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Behavioral and physiological correlates of the geographic distributions of amphibious sea kraits (*Laticauda* spp.)

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ABSTRACT

The physiological costs of living in seawater likely influenced the secondary evolutionary transitions to marine life in tetrapods. However, these costs are alleviated for species that commute between the land and the sea, because terrestrial habitats can provide frequent access to fresh water. Here, we investigate how differences in the ecology and physiology of three sea krait species (*Laticauda* spp.) interact to determine their environmental tolerances and geographic distributions. These three species vary in their relative use of terrestrial versus marine environments, and they display concomitant adaptations to life on land versus at sea. A species with relatively high dehydration rates in seawater (*Laticauda colubrina*) occupied oceanic areas with low mean salinities, whereas a species with comparatively high rates of transcutaneous evaporative water loss on land (*Laticauda semifasciata*) occupied regions with low mean temperatures. A third taxon (*Laticauda laticaudata*) was intermediate in both of these traits, and yet occupied the broadest geographic range. Our results suggest that the abilities of sea kraits to acquire fresh water on land and tolerate dehydration at sea determine their environmental tolerances and geographic distributions. This finding supports the notion that speciation patterns within sea kraits have been driven by interspecific variation in the degree of reliance upon terrestrial versus marine habitats. Future studies could usefully examine the effects of osmotic challenges on diversification rates in other secondarily marine tetrapod species.

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1. Introduction

Oceanic salinity imposes an osmotic challenge to vertebrates living in seawater (Schmidt-Nielsen, 1983). This is especially true for marine tetrapods, a group that has evolved a diversity of structures that help to maintain osmotic balance (sophisticated nephrons in mammals, Ortiz, 2001; salt glands in reptiles, Peaker and Linzell, 1975). Regardless of the efficiency of these excretory structures, living in seawater inevitably entails significant physiological costs (Gutiérrez et al., 2011; Ortiz, 2001; Schmidt-Nielsen, 1983). Hyperosmotic conditions not only affect the day-to-day life of marine vertebrates, but also likely influenced their evolutionary transition to marine life (Brischoux et al., 2012a). For example, despite having salt-secreting glands, the diversity and geographic distributions of extant sea snakes are constrained by oceanic salinity (Brischoux et al., 2012a).

Although osmotic challenges apply to most or all marine tetrapods, some ecological situations alleviate these constraints. For example,

species that regularly commute between saline and terrestrial environments have increased opportunities to frequently access freshwater (i.e., shorebirds, Gutiérrez et al., 2011; sea kraits, Bonnet and Brischoux, 2008; Liu et al., 2012). In such situations, interactions between dehydration at sea and freshwater acquisition on land can influence individual movement rates (e.g., a dehydrated individual will commute more often to a source of freshwater). On a broader spatial scale, such interactions also may affect the extent of a species' geographic range. For example, species that are sensitive to dehydration at sea might be able to withstand saline conditions in the marine environment if their terrestrial habits allow regular access to freshwater sources. Such circumstances should allow species to occupy areas that are extremely saline relative to their dehydration rates, thereby increasing the extent of their geographic distributions, provided that suitable terrestrial habitats are available.

Sea kraits (*Laticauda* spp.) provide an excellent opportunity to investigate how the relative use of terrestrial versus marine environments influences environmental tolerances and geographic distributions. First, sea kraits are characterized by obligatory use of both land (to bask, digest prey, mate, and oviposit) and sea (where they forage for fish) (Heatwole, 1999). Second, this clade is divided into three major complexes (Heatwole et al., 2005), which broadly overlap in geographic range, but differ in their relative use of terrestrial versus marine

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environments. Species from the “*L. colubrina* complex” (N = 4 species) are more terrestrial; species from the “*L. semifasciata* complex” (N = 2 species) are more aquatic; and *L. laticaudata* (disregarding the closely related, lake-locked *Laticauda crockeri*) is intermediate (Greer, 1997; Heatwole, 1999). Third, experimental studies have shown that the three nominal species lie along a gradient of adaptations to life on land versus at sea (Lillywhite et al., 2008, 2009). Finally, life in seawater poses a major physiological challenge to sea kraits (Brischoux et al., 2012b; Dunson, 1975), and thus limits their distribution (Brischoux et al., 2012a; Lillywhite et al., 2008).

