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Variations of natremia in sea kraits (*Laticauda* spp.) kept in seawater and fresh water

François Brischoux [a,*], Marine J. Briand [a,b], Gopal Billy [a], Xavier Bonnet [a]

[a] Centre d'Etudes Biologiques de Chizé, CEBC-CNRS UPR 1934, 79360 Villiers en Bois, France
[b] Université de la Nouvelle-Calédonie, Laboratoire LIVE, LABEX Corail, BP R4, 98851 Nouméa cedex, Nouvelle-Calédonie

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ABSTRACT

Marine tetrapods evolved specific excretory structures (e.g. salt glands) that maintain salt concentrations within a narrow range of variation. However, recent investigations showed that in some lineages (sea snakes), individuals dehydrate in seawater and cannot equilibrate their hydromineral balance without access to fresh water. How these marine species cope with salt gain is therefore puzzling. We sampled two species of amphibious sea kraits (*Laticauda saintgironsi* and *L. laticaudata*) in the field. We also experimentally investigated patterns of salt regulation, specifically variations in natremia (plasma sodium) and body mass (net water flow), in individuals transferred first to fresh water and then to seawater. Our results show that free-ranging sea kraits display hypernatremia (up to 205 $mmol \cdot l^{-1}$). Experimental data showed that natremia markedly decreased in snakes exposed to fresh water and increased when they were transferred to saltwater, thereby demonstrating a marked flexibility in their relation to environmental conditions. A literature survey indicated that all free-ranging marine snake species usually display hypernatremia despite having functional salt glands. Overall, sea snakes exhibit a marked tolerance to salt load compared to other marine tetrapods and apparently trigger substantial salt excretion only once natremia exceeds a high threshold. We hypothesise that this high tolerance significantly decreases energetic costs linked to salt gland functioning.

1. Introduction

One of the paramount challenges for marine tetrapods (i.e., mammals, birds, turtles, snakes, lizards and crocodiles) is to maintain hydromineral balance within vital boundaries (Schmidt-Nielsen, 1983). Because seawater is hyperosmotic to body fluids, marine species tend to gain salt and lose water (Schmidt-Nielsen, 1983). As a consequence, in most marine vertebrates, hydromineral balance regulation requires expenditure of energy (Schmidt-Nielsen, 1983). Marine tetrapods display a variety of structures that actively excrete excess salt. For instance, marine mammals possess a sophisticated countercurrent system with elongated nephrons that excrete large loads of ions in hypertonic urine (Ortiz, 2001). Reptiles do not produce highly concentrated urine, but they have evolved a diversity of cephalic salt glands that excrete concentrated salt solutions (Peaker and Linzell, 1975; Babonis and Brischoux, 2012).

Owing to their developed salt excreting abilities, marine tetrapods have long been thought to maintain their water balance without consuming fresh water (Randall et al., 2002; Houser et al., 2005). This long-standing dogma has been recently challenged in some lineages (Lillywhite et al., 2012). Detailed studies performed on snakes showed that marine species cannot equilibrate their hydromineral balance without access to fresh water (Lillywhite et al., 2008, 2012). Dehydration in seawater has been documented in amphibious sea snakes (sea kraits) as well as in fully marine species (hydrophiines) (Lillywhite et al., 2008, 2012; Brischoux et al., 2012a). Interestingly, dehydration rates are dependent on the degree of emancipation from the ancestral terrestrial environment, both within and across phylogenetic lineages (Brischoux et al., 2012a; Lillywhite et al., 2012). Life in seawater can thus impose significant physiological costs that have likely influenced the secondarily evolutionary transition to marine life in tetrapods (Brischoux et al., 2012b).

