

## Evidence for Control of Cutaneous Oxygen Uptake in the Yellow-Lipped Sea Krait *Laticauda colubrina* (Schneider, 1799)

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**ABSTRACT.**—Some sea snakes and sea kraits (family Elapidae) can dive for upward of two hours while foraging or feeding, largely because they are able to absorb a significant percentage of their oxygen demand across their skin surfaces. Although cutaneous oxygen uptake is a common adaptation in marine elapids, whether its uptake can be manipulated in response to conditions that might alter metabolic rate is unclear. Our data strongly suggest that Yellow-Lipped Sea Kraits, *Laticauda colubrina* (Schneider, 1799), can modify cutaneous uptake in response to changing pulmonary oxygen saturation levels. When exposed to stepwise 20% decreases in aerial oxygen saturation from 100% to 40%, Yellow-Lipped Sea Kraits spent more time emerged but breathed less frequently. A significant graded increase in cutaneous uptake was seen between 100% and 60% saturation, likely attributable to subcutaneous capillary recruitment. The additional increase in oxygen uptake between 60% and 40% was not significant, indicating capillary recruitment is likely complete at pulmonary saturations of 60%. During a pilot trial, a single Yellow-Lipped Sea Krait exposed to an aerial saturation of 25% became severely stressed after 20 min, suggesting a lower saturation tolerance level between 40% and 25% for the species. Reducing subcutaneous perfusion could optimize swimming performance during foraging, whereas redirecting blood to skin surfaces would maximize dive times when subduing prey or avoiding aerial predators.

The family Elapidae includes more than 60 species of sea snakes and sea kraits (Sanders et al., 2013), making it the most successful group of extant reptiles to reinvade the marine environment. Sea snakes are entirely marine, whereas sea kraits are amphibious, spending approximately half of their time at sea and the other half on land (Shetty and Shine, 2002; Cook et al., 2015). When at sea, both groups spend a majority of their time submerged, foraging for prey and surfacing only briefly to replenish pulmonary oxygen stores. Sea snakes and sea kraits exhibit several adaptations that play an important role in extending diving times, including the ability to uptake oxygen across cutaneous surfaces (Rubinoff et al., 1986; Heatwole, 1999; Dabruzzo et al., 2012), highly modified lungs (Dunson, 1975; Graham et al., 1975; Heatwole, 1981), increased metabolic efficiency (Dunson, 1975; Dabruzzo et al., 2012), increased hematocrit, and high hemoglobin oxygen affinity (Wang et al., 2013; also see Lillywhite and Tamir 1994). Of these, cutaneous oxygen uptake is thought to play a principal role in increasing dive duration in sea snakes and sea kraits (Seymour 1974; Feder and Burggren 1985b). Studies are unclear, however, if marine elapids can manipulate cutaneous uptake in response to conditions that might alter their metabolic demand, and if so, to what extent uptake may be modified.

Reptiles may improve cutaneous oxygen uptake by maximizing diffusion driving pressures. This can be accomplished by reducing effective diffusion distance between the stratum corneum and subcutaneous capillaries or by altering hemoglobin dissociation properties. Alternatively, driving pressures can be improved by lowering blood oxygen tensions through increased activity or right-to-left blood shunting that serves to bypass the pulmonary circuit returning oxygen-poor systemic blood to the body (see Lillywhite and Tamir, 1994; Pratt and Franklin, 2010). Maximum uptake rates are constrained by the innate properties of the respiratory surface, and the system eventually becomes diffusion limited. Aquatic cutaneous

respiration in Yellow-Bellied Sea Snakes, *Pelamis platura* (Linnaeus, 1766), as well as Loggerhead Musk Turtles, *Sternotherus minor* (Agassiz, 1857), is diffusion limited, with oxygen uptake decreasing linearly as oxygen tension in water is reduced (Graham, 1974; Belkin, 1968, respectively). Diffusion-limited systems also are temperature independent (Seymour, 1982), such that temperature-induced increases in total metabolic demand have little or no influence on oxygen uptake. Arafura Filesnakes, *Acrochordus arafurae* (McDowell, 1979), for example, show minimal increases in cutaneous uptake (temperature quotient = 1.18), even though total metabolic demand more than doubles (temperature quotient = 2.52) between 20°C and 32°C (Pratt and Franklin, 2010). With the possible exception of cardiac shunts which have not been shown to increase dive times in aquatic reptiles (Hicks, 2002), increasing diffusion driving pressure is not an efficient approach to making rapid, short-term adjustments in cutaneous oxygen uptake.