Herein, we investigate how differences in the ecology (relative use of terrestrial versus marine environments) and physiology (dehydration rates on land versus at sea) of sea kraits are related to their environmental tolerances (salinity and temperature), and ultimately, their geographic distributions.

2. Materials and methods

2.1. Study species and physiological data

Sea kraits (Laticaudinae) are amphibious snakes common throughout coral reefs of the Eastern Indian and Western Pacific Oceans (Heatwole, 1999). Sea kraits forage at sea for fish, but return to land to digest, rest, slough their skins, mate, and lay eggs (Heatwole, 1999). Importantly, these snakes rely on the frequent use of both environments (typically returning to land once every two weeks, Brischoux et al., 2007; Shetty and Shine, 2002).

Data on dehydration rates in seawater and rates of transcutaneous evaporative water loss on land in *L. colubrina*, *L. laticaudata* and *L. semifasciata* were measured experimentally using field-caught animals (see Lillywhite et al., 2008, 2009 for further details). These three species differ significantly in their relative use of terrestrial versus marine environments (Greer, 1997; Liu et al., 2012).

2.2. Geographic range and environmental data

Data on the distribution of each species of sea krait were taken from extent-of-occurrence range maps assembled by the IUCN Sea Snake Specialist Group (<http://www.iucnredlist.org/technical-documents/spatial-data>). Salinity and sea surface temperature (SST) were averaged within each species' geographic range using long-term gridded climate data available from Bio-ORACLE (Tyberghein et al., 2012). We did not use terrestrial temperature data because we lacked information on the terrestrial distributions of sea kraits. Instead, we used SST data as a proxy for air temperatures on land. The relationship between sea surface and terrestrial air temperatures should be particularly strong within the areas occupied by sea kraits because these species are largely restricted to coastlines (Bonnet et al., 2009; Lane and Shine, 2011a). Oceanic range sizes were calculated using an equal-area Behrmann projection.

3. Results

Dehydration rates in seawater were inversely related to the mean salinity within each species' oceanic range (Fig. 1a). The mean salinity within the range of *L. laticaudata* was intermediate between that of *L. colubrina* and *L. semifasciata* (ANOVA with the mean salinity in each grid cell as the dependent variable and species as the predictor, $F_{2,158,329} = 347.65$, $p < 0.0001$, Fig. 1a).

The mean SSTs within each species' range were inversely related to the mean rates of transcutaneous evaporative water loss (Fig. 1b). The mean SST within the range of *L. laticaudata* was again intermediate between that of *L. semifasciata* and *L. colubrina* (ANOVA with the mean SST in each grid cell as the dependent variable and species as the predictor, $F_{2,158,329} = 4039.8$, $p < 0.0001$, Fig. 1b).