Dehydration rates of marine snakes in seawater have been mainly assessed through variation in body mass, an integrative parameter that primarily informs about net water loss (Lillywhite et al., 2008, 2012; Brischoux et al., 2012a). However, underlying variations of concentrations of ions or osmolytes in body fluids that exert a crucial influence on the maintenance of osmotic balance should be investigated (Schmidt-Nielsen, 1983; Ortiz, 2001; Dantzler and Bradshaw, 2009). Although salt strongly influences osmolality, many other osmolytes, such as proteins, carbohydrate and nitrogenous wastes can also be involved (Schmidt-Nielsen, 1983). Conversely, in the marine environment, sodium is one of the primary ions that can be passively gained through permeable surfaces (Schmidt-Nielsen, 1983, but see Dunson and Robinson,

* Corresponding author at: CEBC-CNRS UPR 1934, 79360 Villiers en Bois, France. Tel.: +33 5 49 09 78 40; fax: +33 5 49 09 65 26.
E-mail address: francois.brischoux@gmail.com (F. Brischoux).

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1976; Dunson and Stokes, 1983). Therefore, natremia (plasma sodium concentration) should directly reflect the outcome of the main osmotic challenge faced by marine tetrapods (Schmidt-Nielsen, 1983), including marine snakes (Dunson, 1968, 1980; Dunson et al., 1971; Dunson and Dunson, 1973, 1974, 1975; Duggan and Lofts, 1978; Babonis et al., 2011). In support of this view, sodium excretion rates and thus presumably salt gain have been shown to influence sea snakes environmental tolerances (Brischoux et al., 2012b).

We investigated salt gain and salt regulation by monitoring natremia in marine snakes transferred from fresh water to seawater. Amphibious sea snakes (sea kraits, *Laticauda* spp.) provide an excellent opportunity to investigate physiological tolerances to salinity constraints within a restricted phylogenetic framework (Brischoux et al., 2012a, 2013). First, the high surface to volume ratio due to the snake body plan likely increases salt gain through permeable surfaces (Brischoux and Shine, 2011). Second, sea kraits obligatorily use both marine and land environments to forage, digest, and reproduce (Heatwole, 1999). Importantly, they dehydrate in the field and drink fresh water when available in order to restore their osmotic balance (Bonnet and Brischoux, 2008; Lillywhite et al., 2008; Brischoux et al., 2012a). Third, species from this clade differ in their relative use of terrestrial versus marine environments and display a concomitant gradient of adaptations to marine life (Lillywhite et al., 2008, 2009; Brischoux et al., 2013). Finally, life in seawater poses strong physiological challenges to sea kraits (Dunson, 1975; Brischoux et al., 2012a) and likely limits their distribution (Brischoux et al., 2012b, 2013). We examined natremia of free-ranging individuals and patterns of salt gain of individuals experimentally transferred from fresh water to seawater in two-closely related species of sea kraits (*Laticauda laticaudata* and *L. saintgironsi*) which vary in their degree of habitat use (marine versus terrestrial) and their susceptibility to dehydration in seawater.

Specifically, we predicted that the more marine *L. laticaudata*, which displays relatively lower dehydration rates in seawater, should display a higher resistance to salt gain in seawater and a higher salt tolerance compared to the more terrestrial *L. saintgironsi*. Conversely, we expected both species to restore normonatremia when kept in a presumably less constraining medium such as fresh water.

2. Materials and methods

2.1. Captive animals

Ten adult male *L. saintgironsi* and 10 adult male *L. laticaudata* were caught on Signal islet, New Caledonia (22°17′45 S; 166°17′34 E) between November 18th and November 20th 2011. Upon capture, the stomach of each individual was palpated in order to ensure that no recently fed individuals were included in the experiment. The snakes were weighed and subsequently kept in calico bags. On November 21th 2011, the snakes were brought back at the Aquarium des Lagons Research Facility (Nouméa, New Caledonia) where all experimental procedures were performed.

