

METABOLIC THERMAL SENSITIVITY OPTIMIZES SEA KRAIT AMPHIBIOUS PHYSIOLOGY

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ABSTRACT: Yellow-lipped Sea Kraits (*Laticauda colubrina*) are tropical amphibious snakes that divide their time between land and sea. When moving between habitats, the kraits experience rapid and sometimes extreme shifts in body temperature that can have profound metabolic effects. We quantified cutaneous and pulmonary oxygen uptake in sea kraits from Hoga Island, southeast Sulawesi, Indonesia, at temperatures commonly encountered in aquatic (27.6°C) and aerial (35.2°C) habitats. Total oxygen uptake rate was 49.14 mL Kg⁻¹ h⁻¹ at 27.6°C and 115.27 mL Kg⁻¹ h⁻¹ at 35.2°C. Pulmonary and cutaneous uptake rates were 44.58 and 104.70, and 4.56 and 10.57 mL Kg⁻¹ h⁻¹, at 27.6 and 35.2°C, respectively. Sea kraits had a temperature coefficient (Q₁₀) of approximately 3, suggesting that metabolic rates triple with every 10°C temperature increase. High Q₁₀ values may minimize time on land by increasing digestion and nutrient absorption rates as well as promoting faster healing and injury recovery times. Cooler reef temperatures would decrease metabolic demand, thus increasing submergence and foraging times.

Key words: Bimodal respirometry; Cutaneous oxygen uptake; *Laticauda colubrina*; Q₁₀; Sulawesi, Indonesia

THE SUBFAMILY Laticaudinae is comprised of eight amphibious sea krait species from two genera, *Laticauda* and *Pseudolaticauda* (Heatwole et al., 2005; Kharin and Czeblukov, 2006; Pyron et al., 2011). The Yellow-lipped Sea Krait (*Laticauda colubrina*) has the widest known distribution of the group, ranging throughout the Malay Archipelago into the southwestern Pacific, and north to the Philippines and Taiwan (Heatwole et al., 2005). These kraits forage for eels among crevasses on coral reefs (Heatwole et al., 2005; McCoy, 2006), remaining submerged for 15–20 min and diving to depths of up to 30 m (Heatwole, 1999; Brischoux et al., 2007). Extended dive times are due in part to oxygen storage in the saccular lung (Graham, 1974; Heatwole, 1981), as well as the ability to uptake 10% or more of their total oxygen demand across skin surfaces (Heatwole and Seymour, 1978; Feder and Burggren, 1985). Indeed, cutaneous respiration is considered to be a key adaptation promoting long submersion times in the group (Heatwole and Seymour, 1978). Yellow-lipped Sea Kraits are also the most terrestrial of their family (Heatwole et al., 2005), spending nearly equal amounts of time

on land and sea. Observations by Saint Girons (1964) as well as more recent radiotelemetry studies by Shetty and Shine (2002a) have shown that these kraits remain on land for several days to digest recently captured prey, recover from injury, slough skin, court mates, or lay eggs (Lading et al., 1991; Shetty and Sivasundar, 1998; Shetty and Shine, 2002b).

Thermal requirements for Yellow-lipped Kraits are poorly defined in the literature. Data are typically limited to collections of water temperatures at capture sites often from different depths, locations, and seasons. Consequently, water temperatures reported within the kraits' geographic distribution vary widely, with extremes ranging from a low of 15°C in the Philippines (Punay, 1975) to a high of 31°C in Fiji (Shetty and Shine, 2002a). Regardless of location, kraits likely experience relatively stable water conditions while on the reef (Heatwole, 1999; Shetty and Shine, 2002a). Moving onto land, however, can expose kraits to rapid and sometimes harsh temperature shifts. Pough and Lillywhite (1984) noted that some kraits will experience increases of up to 15°C in body temperature throughout the day. Shetty and Shine (2002a) measured daytime air temperatures of 37°C on Fiji, but suggested that Yellow-lipped Sea Kraits may keep body temperatures around 30°C by seeking shelter from direct sun. Even

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when sheltered from the effects of direct insolation kraits may experience high temperatures approaching the 40°C lethal limit for this group (Bonnet et al., 2009). For example, closely related Blue-lipped Sea Kraits (*Laticauda laticaudata*) on New Caledonia often attain body temperatures of 35°C while on land (Brischoux et al., 2007), and in one case a krait maintained body temperatures between 37.1 and 37.9°C for 3 d (Brischoux et al., 2009). In their extensive monograph on Yellow-lipped Sea Krait ecology, Heatwole and coworkers (2005) note that little attention has been paid to thermal relationships in this species.