A second tactic for enhancing oxygen uptake is improving conductance across cutaneous surfaces. Uptake rates in these systems are determined by the degree of subcutaneous capillary perfusion and may become perfusion limited. Many reptiles, however, exhibit the ability to precisely control the degree and location of capillary perfusion (Bartholomew, 1982; Feder and Burggren, 1985a), making these systems much more amenable to timely adjustments in cutaneous oxygen uptake. Perfusion-limited systems actively improve conductance by opening capillary beds to increase functional surface area for diffusion (Feder and Burggren, 1985a; Heatwole, 1999; Pratt and Franklin, 2010). Changes in conduction can be rapidly matched to oxygen demand (i.e., show a graded response) and are independent of animal activity. Moreover, perfusion influenced systems are sensitive to temperature induced increases in metabolic uptake and often exhibit high temperature quotient values (Seymour, 1982).

Mechanisms for cutaneous uptake by reptiles have been reviewed by Seymour (1982) as well as Feder and Burggren (1985a,b), and both present evidence for diffusion-limited cutaneous uptake in some aquatic snakes. Conversely, Heatwole

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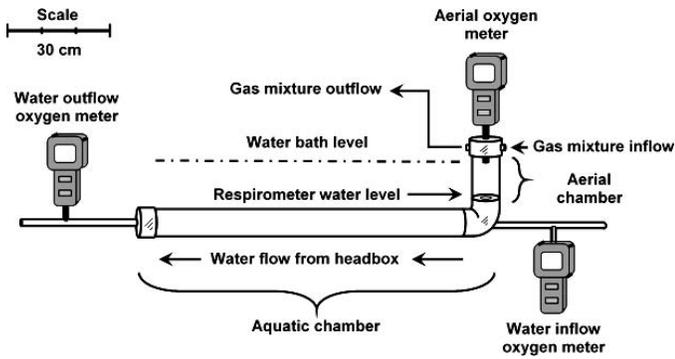


FIG. 1. Respirometer design used to estimate cutaneous oxygen uptake in Yellow-lipped Sea Kraits, *Laticauda colubrina* (Schneider, 1799). During experimental trials animals were exposed to stepwise decreases in aerial oxygen saturation treatments of 100, 80, 60, and 40% to simulate pulmonary saturations experienced while diving. Saturation levels were generated by mixing nitrogen with air flowing through the aerial chamber. Cutaneous uptake was quantified using standard flow-through respirometry techniques. See text for details.

(1999) states that sea snakes (and presumably sea kraits) have the means to fine-tune skin circulatory patterns to meet their immediate respiratory needs while diving. The relationship between cutaneous uptake and ambient gas tensions has not been adequately studied (Seymour, 1982), and supporting data for either argument are largely indirect or anecdotal. The purpose of our study was to test the hypothesis that Yellow-Lipped Sea Kraits, *Laticauda colubrina* (Schneider, 1799), exposed to decreasing aerial oxygen saturation levels will exhibit significant increases in cutaneous oxygen uptake. Yellow-Lipped Sea Kraits are well suited for this study as they are abundant throughout the tropical Pacific where they specialize in preying on eels along reefs and rocky shorelines. In addition, some individuals have been observed to remain submerged for periods of up to two hours (Heatwole, 1975b, 1981; Brischox et al., 2008) and can derive up to 12% of their total metabolic demand from oxygen uptake across cutaneous surfaces (Dabruzzo et al., 2012). Our study objectives were to 1) quantify changes in ventilation and cutaneous oxygen uptake responses of Yellow-Lipped Sea Kraits to progressive hypoxia, 2) identify the pattern and magnitude of these changes, 3) determine whether the patterns follow those predicted for perfusion- or diffusion-limited systems, and 4) discuss the results in relation to diving behavior.