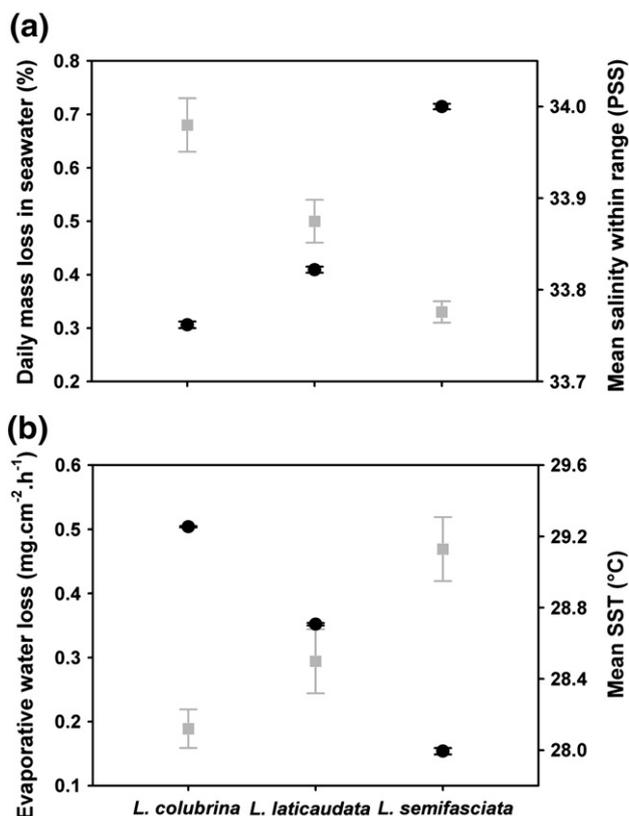


Fig. 1. Characteristics of the environmental conditions within the geographic ranges of sea kraits (*Laticauda* spp.). (a) Gray squares: daily mass loss in seawater for each species (modified from Lillywhite et al., 2008), and black circles: the mean salinity within each species' range. (b) Gray squares: transcutaneous evaporative water loss (modified from Lillywhite et al., 2009), and black circles: the mean sea surface temperature (SST) within each species range. Values shown are means \pm SE.

The three species also diverged in geographic range size (Fig. 2). *L. laticaudata* occupied the broadest geographic range, whereas *L. colubrina* had a range that was intermediate in size between that of *L. semifasciata* and *L. laticaudata*.

4. Discussion

The three species of sea kraits included in our analyses differ in their reliance on aquatic versus terrestrial habitats, and exhibit a counter-gradient of physiological attributes related to water balance (Lillywhite et al., 2008, 2009). The more terrestrial *L. colubrina* is

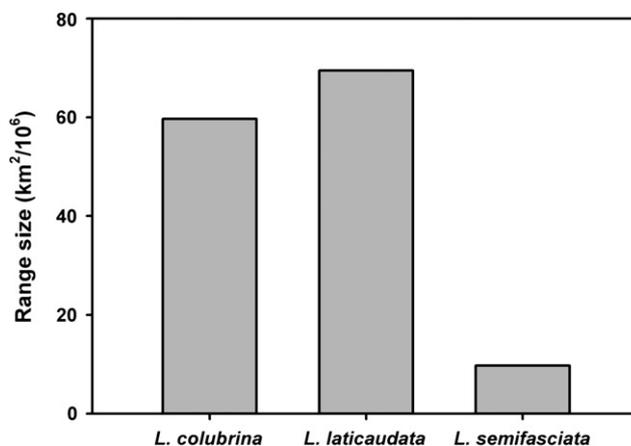


Fig. 2. Geographic range size of three species of sea kraits (*Laticauda* spp.).

resistant to desiccation on land, but sensitive to dehydration in seawater, relative to the other species. Conversely, the more aquatic *L. semifasciata* is resistant to dehydration in seawater, but relatively more sensitive to desiccation on land. *L. laticaudata* is intermediate in both traits (Fig. 1). Accordingly, the mean salinity within each species' oceanic range follows the reverse trend to that observed for dehydration rates in seawater (Fig. 1a). Sea surface temperature (a proxy for thermal conditions on land) within each species' range also follows the reverse trend to that observed for rates of transcutaneous evaporative water loss (Fig. 1b). Taken together, these results support the hypothesis that physiological constraints imposed by salinity and temperature limit the distribution and dispersal of sea kraits.