The scarcity of information on sea krait thermal ecology is somewhat surprising, given the interest in this group and the profound effect temperature change can have on ectotherms. Ectotherm metabolic rates typically double with every 10°C increase in ambient temperature (Schmidt-Nielsen, 1997), and it is likely that Yellow-lipped Sea Krait metabolism is also strongly influenced by environmental temperature change. Although cutaneous metabolic rates of Yellow-lipped Sea Kraits have been previously determined by Heatwole and Seymour (1978), no study to date has measured pulmonary or total oxygen consumption rates for this species, or investigated the effect of temperature on metabolic rate. The purpose of our research was to examine the effects of changing environmental temperature on Yellow-lipped Sea Krait metabolism. Specific study objectives were (1) to estimate total metabolic rate from simultaneous determinations of oxygen uptake across pulmonary and cutaneous surfaces and (2) to quantify effects of acute temperature change on metabolic rate.

MATERIALS AND METHODS

Collection and Holding Conditions

Five nongravid female (Angilletta and Sears, 2000) and 10 male Yellow-lipped Sea Kraits with a mean (\pm standard error) snout-vent length of 79.8 (\pm 1.93) cm and mass of 202.0 (\pm 23.66) g were collected at night on Hoga Island, Southeast Sulawesi, Indonesia (05°27'53"S, 123°46'33"E; datum = WGS84). Kraits were taken to the Hoga Island Research Laboratory where they were individually housed in 50-L clear plastic

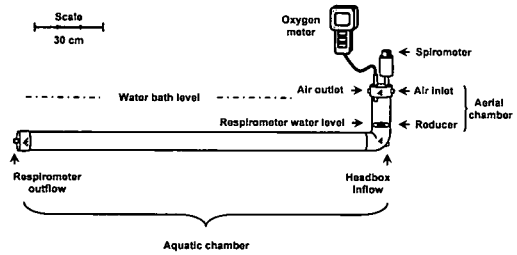


FIG. 1.—Bimodal respirometer used to estimate cutaneous and pulmonary oxygen uptake in the sea krait *Laticauda colubrina*. Pulmonary measures were made as kraits consumed oxygen from air contained within the closed aerial chamber. Chamber air was intermittently exchanged when oxygen levels approached 70% saturation. Cutaneous uptake was quantified with the use of standard flow-through respirometry techniques. See text for complete details.

bins containing clean beach sand and sea water. Sea water was changed twice daily, and all bins were kept at approximate reef temperatures of 26–27°C (Eme and Bennett, 2009). Experimental animals were fasted for 72 h before being placed in trials, and were returned to their site of capture following experiments.

Respirometer Description

A modified version of the bimodal, intermittent-closed respirometer design of Lefevre and coworkers (2011) was used to measure resting oxygen uptake rates ($\text{mL Kg}^{-1} \text{h}^{-1}$) across cutaneous and pulmonary surfaces simultaneously (Fig. 1). Metabolic rates were measured in quiescent, fasted kraits throughout the day, and were considered to fall under the classic definition of resting metabolic rate (see Bennett and Dawson, 1976; Zaidan, 2003; Dorcas et al., 2004). The respirometer was constructed of transparent, high-density (1.45 gm/cm^3) polychloroethanediyl tubing (6.03-cm outside diameter) with a wall thickness of 0.51 cm. Polychloroethanediyl has been shown to be a useful material for the construction of oxygen measuring systems owing to its negligible oxygen absorption and desorption properties (Stevens, 1992). The respirometer was large enough to allow kraits free movement, but small enough to discourage excessive activity (Steffensen, 1989; Cech, 1990). Temperature fluctuations were minimized by placing the respirometer into a recirculating water bath (190 \times 16 \times 24 cm) heated by a 300-W submersible heater (AZOO brand, Taikong Corporation). An opaque

curtain surrounding the bath allowed for observations while reducing potential disturbance to the krait.