#### MATERIALS AND METHODS

**Collection and Holding Conditions.**—Five male and eight nongravid female Yellow-Lipped Sea Kraits with a mean ( $\pm$  SE) snout-vent length of 73.2 ( $\pm$  2.17) cm and mean mass of 208 ( $\pm$  23.5) g were collected on Hoga Island, Southeast Sulawesi, Indonesia (05°27'53"S, 123°46'33"E; datum WGS 84). Collections were made over several weeks as Yellow-Lipped Sea Kraits moved ashore at low tide. While in captivity, the animals were housed at the Hoga Island Research Laboratory in individual 40-L plastic bins (33.5  $\times$  30.0  $\times$  40.0 cm) containing 2–3 cm of fresh water (Lillywhite et al., 2008) at approximate reef temperatures of 26 °C ( $\pm$  0.5; Eme and Bennett, 2009). Bins were cleaned and water changed twice daily. All animals remained at holding conditions for at least 72 h, but no more than 96 h, prior to experimental trials and were fasted over the holding period.

**Experimental Design.**—Repeated measures, flow-through respirometry was used to estimate cutaneous oxygen uptake of 12 Yellow-Lipped Sea Kraits exposed to stepwise 20% decreases in aerial oxygen saturation from 100% to 80%, 60%, and 40%. We collected ventilation responses for each treatment interval, including emergence time, relative breathing rate (breaths taken/time emerged) and absolute breathing rate (breaths taken/treatment time). Minimum aerial saturation level and fasting time were based on pilot trial observations of a single male Yellow-Lipped Sea Krait fasted for 24 h and exposed to decreasing aerial oxygen saturations of 100%, 75%, 50%, and 25% (see Results below). We did not include data from the pilot trial in analyses of cutaneous uptake or ventilation responses.

**Respirometer Design and Protocols.**—Metabolic measurements were made between 0500 h and 1800 h local time on fasted, resting animals making occasional routine movements such as emerging the head for breathing. The respirometer we used in this study is similar to that previously described by Dabruzzo et al. (2012) and consisted of a 0.15-L aerial and 2.45-L aquatic chamber of transparent, high-density (1.45 g/cm<sup>3</sup>) polychloroethanedyl tubing (6.03 cm outside diameter). The system was sufficiently large to allow free movement but small enough to discourage excessive activity (Steffensen, 1989; Cech, 1990). Yellow-Lipped Sea Kraits breathed a nitrogen–oxygen mixture in the aerial chamber, whereas the body remained submerged in the flow-through aquatic chamber (Fig. 1). Nitrogen was mixed with room air to establish subatmospheric aerial oxygen levels (see Gratz, 1979; Pinder and Burggren, 1986). Yellow Springs Instruments (YSI, Inc., Yellow Springs, OH), Model 550A, oxygen meters were used to measure oxygen saturation (%) in the aerial chamber, as well as inflow and outflow seawater oxygen concentrations (mL/L), and water sample values were corroborated by Winkler titration (Cox, 1990). We used an opaque blind to isolate animals from outside activity during trials, while allowing discreet observations of behavior. Two observers continuously monitored and recorded treatment duration, number of emergent events per treatment, breaths per emergent event, and total emerged time per treatment. We then used these data to calculate the percentage of emerged time (%), as well as absolute and relative breathing rates in breaths per minute (bpm).

Each Yellow-Lipped Sea Krait was habituated in the respirometer overnight (Hare et al., 2004; Dabruzzo et al., 2012), breathing room air (i.e., 100% oxygen saturation) from the aerial chamber while fully saturated, filtered seawater flowed from a headbox through the aquatic chamber. Water flow rates were adjusted between 0.025 and 0.075 L/min to establish a dissolved oxygen concentration difference of 10% to 15% between inflow and outflow streams (Steffensen, 1989; Cech, 1990). Outflow water entered a sump where it was filtered (40- $\mu$ m plankton netting), aerated, and recycled to the headbox. We maintained temperatures by submerging the respirometer into a 27°C, constant temperature water bath. The next morning we determined three cutaneous uptake values over 30-min intervals as the animal breathed room air and calculated cutaneous uptake (mL/min) from the following equation (Cech, 1990):