2.2. Experimental protocols

Our experimental treatment was split into two successive phases. Snakes were placed in fresh water for two days in order to allow them to drink ad libitum. This first step will be abbreviated "2-d-FW"therafter. After the 2-d-FW treatment, snakes were handled and blood sampled through intra-cardiac punctures using 30G-needles. The blood (~300 μL representing <0.2% of a snake's body mass) was immediately centrifuged (3 min at 8000 g) and the plasma was separated and stored at −25 °C. Each snake was weighed and randomly allocated to the next experimental step.

In this second treatment, we subjected the sea kraits to different salinity levels (either fresh water or full strength seawater, thereafter FW and SW) during 12 days; an ecologically relevant duration similar to that of a foraging trip at sea (Brischoux et al., 2007). To limit cage effect, each treatment was repeated in two aquaria. Five individuals per species were subjected to each treatment (2 to 3 snakes per aquarium). Aquaria were fitted with a platform placed approximately 1 to 2 cm below the water's surface, providing to the snakes with a resting place, notably to breathe without swimming, while remaining in permanent contact with water. At the end of this treatment, snakes were recaptured, and blood sampled as described above. We did not detect any effects of the aquaria per treatment on the parameters analyzed (all $p > 0.7$) therefore pairs of aquaria were pooled for each treatment for analyses.

Two *L. laticaudata* (one for each treatment) and one *L. saintgironsi* (FW treatment) escaped during the experiment and followed the water drain which opens in the Lagoon therefore thereby reducing our final sample 4 FW and 4 SW *L. laticaudata* and 4 FW and 5 SW *L. saintgironsi*. The remaining snakes were released at the site of capture after the experiment.

2.3. Field animals

To compare natremia between experimental and free-ranging individuals, we also sampled snakes directly in the field at a near-by site (Amédée islet, 22°28′38 S, 166°28′06 E) where a tourist facility allowed us to use a similar protocol for collecting blood as described above. We collected blood from 4 male *L. saintgironsi* and 2 male *L. laticaudata* shortly after capture (<3 min).

2.4. Natremia

Plasma sodium concentrations were assessed with an ISE module on a Pentra C 200 (Horiba Medical Ltd) compact chemistry analyzer.

3. Results

3.1. General observations

When placed in fresh water (onset of the 2-d-FW period) all individuals drank abundantly, often before exploring their new environment and despite the stress of capture. During the 2-d-FW period, many individuals defecated as indicated by large amounts of nitrogenous wastes (insolubilized urates) quickly accumulating at the bottom of the aquariums.

3.2. Variations in body mass

Despite fresh water uptake, we detected a slight loss of body mass between capture and the end of the 2-d-FW period (possibly due to defecation), significant in *L. laticaudata* solely (*L. saintgironsi*: body mass 1 = 153.0 ± 21.4 g, body mass 2 = 151.3 ± 21.8, paired t-tests, $t = 1.47$, $df = 13$, $p = 0.16$; *L. laticaudata*: body mass 1 = 206.5 ± 38.2 g, body mass 2 = 201.2 ± 35.3, paired t-tests, $t = 3.15$, $df = 14$, $p = 0.007$).

In both species, we detected a significant loss of body mass during the second step of the experiment, but with no treatment effect (repeated measures ANOVA, Time effect: $F_{1,\ 7} = 47.67$, $p < 0.001$, Time*Treatment: $F_{1,\ 7} = 0.36$, $p = 0.56$, body mass 3 = 143.9 ± 6.9 g for *L. saintgironsi*; Time effect: $F_{1,\ 10} = 150.31$, $p < 0.0001$, Time*Treatment: $F_{1,\ 10} = 0.51$, $p = 0.49$, body mass 3 = 187.2 ± 10.3 g for *L. laticaudata*).