Flow-through respirometry was used to quantify cutaneous oxygen uptake for kraits in the aquatic chamber (165 cm in length; 4.30-L volume). Seawater from a 4-L head box flowed through the aquatic chamber at a rate of 0.065 (± 0.0025) L/min, with water flow controlled by a 9.5-mm ID polypropylene stopcock valve on the chamber's outflow side. Seawater used in respirometry trials was filtered through 40- μ m mesh netting to remove planktonic organisms. Water leaving the respirometer flowed into a 6-L sump and was pumped back up to the headbox (Harbor Freight Submersible Fountain Pump, Model 258-GPH), where it was filtered and aerated. The flow-through design allowed for longer trial times, faster temperature adjustments, and improved water quality maintenance compared to previous static respirometer designs used to measure sea snake metabolism (Heatwole and Seymour, 1975).

Pulmonary oxygen consumption was estimated with the use of a closed 0.15-L, vertical aerial chamber (Fig. 1) in which an air pump (Whitewater, Model LT-11) intermittently renewed chamber atmosphere following each emergence event. Polypropylene inflow and outflow valves (SmartProducts, Incorporated, 302 series) maintained one-way chamber air flow, and an oxygen analyzer (Yellow Springs Instruments, Model 550A) continuously monitored chamber oxygen levels during each trial. A reducer between the aerial and aquatic chambers decreased the internal respirometer diameter by two-thirds, thereby minimizing the surface area for gas exchange between chambers while still providing adequate space for each krait to emerge its head.

Bimodal Respirometry Trials

The evening prior to each trial, kraits were placed in the respirometer with the aerial chamber opened to the atmosphere, and left overnight to habituate at 27.6°C (Hare et al., 2004). During this time, water flow rate through the aquatic chamber was adjusted to achieve an oxygen concentration difference of 10–15% between inflow and outflow water (Steffensen, 1989; Cech, 1990). The following

morning between 0800 h and 0900 h local time, the experimental trial was started by flushing and sealing the aerial chamber. To avoid confounding directional effects, metabolic rates of one-half of the study animals were determined first at 27.6 (± 0.08)°C and again following an acute temperature increase to 35.2 (± 0.14)°C. Remaining kraits were subjected to the reciprocal temperature protocol. Temperature changes in the respirometer were made over the course of 60 min, after which kraits remained at the new temperature for an additional 45 min prior to metabolic rate determinations—a time sufficient to assure that water and body temperatures had reached equilibrium. A blank respirometry trial (identical in all respects but without the krait) was run prior to the first krait trial, and following every third animal thereafter (i.e., six blank runs). The mean metabolic rate taken from blank trials was used to account for planktonic and bacterial metabolism taking place in the water.

Two observers continuously monitored the krait and recorded behavior as well as emersion times during trials. In addition, krait ventilatory efforts were evaluated with the use of a 0.6-L water-seal spirometer (Fig. 1). Breathing frequency (as breaths per minute, bpm) was easily documented, but the spirometer lacked the necessary precision to ascertain reliable tidal volume measures. Nevertheless, observers could accurately identify relative depth of breathing and the frequency patterns. Kraits were allowed to rebreathe chamber air until saturation levels approached 80%. At the next submergence event, oxygen levels were restored by flushing air through the aerial chamber (Graham, 1974). Oxygen consumed (mL) during each breathing event was calculated using the following equation:

Pulmonary oxygen consumption (mL) =

$$(F_iO_2 - F_fO_2) \times V \times 208.7,$$

where F_iO_2 is the initial fractional oxygen concentration at the beginning of a breathing event, F_fO_2 is the final fractional oxygen concentration at the end of a breathing event, V is the aerial chamber volume (mL), and 208.7 is the oxygen concentration in air (mL/L). Total pulmonary oxygen uptake (mL/min)

was then calculated as the sum of the individual consumption values divided by the total trial time in minutes.

Cutaneous oxygen exchange (mL/min) was estimated from simultaneous inflow and outflow water samples from the aquatic chamber collected at 35-min intervals ($n = 5$ at each temperature treatment) in 300-mL Biological Oxygen Demand bottles. Dissolved oxygen values (± 0.005 mL/L) were then determined with the use of standard Winkler titration methods (Cox, 1990), and krait oxygen consumption rate across the skin was calculated from the following equation (Cech, 1990):

cutaneous oxygen uptake (mL/min) =

$$(O_{2i} - O_{2f}) \times \dot{V}_w,$$

where O_{2i} is oxygen concentration of inflow water (mL/L), O_{2f} is oxygen concentration of outflow water (mL/L), and \dot{V}_w is the water flow rate through the respirometer (L/min). The treatment-appropriate blank value was subtracted from the total cutaneous oxygen uptake for each krait to remove any metabolic contributions from bacteria or plankton.