$$\text{Cutaneous uptake (mL/min)} = (O_{2i} - O_{2f}) \times \dot{V}_w$$

where  $O_{2i}$  is the average oxygen concentration of inflow water (mL/L),  $O_{2f}$  is the average oxygen concentration of outflow water (mL/L), and  $\dot{V}_w$  is the water flow rate through the respirometer (L/min). We adjusted the average of the three cutaneous uptake values to standard temperature and pressure, dry. High variability among snake mass-adjustment exponents

TABLE 1. Five-number summary of cutaneous oxygen uptake, emergence time, relative (breaths taken/time emerged), and absolute (breaths taken/treatment time) breathing rates of 12 Yellow-Lipped Sea Kraits, *Laticauda colubrina* (Schneider, 1799), exposed to stepwise decreases in aerial oxygen saturation of 100%, 80%, 60%, and 40%.

Treatment	Quantiles				
	10%	25%	Median	75%	90%
Oxygen saturation					
Cutaneous oxygen uptake (mL/kg/h)					
100%	1.67	2.88	5.07	8.91	31.98
80%	2.51	2.83	5.32	11.00	38.96
60%	3.53	3.79	5.43	13.90	29.74
40%	3.33	4.34	5.45	14.67	28.53
Percentage of treatment time emerged					
100%	1.7	2.3	4.0	12.7	19.4
80%	3.0	5.9	17.0	38.4	96.8
60%	11.2	16.4	30.2	55.5	75.6
40%	4.3	22.6	40.5	57.2	94.7
Relative breathing rate in breaths per minute					
100%	2.32	2.76	4.12	9.81	13.85
80%	0.20	1.35	2.60	6.69	9.67
60%	0.49	0.68	1.19	1.94	2.48
40%	0.76	0.98	1.25	1.91	7.69
Absolute breathing rate in breaths per minute					
100%	0.11	0.13	0.24	0.35	0.45
80%	0.20	0.28	0.31	0.77	0.84
60%	0.19	0.22	0.30	0.35	0.54
40%	0.29	0.31	0.40	0.65	0.85

prevented the use of a common exponent (Andrews and Pough, 1985); therefore, we divided cutaneous oxygen uptake in mL/min by mass to determine mass-specific cutaneous uptake (mL/kg/h) at 100% oxygen saturation. Weight-specific measures have good comparative value and are widely reported in sea krait and sea snake metabolic studies (e.g., Heatwole and Seymour, 1975b, 1978; Heatwole, 1999; Dabruzzi et al., 2012). In each subsequent treatment, we reduced aerial chamber oxygen levels by 20% over a period of 5 to 10 min by metering nitrogen into the air stream using a Dwyer model 5775 flow meter (Dwyer Instruments, Inc., Michigan City, IN). The animal was then allowed to adjust to the new oxygen treatment level (i.e., 80%, 60%, or 40% oxygen saturation) for 60 min, and the cutaneous measurement process was repeated over the next 90 min. We ran a respirometry blank, identical in all respects but without an animal, prior to the first trial and every fourth trial thereafter for a total of four blank runs. We subtracted the mean blank metabolic rate for each oxygen saturation level from the cutaneous uptake values to correct for any planktonic and bacterial metabolism in the seawater. The respirometer was disassembled after each trial, washed thoroughly with antibacterial soap, rinsed, and left to air dry (Steffensen, 1989; Cech, 1990).

**Statistical Analyses.**—Cutaneous metabolic uptake and ventilation response data sets did not meet the assumptions for parametric analysis; therefore, we represent data sets as five number summaries of 10%, 25%, 50% (median), 75%, and 90% quartiles. We used Friedman's multiple median comparison procedure to test the general null hypothesis that treatment endpoint median locations did not differ significantly (Friedman, 1937, 1939). Where differences were found, we determined relationships between treatment medians by using Tukey's pairwise separation on ranked data (Zar, 2010). For all statistical tests  $\alpha = 0.05$ .