3.3. Natremia

In *L. saintgironsi*, the mean natremia of individuals sampled in the field was significantly higher compared to the mean value for individuals sampled after two days in fresh water (ANOVA, $F_{1,\ 20} = 36.27$,

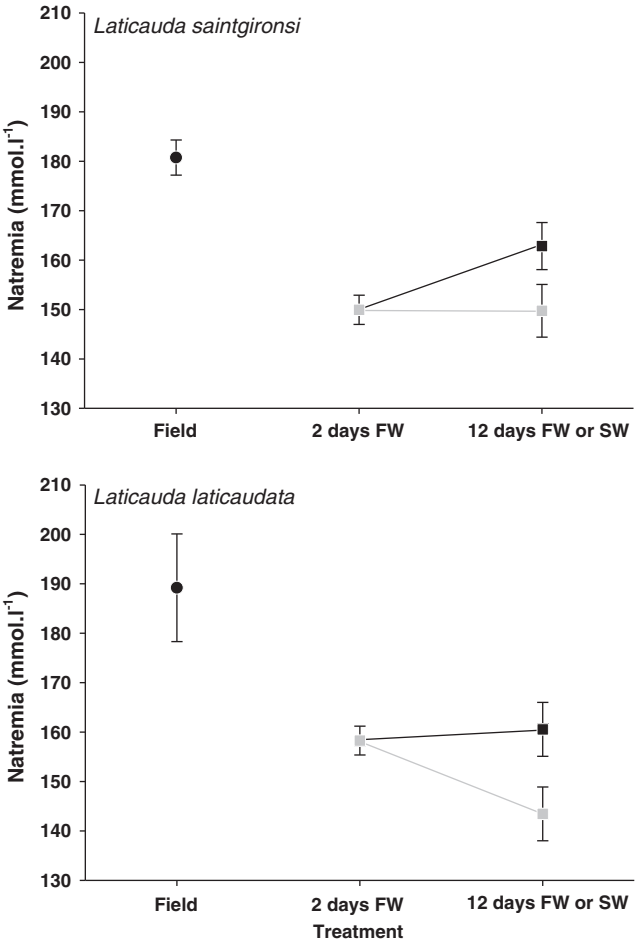

Fig. 1. Natremia (plasma sodium concentration, mmol·l^{-1}) of sea kraits (*L. saintgironsi* and *L. laticaudata*) sampled in the field (black circles), and under experimental conditions (black and grey squares). FW and SW stand for fresh water and seawater; and are represented by grey and black symbols respectively. Connected dots indicate that the same individuals were sampled for those treatments. See text for details.

$p < 0.0001$, Fig. 1), and was higher compared to the value recorded in individuals transferred and kept in sea water for 12 additional days (ANOVA, $F_{1, 16} = 18.22$, $p < 0.001$, Fig. 1). Focusing on the experimental individuals, we found a significant treatment effect (repeated measures ANOVA, effect of treatment through time $F_{1, 6} = 6.06$, $p = 0.04$, Fig. 1). Post hoc tests revealed that the natremia of snakes kept in fresh water did not change after 12 days (Fisher's LSD, $p = 0.55$); by contrast salt gain increased in snakes transferred to saltwater ($p < 0.01$, Fig. 1).

In *L. laticaudata*, we also found that the mean natremia of individuals sampled in the field was higher compared to individuals sampled two days after transfer to fresh water (ANOVA, $F_{1, 13} = 24.64$, $p < 0.0001$, Fig. 1), and also compared to snakes 12 days after transfer to seawater (ANOVA, $F_{1, 8} = 17.79$, $p < 0.003$, Fig. 1). Focusing on the experimental individuals, we found a significant treatment effect (repeated measures ANOVA, effect of treatment through time $F_{1, 5} = 5.05$, $p = 0.05$, Fig. 1). Post hoc tests showed that the natremia of snakes kept in fresh water decreased after 12 days (Fisher's LSD, $p = 0.03$), while it stayed constant in individuals transferred to seawater ($p = 0.71$, Fig. 1).