Total oxygen consumption for each krait at high and low treatment temperatures was calculated as the sum of the pulmonary and cutaneous oxygen uptake values. Relative percentage of oxygen taken up across the skin was then calculated as the quotient of cutaneous and total oxygen consumption. Andrews and Pough (1985) found high variability among mass exponents relating metabolic rate to snake mass, and concluded that a common mass exponent cannot be assumed for intraspecific comparisons. Therefore exponent-based adjustments were not made, and we report oxygen consumption values as weight specific values ($\text{mL Kg}^{-1} \text{h}^{-1}$) after Heatwole and Seymour (1975, 1978) and Heatwole (1999).

Temperature coefficients (Q_{10}) were estimated with the use of the equation (Withers, 1977; Schmidt-Nielsen, 1997)

$$Q_{10} = (K_2 \div K_1)^{10/(T_2 - T_1)},$$

where Q_{10} is the temperature coefficient, and K_2 and K_1 are mean metabolic rates at temperatures T_2 (35.2°C) and T_1 (27.6°C), respectively. Following each trial, krait mass (± 0.1 g), standard snout-vent length (± 0.1 cm),

and sex were determined. The respirometer was then disassembled, washed with antibacterial soap, thoroughly rinsed, and left to air dry (Steffensen, 1989; Cech, 1990).

Statistical Analyses

Paired *t*-test analysis was used to compare differences between temperature treatments for cutaneous, pulmonary, and total oxygen consumption rates, percentage cutaneous oxygen uptake, as well as average ventilation rate and time emerged. Statistical decisions were based on *t*-test comparisons adjusted for multiplicity using the Bonferroni correction (adjusted *P* value = 0.008). Values are reported as mean \pm standard error.

RESULTS

Yellow-lipped Sea Kraits remained largely quiescent during resting metabolic rate determinations, spending approximately 35% of the trial time with their head completely or partially emerged, often with only the nares exposed. Kraits in eight of the trials exhibited no movement other than to break the water surface to breathe. In remaining trials, krait activity accounted for only 0.2% of the total trial time. Short intervals of limited activity are not considered to violate resting metabolic rate conditions (Zaidan, 2003; Dorcas et al., 2004); therefore no adjustments were made for activity. Average emergent times were 154.0 ± 6.23 and 156.0 ± 5.78 min at 27.6 and 35.2°C, respectively, and were not statistically different (paired, one-tailed *t*-test; $t_{14} = -0.22$; $P = 0.83$). Ventilatory patterns of emerged sea kraits were typified by a single larger breath followed by one to three smaller exchanges, a pattern similar to that described by Heatwole (1999). Respective average ventilation rates of sea kraits at 27.6 and 35.2°C were 1.0 ± 0.12 and 1.4 ± 0.15 bpm. Ventilation rates were also statistically indistinguishable between temperature treatments (paired, two-tailed *t*-test; $t_{14} = -2.22$; $P = 0.09$).

Oxygen uptake across pulmonary and cutaneous surfaces was markedly influenced by temperature (Table 1). A paired, one-tailed *t*-test revealed a significant increase in total metabolic demand between 27.6 and 35.2°C ($t_{14} = 7.67$; $P < 0.0001$). A similar response

TABLE 1.—Cutaneous, pulmonary, and total oxygen uptake values (mean \pm SE) for 15 Yellow-lipped Sea Kraits, *Laticauda colubrina*, acclimated at $27.6 \pm 0.08^\circ\text{C}$ and acutely exposed to $35.2 \pm 0.14^\circ\text{C}$. Metabolic values in each category differed significantly between temperature treatments ($P < 0.0001$). Temperature coefficient (Q_{10}) values were calculated for all metabolic categories from mean metabolic values measured at low and high temperatures.

Type	Temperature ($^\circ\text{C}$)	Total oxygen uptake (mL $\text{Kg}^{-1} \text{h}^{-1}$)	Q_{10}
Cutaneous	27.6	4.56 (± 0.58)	
	35.2	10.57 (± 1.10)	3.13
Pulmonary	27.6	44.58 (± 15.36)	
	35.2	104.70 (± 21.85)	2.99
Total	27.6	49.14 (± 15.65)	
	35.2	115.27 (± 22.06)	3.07

was seen in both cutaneous uptake across the skin ($t_{14} = 6.89$; $P < 0.0001$), as well as pulmonary oxygen uptake across lung surfaces ($t_{14} = 7.01$; $P < 0.0001$). Pulmonary and cutaneous uptake exhibited relatively high levels of temperature sensitivity, with Q_{10} values for pulmonary, cutaneous, and total oxygen uptake all approximately equal to 3 (Table 1), i.e., metabolic demand could be expected to triple with each 10°C increase in ambient temperature.