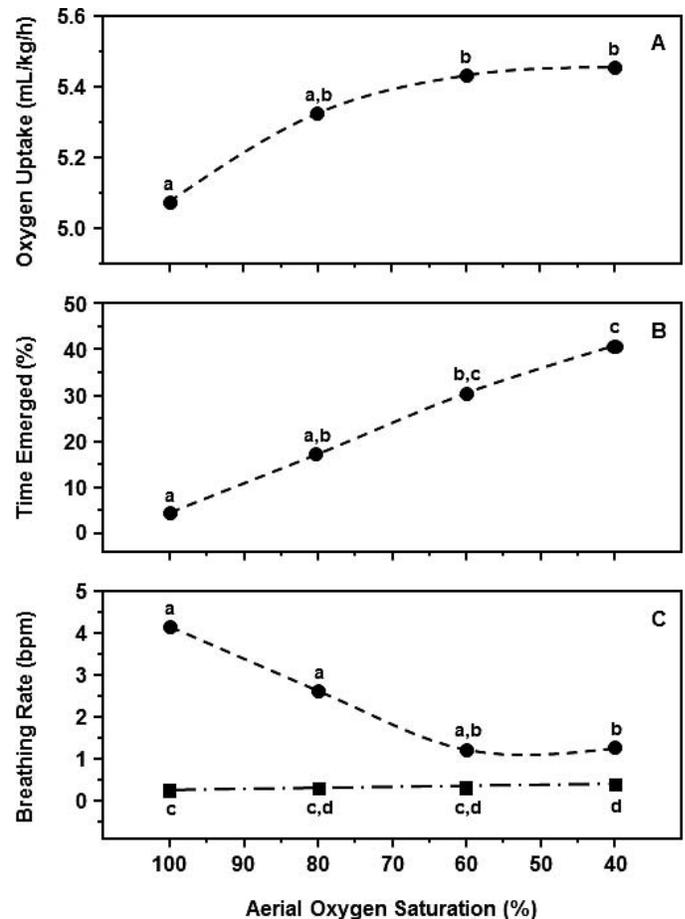


FIG. 2. Ventilation responses of 12 Yellow-lipped Sea Kraits, *Laticauda colubrina* (Schneider, 1799), exposed to stepwise decreases in aerial oxygen saturation. Median values for cutaneous oxygen uptake (A), emergence time (B), relative breathing rate (breaths taken ÷ time emerged) (C ●), and absolute breathing rate (breaths taken ÷ treatment time) (C ■) are plotted on aerial saturation treatments of 100, 80, 60, and 40%. Medians with like lower case letters do not differ significantly within plots ( $\alpha = 0.05$ ).

## RESULTS

Pilot data from the male Yellow-Lipped Sea Krait subjected to stepwise decreases in aerial saturation of 100%, 75%, 50%, and 25% showed that aerial oxygen saturation levels of 25% were insufficient to support the animal's routine activity level. We observed obvious signs of distress including agitated swimming behavior, rapid breathing rate, persistent escape efforts, and vomiting after only 20 min of exposure to the low oxygen saturation treatment. Furthermore, the vomitus consisted of a Broadnose Worm Eel, *Myrichthys colubrinus* (Boddaert, 1781), in the early stages of breakdown, suggesting that digestion was not complete after 24 h of fasting at  $\approx 26^\circ\text{C}$ . When aerial saturation was restored to 100%, activity and breathing rate decreased to near pretrial levels within about 60 min; when subsequently released, the animal swam quickly toward the reef.

Yellow-Lipped Sea Kraits exhibited an inverse logarithmic relationship between cutaneous oxygen uptake rate and aerial oxygen saturation level (Table 1). As aerial saturations decreased, median cutaneous oxygen uptake showed a significant 8% increase (Friedman's multiple median comparison;  $\chi^2 = 11.80$ ;  $df = 3$ ;  $P = 0.0081$ ). The inverse relationship between

cutaneous uptake and aerial saturation produced a graded pattern of overlapping statistical relationships. Tukey's pairwise separation on ranked data found no significant differences between median cutaneous uptake at 100% and 80% saturation, or between the 80%, 60%, and 40% saturation groups. Median uptake at 60% and 40% aerial saturation was significantly higher than the 100% saturation group (Fig. 2A). In spite of a 60% reduction in inspired oxygen concentration, Yellow-Lipped Sea Kraits displayed no outward signs of agitation or stress during the metabolic trials.