Because salinity poses a physiological challenge to sea kraits, these species have to restore their osmotic balance by acquiring fresh water during unpredictable rainfall events (Bonnet and Brischox, 2008; Guinea, 1991). However, the ease with which fresh water can be acquired depends on the degree of terrestriality of the species (Bonnet and Brischox, 2008). Precipitation is more likely to fall over tropical islands than over open ocean, and even minor rainfall events can provide fresh water for sea kraits in coastal environments (Bonnet and Brischox, 2008). In the ocean, on the other hand, heavy rainfall and appropriate environmental conditions are required to form freshwater lenses. As a consequence, the more terrestrial *L. colubrina* is more likely to acquire fresh water and restore its osmotic balance than is the more marine *L. semifasciata*, and to a lesser extent *L. laticaudata* (Brischox et al., 2012b). In addition, high rates of evaporative water loss are likely to limit the ability of *L. semifasciata* to spend significant amounts of time on land, preventing this species from accessing fresh water following rainfall events. Conversely, long periods in seawater, either during foraging trips or during dispersal over larger oceanic areas, will dehydrate *L. colubrina* more rapidly than *L. semifasciata*, and to a lesser extent *L. laticaudata* (Brischox et al., 2012b). Thus, the differential abilities of sea kraits to acquire fresh water on land and tolerate dehydration at sea are likely to influence the extent of their geographic distributions. In support of this view, the intermediate species *L. laticaudata*, moderately efficient at accessing freshwater on land (Bonnet and Brischox, 2008), but also moderately resistant to dehydration at sea, occupies the widest geographic range (Fig. 2).

Recent genetic analyses have shown that the distribution of terrestrial habitats within the oceanic range of *L. laticaudata* has little impact on gene flow (Lane and Shine, 2011b). Conversely, the more terrestrial “*L. colubrina* complex” (*L. colubrina*, *Laticauda frontalis*, *Laticauda guineai* and *Laticauda saintgironsi*) shows stronger geographic differentiation in allelic frequencies, associated with island groups (Lane and Shine, 2011b). Although we lack genetic data for the “*L. semifasciata* complex” (*L. semifasciata* and *Laticauda schistorhincha*), the existence of two species in this complex also suggests geographic differentiation. Taken together, these patterns suggest that the ability to restore osmotic balance during rainfall events might be more important for individual survival during infrequent dispersal events over large oceanic areas than is the resistance to dehydration in seawater. Accordingly, the restricted ranges of *L. semifasciata* and *L. schistorhincha* suggest that limitations on acquiring fresh water on land constrain successful dispersal in the more marine laticaudines. The intermediate ecology of *L. laticaudata* allows this species not only to colonize the widest range, but also to maintain gene flow among populations (Lane and Shine, 2011b). Collectively, these observations support the hypothesis that sea krait speciation patterns have been driven by differences in the importance of terrestrial versus marine habitats in the species' ecology (Lane and Shine, 2011b).

There are, however, several caveats to our conclusions. First, our analysis is based on correlations, and we have no direct evidence of causation. For example, it remains possible that sea snake distributions are determined by factors unrelated to osmotic challenges and that the correlations we see reflect adaptation of snake physiology to the osmotic conditions that each species experiences over its range; that is,

interspecific differences in osmoregulatory ability may be consequences rather than causes of the interspecific differences in geographic distribution. It is likely that the osmoregulatory abilities of extant snakes are evolving in relation to their present distributions. Second, our comparisons are based upon a small number of species, and the validity of our interpretations can only be tested by expanding the suite of taxa that are studied. The multiple evolutionary invasions of the marine environment throughout the tetrapod phylogeny provide abundant opportunities for such studies. For example, if it is generally true that an ability to cope with the osmotic challenges associated with marine life has influenced geographic ranges and speciation patterns of secondarily marine organisms (Brischox et al., 2012a), such processes might have contributed to the remarkably rapid radiation of hydrophiine sea snakes (Sanders et al., 2008, 2010). Future studies could usefully compare osmoregulatory capacities to geographic distributions in these and other species of secondarily marine tetrapods.

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