Yellow-lipped Sea Krait pulmonary oxygen uptake was an order of magnitude higher than respiration across cutaneous surfaces (Table 1). Interestingly, the relative percentages of oxygen absorbed across skin surfaces showed no significant change (paired, one-tailed t -test; $t_{14} = 1.76$; $P = 0.100$) even as oxygen tensions decreased with increasing water temperature. Therefore, percentage oxygen uptake values from temperature treatments were pooled, for a cutaneous oxygen uptake value of $13.5 \pm 1.67\%$ (Fig. 2).

DISCUSSION

Sea krait bioenergetics are not well studied, with work limited in both the type of data collected, as well as the number of species tested. Total resting metabolic rates have not been empirically quantified for any sea krait species, and oxygen uptake across cutaneous surfaces alone has been empirically measured for only two species. Heatwole and Seymour (1978) reported cutaneous uptake of 7.4 and 7.0 mL $\text{Kg}^{-1} \text{h}^{-1}$ for Yellow-lipped and

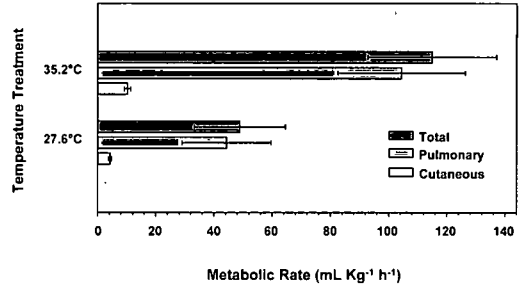


FIG. 2.—Mean total resting metabolic rate (oxygen uptake) of the sea krait, *Laticauda colubrina*, measured at two temperatures and partitioned into pulmonary and cutaneous oxygen uptake components. Error bars represent \pm one standard error.

Blue-lipped Sea Kraits, respectively, at temperatures ranging from 22.5 – 27.5°C . Our cutaneous uptake rate at 27.6°C was somewhat lower ($4.56 \text{ mL } \text{Kg}^{-1} \text{h}^{-1}$), perhaps because of methodological differences between studies. In our study kraits were habituated overnight which has been demonstrated to result in lower metabolic rates (Hare et al., 2004), and the respirometer design also discouraged excessive movement. Kraits showed no obvious signs of stress during trials and exhibited consistent behavioral and breathing patterns. Yellow-lipped Kraits in the Heatwole and Seymour (1978) experiments experienced greater temperature variability, were not habituated to the respirometer, or allowed access to air, factors that may have resulted in higher activity levels and metabolic rates.

Relative cutaneous uptake values for kraits (and several sea snakes) have been historically derived with the use of total metabolic rates interpolated from a terrestrial snake regression (Bennett and Dawson, 1976). Feder and Burggren (1985) estimate that cutaneous uptake accounts for 13 and 12% of the total oxygen demand of Yellow-lipped and Blue-lipped Sea Kraits, respectively. Our empirical data, showing Yellow-lipped Kraits pick up an average 13.5% of their total oxygen demand across skin surfaces (Fig. 2), are in good agreement with this estimate. The same fidelity is not, however, apparent for true sea snakes (subfamily Hydrophiinae). The Bennett and Dawson (1976) regression produces cutaneous uptake percentages between 29 and 34% (Feder and Burggren, 1985), a range strikingly higher than the 5–22%

derived from empirical sea snake data (Heatwole and Seymour, 1975). Reasons for the disparity are not immediately clear, but it appears that indirect calculations are a better predictor of total metabolic rates for the more terrestrial sea kraits than for the true sea snakes.