4. Discussion

Physiological capacity for excreting salt is essential for marine vertebrates (Peaker and Linzell, 1975; Schmidt-Nielsen, 1983; Ortiz, 2001). Owing to their salt glands, sea snakes were expected to be able to maintain their natremia within a narrow range when exposed to various salinities. Unexpectedly, our results show that 1) free-ranging sea kraits can display elevated natremia (up to 205 mmol·l^{-1}, Fig. 1), and 2) that sea kraits can undergo important changes of natremia in response to the salt content of their aquatic environment (Fig. 1). Interestingly, such marked changes occurred relatively independently from variations in body mass, suggesting possible decoupling between natremia and net water flows between body compartments and the environment (Lillywhite et al., 2008, 2012).

The elevated natremia we recorded on free-ranging individuals could be merely a concentration of body fluid due to dehydration. Indeed, amphibious species such as sea kraits dehydrate both on land (Lillywhite et al., 2009) and at sea (Lillywhite et al., 2008; Brischoux et al., 2012a). To cope with dehydration, and restore their water balance, sea kraits drink fresh water when available (Bonnet and Brischoux, 2008; Lillywhite et al., 2008, this study). In our study, intake of fresh water presumably allows adjustment of natremia down to ~150 mmol·l^{-1} (Fig. 1), a level considered as normal in snakes (Campbell, 2004). Although teasing apart the respective role of water loss (and thus concentration of body fluids) versus salt gain on natremia was not possible on the free-ranging individuals we sampled, our results suggest that despite having a functional salt gland, sea kraits display a high tolerance to hypernatremia.

Although both species are amphibious and share basic ecological traits (foraging at sea versus other activities on land: Heatwole, 1999), they also vary in their degree of emancipation from the terrestrial environment, *L. saintgironsi* being more terrestrial (Shine et al., 2003; Bonnet et al., 2005, 2009; Bonnet and Brischoux, 2008). Each sea krait species also displays specific physiological adaptations: dehydration rate in seawater of *L. saintgironsi* (as assessed for its sister species *Laticauda colubrina*: Lillywhite et al., 2008) should be higher compared to *L. laticaudata* (Lillywhite et al., 2008). These differences are reflected by their relationship to salinity (Brischoux et al., 2012a, 2013). Accordingly, the two species of sea kraits displayed different responses to salinity (Fig. 1). When transferred to seawater, the natremia of *L. saintgironsi* increased by 8.5% but remained stable in snakes kept in fresh water (Fig. 1). Salt gain was unlikely the result of drinking as captive sea kraits refuse to drink seawater (Lillywhite et al., 2008), our findings rather suggest that *L. saintgironsi* gain salt through permeable skin surfaces when kept in seawater for 12 days. In contrast, natremia in *L. laticaudata* rose only 1.2% following 12 days in seawater (Fig. 1). Interestingly, in *L. laticaudata* kept in fresh water, natremia continued to decrease by 9.4% (Fig. 1). These data suggest that either it took longer for *L. laticaudata* to restore osmotic balance through drinking and/or that an influx of fresh water through permeable surfaces had occurred in this species. This latter hypothesis may reveal important trade-offs with skin permeability, and deserves further study (see Dunson and Robinson, 1976; Dunson and Stokes, 1983). Overall, our experiment shows that, over an ecologically relevant time scale (duration of a foraging trip), the more terrestrial *L. saintgironsi* is more susceptible to salt gain through the skin than is the more marine *L. laticaudata*. These results dovetail remarkably well with interspecific differences in dehydration rates in seawater measured elsewhere (Lillywhite et al., 2008; Brischoux et al., 2012a).