As aerial oxygen saturation levels decreased, Yellow-Lipped Sea Kraits significantly increased the percentage of time they remained emerged. Median emergence times in each treatment increased more or less linearly, demonstrating a 10-fold increase in emergence time from 3.5% to over 37% as saturation levels fell from 100% saturation to 40% (Table 1). Friedman's multiple median comparison identified significant differences in median emergence times between treatments ( $\chi^2 = 15.30$ ;  $df = 3$ ;  $P = 0.0016$ ). Tukey's pairwise separation on ranked data reported statistical similarities between the 100% and 80% treatment medians, the 80% and 60% treatment medians, and the 60% and 40% saturation treatment groups (Fig. 2B).

Relative and absolute breathing rates of Yellow-Lipped Sea Kraits showed fundamentally different responses to decreasing oxygen saturations (Table 1). Median relative ventilation rate (i.e., median number of breaths taken per emergent time) decreased with aerial oxygen saturation, falling from 4.12 bpm at 100% oxygen saturation to 1.25 bpm at 40% saturation (Table 1). The differences in relative median ventilation rate between oxygen saturation treatments were significant (Friedman's multiple median comparison;  $\chi^2 = 13.00$ ;  $df = 3$ ;  $P = 0.0046$ ), with Tukey's pairwise separation on ranked data dividing treatment medians into two statistically distinct but overlapping groups. Relative median ventilation rates at oxygen saturation levels of 100%, 80%, and 60%, were statistically similar, as were rates in 60% and 40% saturation treatment groups (Fig. 2C). Interestingly, the absolute breathing rate showed a small but significant increase from 0.24 to 0.40 bpm (Table 1) as oxygen saturation decreased (Friedman's multiple median comparison;  $\chi^2 = 8.40$ ;  $df = 3$ ;  $P = 0.039$ ). Treatment medians at 80%, 60%, and 40% saturation were statistically similar as were 100%, 80%, and 60% median values (Tukey's pairwise separation test on ranked data).

#### DISCUSSION

Although the ability of sea kraits and sea snakes to control oxygen uptake across skin surfaces has been discussed in the scientific literature since the early 1980s (Seymour, 1982; Feder and Burgrenn, 1985a), the empirical data are equivocal. Our results offer a strong argument in support of control in the Yellow-Lipped Sea Krait. Exposing Yellow-Lipped Sea Kraits to stepwise decreases in aerial oxygen saturation levels from 100% to 60% resulted in a significant, graded increase in cutaneous oxygen uptake (Fig. 2). A graded response pattern is consistent with the hypothesis by Feder and Burgrenn (1985a) that subcutaneous capillary recruitment can be used to increase functional surface area for oxygen diffusion, resulting in higher rates of cutaneous oxygen uptake. Decreasing aerial saturation from 60% to 40% produced no further significant increase in uptake, indicating that the subcutaneous capillary architecture in diving Yellow-Lipped Sea Kraits is fully involved, and cutaneous uptake maximized at pulmonary oxygen saturations

of approximately 60%. Yellow-Lipped Sea Kraits exposed to aerial saturations of 40% for 150 min showed no adverse reactions, whereas the pilot study animal exhibited signs of severe stress after only 20 min of exposure to 25% oxygen saturation. Similar stress responses have been noted only in forcibly submerged Yellow-Bellied Sea Snakes immediately prior to drowning (Graham, 1974). We doubt, therefore, that diving Yellow-Lipped Sea Kraits would allow pulmonary oxygen stores to reach such stressful levels, and the minimum saturation tolerated before surfacing lies somewhere between 25% and 40%. Any additional dive-related redistributions of blood would likely be associated with intracardiac shunting (Lillywhite and Tamir, 1994; Hicks, 2002; Cook and Brischox, 2014). Intracardiac shunting along with a high hemoglobin affinity for oxygen could potentially extend dive times in some diving snakes by lowering arterial oxygen tension and improving oxygen driving pressure across the skin (Lillywhite and Tamir, 1994; Pratt and Franklin, 2010).