The lack of sea krait data, along with potentially confounding regression-derived values, have contributed to a general perception that kraits are less effective at extracting oxygen across their skin surfaces than true sea snakes. It is reported, for example, that the Yellow-bellied Seasnake, *Pelamis platurus*, picks up 33% of its oxygen demand across skin surfaces (Feder and Burggren, 1985; Schmidt-Nielsen, 1997). The cited value, however, is true for only one small specimen (22.0 cm; 7.0 g) from the study group. The relative cutaneous uptake contribution for all snakes in the study varied with surface area, and ranged from 12 to 33%, with a less extreme mean value near 20% (Graham, 1974; Heatwole, 1999). Furthermore, the mean percentage cutaneous uptake for Yellow-lipped Sea Kraits in our study is well within the 5–22% range of the eight sea snake species for which data exist (see Graham, 1974; Heatwole and Seymour, 1975; Heatwole, 1999). The comparison suggests kraits and sea snakes may have cutaneous respiratory attributes that are more similar than generally believed.

In addition to sea snakes and sea kraits, bimodal respiration is used by many semiaquatic reptiles to extend active foraging dive times. Several semiaquatic snakes exhibit significant oxygen uptake across cutaneous surfaces (Winne et al., 2001; Gibbons and Dorcas, 2004), and some turtle species are known to respire across skin and cloacal surfaces (Stone et al., 1992; Gordos and Franklin, 2002; Gordos et al., 2007). The ability of active sea kraits to remain submerged for extensive periods can be attributed to several key adaptations, including oxygen storage in the saccular lung (Graham, 1974; Heatwole, 1981) and cutaneous respiration (Heatwole and Seymour, 1978). Alterations in circulation (Heatwole, 1999) and increased hematocrit levels (Brischoux et al., 2011) have also been implicated as possible diving adaptations. It can be argued that metabolic thermal sensitivity is likewise an important adaptation enhancing diving performance of sea kraits. In effect, the high temperature coefficient allows sea kraits to

optimize physiological interactions by taking advantage of the thermal differential that exists between terrestrial and reef environments.

For many ectotherms, including reptiles, behavioral thermoregulation has been shown to optimize physiological performance. Although optimal temperatures for many functions fall within a relatively narrow range of selected body temperatures (Dawson, 1975; Huey, 1982; Stevenson et al., 1985), others do not, suggesting that differing thermosensitivity between interacting processes may benefit ectotherms (Huey, 1982; Di Santo and Bennett, 2011). For example, differing thermal sensitivities between assimilation and gut passage rates likely improve overall digestive efficiency in the Rubber Boa, *Charina bottae* (Dorcas et al., 1997), and the Common Green Iguana, *Iguana iguana* (van Marken Lichtenbelt et al., 1997). A high resting metabolic Q_{10} value may minimize time on land by increasing sea krait digestion and nutrient absorption rates as well as promoting faster healing and recovery from injury. Returning to cooler reef temperatures would, in turn, decrease terrestrial metabolic rates by two-thirds, promoting longer dive times and increased foraging times, and reducing predator exposure by shortening surface intervals (Punay, 1975; Lading et al., 1991; Brischoux et al., 2011). Low-temperature metabolic responses similar to those seen in sea kraits may be a widespread adaptation to a diverse set of environmental conditions. Some reptiles, for example, conserve energy by selecting cooler daily temperatures (Regal, 1966; Christian et al., 1984), whereas others lower metabolic rates to survive winter conditions (Rollinson et al., 2008; Reyes and Milsom, 2009). In this regard tropical kraits share some interesting similarities with cold-adapted temperate reptile species.

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LITERATURE CITED

- Andrews, R.M., and F.H. Pough. 1985. Metabolism of squamate reptiles: Allometric and ecological relationships. *Physiological Zoology* 58:214–231.