A review of plasma sodium concentration of marine snakes kept in fresh water or seawater provides additional insights (Table 1). Free-ranging marine snakes (including file snakes, sea kraits and hydrophines sea snakes) exhibit elevated natremia under natural conditions (Table 1). However, when transferred to fresh water, all of these species restore natremia to normal levels (140–150 mmol·l^{-1}: Campbell, 2004). This suggests that sea snakes share with other tetrapods (marine and terrestrial) relatively similar normonatremia as shown by the remarkable consistency of the levels they attain when hydrated (Table 1, Campbell, 2004). However, in striking contrast to other marine tetrapods (seabirds, marine mammals) sea snakes tolerate strong

Table 1
Summary of published data on plasma sodium concentration in several marine snake species (having salt glands). Most data from seawater (SW) comes from individuals captured in natural conditions; while data from fresh water acclimated (FW) snakes come from laboratory experiments. Data are mean values collected from Dunson, 1968 (a), Dunson and Dunson, 1973 (b), 1974 (c), 1975 (d), Dunson et al., 1971 (e), Duggan and Lofts, 1978 (f), Babonis et al., 2011 (g) and the present study (h).

Habits	Family	Species	Natremia ($mmol \cdot l^{-1}$)	
			FW	SW
Amphibious	Laticaudinae	*Laticauda saintgironsi*[h]	149.7	180.7
		L. laticaudata[h]	143.4	189.2
		L. semifasciata [g]	152.2	158.2
Aquatic	Acrochordidae	*Acrochordus granulatus*[b]	128.0	160.3
	Hydrophinii	*Hydrophis cyanocinctus*[f]	152.2	231.4
		H. elegans[c]	134.0	205.5
		Pelamis platurus[a,d,e]	140.0	232.1

hypernatremia and can sustain very high sodium concentrations in the plasma (Table 1, up to 307 $mmol \cdot l^{-1}$ recorded in free-ranging *Pelamis platurus*). Although marine snakes' distributions and tolerances to salinity have been shown to correlate with the efficiency of their salt glands (Brischoux et al., 2012b), remarkably our results question the usefulness and/or efficiency of their functional salt gland. Empirical and experimental studies (Table 1) suggest that salt glands of sea snakes do not maintain normonatremia as in other marine tetrapods; instead they seem to serve to limit extreme salt loads. For instance according to Dunson et al. (1971), effective salt secretion is initiated once natremia deviate from high thresholds between 170 and 200 $mmol \cdot l^{-1}$ in *P. platurus*.

We hypothesise that restricting active salt excretion to high levels of natremia represents an effective means of saving energy in these low-energy specialists (Pough, 1980). One would have expected more marine adapted species (hydrophiines) to regulate their natremia more precisely. Counter intuitively, "true" sea snakes (hydrophiines) which have relatively more highly developed and thus more efficient salt glands (Brischoux et al., 2012b) also show the highest tolerance to hypernatremia (all >200 $mmol \cdot l^{-1}$, Table 1), while other species, presumably less marine-adapted (acrochordids, laticaudines: Brischoux et al., 2012b), show lower natremia under natural conditions (160–190 $mmol \cdot l^{-1}$, Table 1). We suggest that, in addition to modifications of skin permeability (Dunson and Robinson, 1976; Dunson and Stokes, 1983), and the evolution of salt glands (Babonis and Brischoux, 2012) life in seawater might have substantially modified the tolerance of marine snakes to hypernatremia. A greater tolerance to hypernatremia would be beneficial since active salt excretion would occur only when plasma sodium dangerously exceeds an upper threshold. In turn, this would substantially decrease energetic costs linked to salt gland functioning (Peaker and Linzell, 1975; Gutiérrez et al., 2011) an otherwise continuous expenditure of energy that might be prohibitive in the day-to-day life of these organisms (Pough, 1980). Future studies should test this hypothesis in the context of the evolutionary transition to marine life in secondarily marine vertebrates. For instance, physiological performances (e.g. swimming) should deteriorate at a higher threshold of natremia in true sea snakes compared to other, presumably less marine-adapted species. More generally, our results support the notion that the great flexibility conferred by ectothermy is a major adaptive strategy related to the saving of energy in low-energy specialists (Pough, 1980; Shine, 2005).

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