Several less direct lines of evidence suggest that other aquatic snakes and marine adapted elapids may have the ability to modify cutaneous respiration. Several authors (e.g., Heatwole and Seymour, 1975a; Bruton et al., 2012) have argued that cutaneous uptake in aquatic snakes is diffusion limited and, therefore, insensitive to changes in subcutaneous blood flow. Seymour (1982) points out that diffusion-limited systems should have temperature quotients very near 1. Dabruzzo et al. (2012), however, measured cutaneous metabolic rates in Yellow-Lipped Sea Kraits at 28°C and 35°C and found a temperature quotient of 3.13, further strengthening the case that this species can modify cutaneous uptake. The ability to regulate subcutaneous capillary blood flow is a well-developed mechanism in many reptiles (Feder and Burgrenn, 1985a), although it is not always used for respiratory purposes (Bartholomew, 1982). A number of independent personal observations have described blushing of the skin in aquatic snakes (see Feder and Burgrenn, 1985a). Spine-Bellied Sea Snakes, *Lapemis curtus* (Shaw, 1802), and file snakes *Acrochordus granulatus* (Schneider, 1799), for example, are said to turn "pink", presumably attributable to perfusion of subcutaneous capillaries, although the response stimulus is not well studied (Heatwole and Seymour, 1975b; Lillywhite and Tamir, 1994). Additionally, some sea snakes exhibit exponential increases in cutaneous uptake in response to increased activity, also implying some level of cutaneous uptake control (Seymour, 1982). Yellow-Bellied Sea Snakes, Spine-Bellied Sea Snakes, and Dog-Faced Water Snakes, *Cerberus rynchops* (Schneider, 1799), all exhibit a two- to fivefold increase in oxygen uptake when active (Graham, 1974; Heatwole and Seymour, 1975b, 1978, respectively). These diverse findings point to the skin as an actively regulated oxygen uptake system in some species.

The keratinized skin of vertebrates is relatively thick, and in most cases, oxygen diffusion across skin is poor (Withers, 1992). Some aquatic turtles uptake oxygen across well-vascularized regions of the buccal cavity and cloaca when submerged to compensate for low oxygen diffusion across the shell (Dunson, 1960; King and Heatwole, 1994; Pratt and Franklin, 2010). Buccal and/or cloacal respiration was not apparent in Yellow-Lipped Sea Kraits in our study or in Yellow-Bellied Sea Snakes studied by Graham (1974). Likewise, none of six sea snake species (*Aipysurus duboisii* [Bavay, 1869], *Aipysurus laevis* [Lacépède, 1804], *Acalyptophis peronii* [Duméril, 1853], *Hydrophis elegans* [Gray, 1842], *Hydrophis belcheri* [Gray, 1849], and *Lapemis curtus* [Shaw, 1802]) studied by Heatwole and Seymour (1975b) showed evidence of buccal or cloacal respiration while

submerged. Some diffusion-limited vertebrates, including frogs, increase cutaneous uptake by using well-protected areas of thinner skin as respiratory exchange surfaces (Pinder and Burggren, 1986; Feder, 1995). Although Yellow-Lipped Sea Kraits clearly use skin as an oxygen exchange site when submerged (Seymour, 1974; Heatwole and Seymour, 1975a,b; Dabruzzi et al., 2012), the species has relatively thick skin compared to other marine snakes (Jayne, 1988). The unusual thickness is thought to enhance lateral force transmission for movement on land (Jayne, 1988), as well as increase skin resistance to water loss (Lillywhite et al., 2009). Even so, skin on the dorsal regions is somewhat thinner than skin from lateral and ventral locations (Jayne, 1988), and these variations in thickness may help optimize cutaneous uptake while preserving other important skin functions such as abrasion resistance while on land. Shetty and Shine (2002) have reported that Yellow-Lipped Sea Kraits come ashore at approximately 10- to 12-day intervals to slough skin. Rapid skin turnover likely keeps biofouling to a minimum (Shine et al., 2010), and because old skin is sloughed while on land, there is little chance that the exuvia will interfere with cutaneous respiration. The anatomy and physiology of Yellow-Lipped Sea Krait skin may be unique in that it improves functional performance on land while still maintaining relatively high levels of cutaneous oxygen uptake in water.