- Angilletta, M.J., Jr, and M.W. Sears. 2000. The metabolic cost of reproduction in an oviparous lizard. *Functional Ecology* 14:39–45.
- Bennett, A.F., and W.R. Dawson. 1976. Metabolism. Pp. 127–224 in C. Gans and W.R. Dawson (Eds.), *Biology of the Reptilia*, Volume 5. Physiology A. Academic Press, USA.
- Bonnet, X., F. Brisichoux, D. Pearson, and P. Rivalan. 2009. Beach rock as a keystone habitat for amphibious sea snakes. *Environmental Conservation* 36:62–70.
- Brisichoux, F., X. Bonnet, T.R. Cook, and R. Shine. 2007. Snakes at sea: Diving performances of free-ranging sea kraits. Pp. 5–20 in Proceedings of the 11th Annual Meeting on Health, Science and Technology. Tours University, France.
- Brisichoux, F., X. Bonnet, and R. Shine. 2009. Kleptothermy: An additional category of thermoregulation, and a possible example in sea kraits (*Laticauda laticaudata*, Serpentes). *Biology Letters* 5:729–731.
- Brisichoux, F., G.E.A. Gartner, T. Garland, Jr, and X. Bonnet. 2011. Is aquatic life correlated with an increased hematocrit in snakes? *PLoS ONE* 6:e17077. <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0017077>.
- Cech, J.J. 1990. Respirometry. Pp. 335–356 in C.B. Schreck and P.B. Moyle (Eds.), *Methods for Fish Biology*. American Fisheries Society, USA.
- Christian, K.A., C.R. Tracy, and W.P. Porter. 1984. Physiological and ecological consequences of sleeping-site selection by the Galapagos Land Iguana *Conolophus pallidus*. *Ecology* 65:752–758.
- Cox, G.W. 1990. *Laboratory Manual of General Ecology*, 6th ed. William C. Brown Publishers, USA.
- Dawson, R. 1975. On the physiological significance of the preferred body temperatures of reptiles. Pp. 443–473 in D.M. Gates and R.B. Schmerl (Eds.), *Perspectives of Biophysical Ecology*, Ecological Studies, Volume 12. Springer-Verlag, USA.
- Di Santo, V., and W.A. Bennett. 2011. Is post-feeding thermotaxis advantageous in elasmobranch fishes? *Journal of Fish Biology* 78:195–207.
- Dorcas, M.E., C.R. Peterson, and M.E.T. Flint. 1997. The thermal biology of digestion in Rubber Boas (*Charina bottae*): Physiology, behavior, and environmental constraints. *Physiological Zoology* 70:292–300.
- Dorcas, M.E., W.A. Hopkins, and J.H. Roe. 2004. Effects of body mass and temperature on standard metabolic rate in the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*). *Copeia* 2004:145–151.
- Eme, J., and W.A. Bennett. 2009. Critical thermal tolerance polygons of tropical marine fishes from Sulawesi, Indonesia. *Journal of Thermal Biology* 34:220–225.
- Feder, M.E., and W.W. Burggren. 1985. Cutaneous gas exchange in vertebrates: Design, patterns, control and implications. *Biological Reviews* 60:1–45.
- Gibbons, J.W., and M.E. Dorcas. 2004. *North American Watersnakes: A Natural History*. University of Oklahoma Press, USA.
- Gordos, M., and C.E. Franklin. 2002. Diving behaviour of two Australian bimodally respiring turtles, *Rheodytes leukops* and *Emydura macquarii*, in a natural setting. *Journal of Zoology* 258:335–342.
- Gordos, M.A., M. Hamann, C.S. Schauble, C.J. Limpus, and C.E. Franklin. 2007. Diving behaviour of *Elseya albagula* from a naturally flowing and hydrologically altered habitat. *Journal of Zoology* 272:458–469.
- Graham, J.B. 1974. Aquatic respiration in the sea snake *Pelamis platurus*. *Respiration Physiology* 21:1–7.
- Hare, K.M., S. Pledger, M.B. Thompson, J.H. Miller, and C.H. Daugherty. 2004. Conditioning reduces metabolic rate and time to steady-state in the lizard *Naultinus manukanus* (Reptilia: Gekkonidae). *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 139:245–250.
- Heatwole, H. 1981. Role of the sacculus lung in the diving of the sea krait, *Laticauda colubrina* (Serpentes: Laticaudidae). *Australian Journal of Herpetology* 1:11–16.
- Heatwole, H. 1999. *Sea Snakes*, 2nd ed. Krieger, USA.
- Heatwole, H., and R. Seymour. 1975. Pulmonary and cutaneous oxygen uptake in sea snakes and a file snake. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 51:399–405.
- Heatwole, H., and R.S. Seymour. 1978. Cutaneous oxygen uptake in three groups of aquatic snakes. *Australian Journal of Zoology* 26:481–486.
- Heatwole, H., S. Busack, and H. Cogger. 2005. Geographic variation in sea kraits of the *Laticauda colubrina* complex (Serpentes: Elapidae: Hydrophiinae: Laticaudini). *Herpetological Monographs* 19:1–136.
- Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25–91 in C. Gans and F.H. Pough (Eds.), *Biology of the Reptilia*, Volume 12. Academic Press, USA.
- Khari, V.E., and V.P. Czeblukov. 2006. A new revision of sea kraits of family Laticaudidae Cope, 1879 (Serpentes: Colubroidea). *Russian Journal of Herpetology* 13:227–241.
- Lading, E.A., R.B. Stuebing, and H.K. Voris. 1991. A population size estimate of the Yellow-lipped Sea Krait, *Laticauda colubrina*, on Kalamunian Damit Island, Sabah, Malaysia. *Copeia* 1991:1139–1142.
- Lefevre, S., D.T.T. Huong, T. Wang, N.T. Phuong, and M. Bayley. 2011. Hypoxia tolerance and partitioning of bimodal respiration in the Striped Catfish (*Pangasianodon hypophthalmus*). *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 158:207–214.
- McCoy, M. 2006. *Reptiles of the Solomon Islands*. Pensoft Publishers, Bulgaria.
- Pough, F.H., and H.B. Lillywhite. 1984. Blood volume and blood oxygen capacity of sea snakes. *Physiological Zoology* 57:32–39.
- Punay, E.Y. 1975. Commercial sea snake fisheries in the Philippines. Pp. 489–502 in W.A. Dunson (Ed.), *The Biology of Sea Snakes*. University Park Press, USA.
- Pyron, R.A., F.T. Burbrink, G.R. Colli, A.N. Montes de Oca, L.J. Vitt, C.A. Kuczynski, and J.J. Wiens. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution* 58:329–342.
- Regal, P.J. 1966. Thermophilic response following feeding in certain reptiles. *Copeia* 1966:588–590.
- Reyes, C., and W.K. Milsom. 2009. Daily and seasonal rhythms in the respiratory sensitivity of Red-eared

