = 5242 \text{ m}^2$, and $NRF = 694.9 \text{ m}^2$.

The majority of sea kraits were observed in HRF, which composed about 30% of the total area that we sampled. There we found a total of 148 *L. semifasciata*, 61 *L. laticaudata*, and 17 *L. colubrina*, which comprised the majority of snakes seen among the...
different habitats (Table 1). No sea kraits were seen in either NRF or NR habitats. LR was the most available habitat, but there we found only one L. colubrina and no individuals of the other species. HR habitat had the second greatest abundance of L. colubrina, whereas LRF exhibited the second greatest abundance of L. laticaudata and L. semifasciata (Table 1). There was no correlation between the number of each sea krait species and the area of each habitat type (Spearman correlation: L. colubrina: \( r = 0.375, P = 0.125 \); L. laticaudata: \( r = 0.349, P = 0.156 \); L. semifasciata: \( r = 0.361, P = 0.141 \)).

We counted sea kraits within each habitat (except NR) on six different occasions at the other 100-m transects. Again, the largest number of snakes was counted in HRF and totaled 324 individuals, including 265 L. semifasciata, 38 L. laticaudata, and 21 L. colubrina. Only 15 snakes were observed in LRF, and just two were seen in each of HR and LR. No sea krait was observed in NRF (Fig. 3). The mean of species counts in HRF was greater than in the other types of habitat (Kruskal–Wallis test: L. colubrina: \( \chi^2 = 53.948, P < 0.001 \), L. laticaudata: \( \chi^2 = 51.814, P < 0.001 \), L. semifasciata: \( \chi^2 = 80.836, P < 0.001 \)).

**Discussion**

Animals generally do not use habitat randomly (Rosenzweig 1981; Cody 1985; Graeter et al. 2008), thus assessment of habitat selection requires information about the abundance of animals and how this relates to the availability of habitat (Harvey and Weatherhead 2006). Here, we demonstrate a positive association of sea kraits with habitat that provides both safety and fresh water, thus fulfilling both important requirements. It is clear that sea kraits require fresh water to maintain water balance (Guinea 1991; Bonnet and Brischoux 2008; Lillywhite et al. 2008). Therefore, a habitat with fresh water provides an important resource that potentially attracts sea kraits.

In addition to physiological requirements, finding safe retreat sites also is significant. Clearly, sea kraits of all three species were most abundant at HRF habitat, which implies these snakes are selecting sites
where there occur both numerous retreat sites and availability of fresh water (Table 1 and Fig. 3). Further, *L. colubrina* was secondarily abundant at HR habitat, whereas the other species were secondarily abundant at LRF sites. Finding adequate retreat sites is no doubt important for *L. colubrina*, which is more terrestrial than the other three species but cannot move on land as well as terrestrial elapids (Shine and Shetty 2001) and is susceptible to losses of body water in evaporation (Lillywhite et al. 2009). Adaptations of all sea kraits for effective locomotion in water involve morphological features such as a paddle-shaped tail, which might enhance the propulsive thrust of snakes that are swimming (Heatwole 1999; Shine and Shetty 2001). However, specializations for improving the swimming performance in water possibly reduces the effectiveness of terrestrial locomotion (Jayne 1985; Cundall 1987), which, in turn, might limit the distances that sea kraits move inland from the intertidal zone. Therefore, the configuration of the coastal zone is likely to be very important for the terrestrial sojourns of sea kraits, especially *L. colubrina*.

HR habitats also provide retreat sites for *L. colubrina*, which are present in significant numbers (Table 1 and Fig. 3). This distinction from the other species is likely attributable to two reasons. First, *L. colubrina* has the stronger terrestrial habits, and HR habitat provides safe retreat sites when these snakes are on land. Secondly, these terrestrial sites might offer opportunities for encountering fresh water during periods of rainfall that are not available to snakes that are at sea. Even small amounts of rainfall can create opportunities for drinking, as sea kraits in terrestrial habitats are known to drink from small pools and dripping vegetation caused by precipitation (Guinea 1991; Bonnet and Brischoux 2008). These drinking opportunities would not be available to aquatic snakes, and both *L. laticaudata* and *L. semifasciata* tend to be far less terrestrial than does *L. colubrina*. Sites with other freshwater sources such as springs or estuaries therefore are relatively more important to the distribution of these other two species (Table 1; Lillywhite et al. 2008). Relatively large amounts of precipitation are probably required to create freshwater or brackish-water lenses from which sea kraits might drink while at sea. Thus, for the more aquatic snakes, importance is given to sources of fresh water that run into the sea at coastal locations.

Terrestrial retreat sites are also important for the other amphibious species that are more aquatic and do not crawl onto land so frequently. We observed a *L. semifasciata*, which almost always stays in water, being caught and killed at night by a masked palm civet (*Paguma larvata*) while it was on rocks. Retreat sites can provide safety during brief sojourns out of water, or even when these snakes remain in very shallow water that characterizes the intertidal zone where snakes are most active at night. Further, the HR habitat remains above water during high tide (Fig. 1), and this enables sea kraits to avoid exposing themselves during bouts of intermittent breathing that require visual exposure when these snakes are at sea. The importance of safety is also reflected in the observation that abundant beach rocks provide keystone habitat for two species of sea kraits in New Caledonia (Bonnet et al. 2009).

The availability of intertidal and near-shore retreat sites is further emphasized by the absence of sea kraits at the NR and NRF habitats (Table 1). While the absence of retreat sites at these locations is obvious, it may also be that these habitats provide less productive foraging sites when the snakes are feeding at sea than do habitats with coral reef. Sea kraits specialize on eels and crevice-dwelling fishes, and they sometimes swim long distances to find productive foraging grounds at sea (Reed et al. 2002; Ineich et al. 2007; Brischoux and Bonnet 2008). However, proximity of food resources is likely to be important for snakes having strong fidelity to retreat sites (Shetty and Shine 2002b; Brischoux and Bonnet 2008). Animals that have very strict or strong fidelity to their habitat tend to be more vulnerable to its destruction (Shine et al. 1998; Harwood 2001; Brischoux et al. 2009). In many places, sea kraits have been killed in extremely large numbers, causing
local extinctions (Brischoux et al. 2009). This problem will be exaggerated by strong anthropogenic disturbances on the coast, as well as generally decreased precipitation over the tropics since the 1970s (Hulme et al. 1998). Thus, conservation of sea kraits requires further investigation and understanding of their habitat requirements, which are likely to be more complex than was previously envisioned (Mullin and Seigel 2009).

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References