Notably, emergence time and breathing rate responses of Yellow-Lipped Sea Kraits exhibit a reverse relationship as aerial oxygen saturation levels decreased (Fig. 2), such that emergence time increased by an order of magnitude, but breathing events during each emergent event (i.e., relative breathing rate) fell. The absolute breathing rate, however, remained relatively constant. Putative sites for control of reptile ventilatory drive and ventilation patterns are the central receptors in the carotid arteries and the peripheral chemoreceptors in the cerebral ventricles (Taylor et al., 1999). Although peripheral receptors have been shown to respond to hypoxemia (low blood oxygen content), central receptors are thought to be sensitive to hypercapnia. Conversely, Glass and Johansen (1976) found that hypercapnic gas mixtures of 6% and 8% carbon dioxide exerted a depressant rather than a stimulatory effect on ventilation in Elephant Trunk Snakes (*Acrochordus javanicus*; Hornstedt, 1787) but could not exclude the possibility that other concentrations may have a stimulatory effect. The role of central and peripheral receptors in establishing ventilatory drive or hypoxia responses is not well understood in most reptiles (Milsom, 1991), but Yellow-Lipped Sea Kraits seem to exhibit specific, well-defined ventilatory receptor responses. During trials, kraits breathed a low oxygen, carbon dioxide free, gas mixture and experienced hypoxemia without hypercapnia such that the peripheral receptors triggered an emergence response, but the central receptors remained unaffected, and no increase in overall breathing rate was seen.

Cutaneous respiration is considered to be one of the most important diving adaptations of marine elapids (Seymour, 1974; Heatwole and Seymour, 1975a,b; Dabruzzi et al., 2012), and the ability to modify oxygen uptake may have several benefits. For example, longer dive times may increase foraging efficiency (Cook et al., 2015), although in some cases maximizing capillary recruitment during a dive cycle may not be necessary, or even desirable. Yellow-Lipped Sea Kraits usually make relatively short, 20–30-min dives (Heatwole, 1975b, 1981) during which they forage for eels in coral crevasses and holes (Heatwole, 1999; Brischoux et al., 2007; Cook et al., 2015). Increased cutaneous

uptake during these short-duration dives may have little advantage, and in fact could decrease blood flow needed for other important functions such as swimming. During prey encounters, Yellow-Lipped Sea Kraits are obligated to remain submerged for longer durations as they wait until envenomated prey become incapacitated. Laboratory studies of Yellow-Lipped Sea Kraits show this process can require up to 30 min to complete (Radcliffe and Chiszar, 1980), and although it is impractical to observe them directly under natural conditions (Brischoux et al., 2007), Yellow-Lipped Sea Kraits are likely to need longer submersion times during feeding than during foraging. Indeed, several studies have reported submergence times of up to two hours in Yellow-Lipped Sea Kraits (Heatwole, 1975b, 1981; Brischoux et al., 2008). Reduced activity along with additional oxygen uptake gained through subcutaneous capillary recruitment likely translates into longer submergence feeding times. Longer dive times also may reduce aerial predation threats. Cold-acclimated Mary River Turtle hatchlings (*Elusor macrurus*; Legler and Cann, 1994), for example, are thought to dramatically reduce predator exposure by increasing dive times (Clark et al., 2008). Similarly, longer dive times by sea kraits or sea snakes may reduce threats from aerial predators such as sea eagles (Heatwole, 1975a). Cutaneous uptake may well be a key adaptation allowing elapids to successfully reinvade the sea, but it is the ability to modify uptake that makes the process so uniquely flexible.

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