- Sliders (*Trachemys scripta elegans*). *Journal of Experimental Biology* 212:3339–3348.
- Rollinson, N., G.J. Tattersall, and R.J. Brooks. 2008. Overwintering habitats of a northern population of Painted Turtles (*Chrysemys picta*): Winter temperature selection and dissolved oxygen concentrations. *Journal of Herpetology* 42:312–321.
- Saint Girons, H. 1964. Notes sur l'ecologie et la structure des populations des laticaudinae (Serpents, Hydrophidae) en Nouvelle Calédonie. *La Terre et la Vie* 3:185–214.
- Schmidt-Nielsen, K. 1997. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, UK.
- Shetty, S., and A. Sivasundar. 1998. Using passive integrated transponders to study the ecology of the *Laticauda colubrina*. *Hamadryad* 23:71–76.
- Shetty, S., and R. Shine. 2002a. Activity patterns of Yellow-lipped Sea Kraits (*Laticauda colubrina*) on a Fijian Island. *Copeia* 2002:77–85.
- Shetty, S., and R. Shine. 2002b. The mating system of Yellow-lipped Sea Kraits (*Laticauda colubrina*: Laticaudidae). *Herpetologica* 58:170–180.
- Steffensen, J.F. 1989. Some errors in respirometry of aquatic breathers: How to avoid and correct for them. *Fish Physiology and Biochemistry* 6:49–59.
- Stevens, E.D. 1992. Use of plastic materials in oxygen-measuring systems. *Journal of Applied Physiology* 72: 801–804.
- Stevenson, R.D., C.R. Peterson, and J.S. Tsuji. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the Wandering Garter Snake. *Physiological Zoology* 58:46–57.
- Stone, P.A., J.L. Dobie, and R.P. Henry. 1992. The effect of aquatic O₂ levels on diving and ventilatory behavior in Soft-shelled (*Trionyx spiniferus*), Stinkpot (*Sternotherus odoratus*), and Mud Turtles (*Kinosternon subrubrum*). *Physiological Zoology* 65:331–345.
- van Marken Lichtenbelt, W.D., J.T. Vogel, and R.A. Wesselingh. 1997. Energetic consequences of field body temperatures in the Green Iguana. *Ecology* 78:297–307.
- Winne, C.T., T.J. Ryan, Y. Leiden, and M.E. Dorcas. 2001. Evaporative water loss in two natricine snakes, *Nerodia fasciata* and *Seminatrix pygaea*. *Journal of Herpetology* 35:129–133.
- Withers, P.C. 1977. Measurement of VO₂ and VCO₂, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* 42:120–123.
- Zaidan, F., III. 2003. Variation in Cottonmouth (*Agkistrodon piscivorus leucostoma*) resting metabolic rates. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 134:511–523.

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