

Foraging behaviour and energy budgets of sea snakes: insights from implanted data loggers

T. R. Cook^{1,2}, X. Bonnet³, T. Fauvel³, R. Shine⁴ & F. Brischoux³

1 Institute of Ecology and Environmental Sciences, Evolutionary Ecophysiology Team, University Pierre et Marie Curie, Paris, France

2 Percy FitzPatrick Institute, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

3 Centre d'Études Biologiques de Chizé, UMR 7372 CNRS-ULR, Villiers-en-Bois, France

4 School of Biological Sciences, University of Sydney, Sydney, NSW, Australia

Keywords

sea snakes; foraging behaviour; diving behaviour; ectothermy; energetics; top predators; coral reefs; bio-logging.

Correspondence

Timothee Cook, Institute of Ecology and Environmental Sciences (IEES-Paris), Evolutionary Ecophysiology Team, University Pierre et Marie Curie, Bâtiment A-7ème étage, 7 quai St Bernard, 75005 Paris, France.

Email: timothee.cook@gmail.com

Editor: Mark-Oliver Rödel

Received 27 May 2015; revised 3 July 2015; accepted 8 July 2015

doi:10.1111/jzo.12286

Abstract

Information on the foraging behaviour of sea snakes has the potential to clarify adaptive pathways involved in the evolutionary invasion of marine habitats by terrestrial vertebrates. However, logistical obstacles have precluded studies in this field. To obtain preliminary data of diving behaviour, we surgically implanted temperature-depth loggers into two sympatric, amphibious, benthic foraging sea krait species from New Caledonia. Based on logger recovery from three snakes (1 *Laticauda laticaudata* and 2 *L. saintgironsi*), we obtained data on a total of 1850 dives carried out over eight foraging trips and 39.6 days at sea. Almost 99% of dives were <30 m deep. Average dive depth was 10.7 ± 7.0 m, but snakes dived as deep as 82.6 m. Maximum dive duration was ≥ 123.7 min. At sea, snakes dived continuously, with over 90% of surface recovery periods lasting less than 3 min in *L. saintgironsi* ($n = 1$). Periods at the surface (between successive dives) were longer at night than by day, plausibly reflecting more intense hunting activity by the snake. Locomotor speed, as measured by the rate of vertical descent or ascent during diving, was low (0.15 m s^{-1}). In combination with other data on these species, we estimate that metabolic expenditure was about 10 times greater while the snakes were at sea than on land; and their overall field metabolic rate ($70\text{--}145 \text{ kJ kg}^{-1} \text{ day}^{-1}$) was an order of magnitude less than has been reported for diving endotherms. Despite low sample sizes, our study shows that implanted data loggers can provide novel insights into sea snake biology. Our data emphasize the behavioural and ecological consequences of ectothermy for secondary marine vertebrates. In particular, they illustrate how ectothermy allows species to thrive on rates of energy intake vastly lower than are required for their endothermic competitors.

Introduction

Sea snakes are the largest group of marine reptiles. Most of the approximately 200 species (Murphy, 2012) are 'true' sea snakes (Hydrophiinae), fully marine viviparous reptiles that never leave the ocean (Heatwole, 1999). A second, older phylogenetic lineage consists of oviparous sea kraits (Laticaudinae), which divide their time more or less equally between foraging at sea and resting on land, where they digest prey, slough, mate and lay eggs (Heatwole, 1999). Other transitions from terrestrial to aquatic life are seen in smaller groups (e.g. Homalopsidae, Acrochordidae) and even in occasional species within other lineages (e.g. Elapidae, Natricidae; see Murphy, 2012). The repeated independent colonization of marine habitats provides exceptional opportunities for comparative studies, to clarify the processes involved in a major

phylogenetic transition in habitat types (e.g. Shine & Shetty, 2001; Brischoux *et al.*, 2012).

Foraging behaviour lies at the heart of this transition. All of the secondary marine snakes forage in the ocean, with terrestrial habitats used for other functions. Thus, the exploitation of underwater foraging niches has been an important (although not unique) driver of the transitions from terrestrial to marine life (Vermeij & Dudley, 2000; Lillywhite, Sheehy & Zaidan, 2008). From a management perspective, knowledge of foraging behaviour may help us to understand the reasons for decline of wild populations of sea snakes and what habitats are critical for maintaining viable populations (e.g. Goiran & Shine, 2013; Lukoschek *et al.*, 2013; Nguyen *et al.*, 2014). Available data on foraging behaviour in sea snakes derives from observations made from boats or underwater (Dunson, 1975; Heatwole, 1975). Such data provide important

information on hunting behaviour, but sample sizes are limited by logistical constraints, snake behaviour potentially is influenced by diver presence, and many factors influence observability. Bio-logging (the use of electronic tags for recording behaviour in free-ranging animals: Ropert-Coudert & Wilson, 2005) offers the potential for cost-effective detailed documentation of snake behaviour over long periods that can complement data collected by hand. Although bio-logging has been used repeatedly to study diving behaviour in marine birds, mammals and turtles (Ropert-Coudert *et al.*, 2009), it has only been used once for this purpose in a free-ranging sea snake species, in the pioneering work by Rubinoff, Graham & Motta (1986, 1988) on the yellow-bellied sea snake *Pelamis platurus* (see recent review by Cook & Brischoux, 2014).

In the present study, we use bio-logging to investigate the foraging behaviour of free-ranging sea kraits (*Laticauda* spp.). Sea kraits are restricted to coral reef ecosystems of the tropical Eastern Indian and Western Pacific oceans, where they forage on benthic prey (anguilliform fish: Reed *et al.*, 2002, Ineich *et al.*, 2007). The snakes alternate bouts of foraging at sea with bouts on land, when they digest, slough, drink freshwater, breed (Heatwole, 1999; Shetty & Shine, 2002; Bonnet, 2012) and are safe from marine predators. In New Caledonia, two species live in sympatry on small islets, which are distributed across the lagoon: *Laticauda laticaudata* (the blue sea krait) and *L. saintgironsi* (the yellow sea krait: Saint Girons, 1964). Dietary studies on snakes reveal that *L. laticaudata* feeds primarily on anguilliform species living on soft-bottom habitats, whereas *L. saintgironsi* prefers anguilliform species found on hard-bottom habitats (Brischoux, Bonnet & Shine, 2007a; Brischoux *et al.*, 2011a). We deployed temperature-depth recorders on adult individuals of both species in 2006 (see Brischoux *et al.*, 2007b) and in 2010. Despite the small sample size of individuals equipped and recovered ($n = 3$), the data are extensive for each of those three individuals. Hence, we can conduct a preliminary exploration of sea krait diving behaviour and time budgets, and thus energy budgets.

Materials and methods

Data collection

Fieldwork was conducted in 2005–2006 and 2009–2010 on Signal islet (22°17'46" S, 166°17'35" E), located in the lagoon off the main island (Grand Terre) of New Caledonia. Snakes were captured by hand on the beach, when they were commuting to and from the sea. Six sea kraits (three *L. laticaudata* and two *L. saintgironsi* in 2006 and one *L. saintgironsi* in 2010) were equipped with a temperature-depth recorder together with a radio-transmitter (see Table 1 for data on snakes and tags used). Overall, combined mass of both tags represented 2–5% of snake body mass, below the recommended maximum level (Kenward, 1987).

Devices were implanted intraperitoneally following Reinert & Cundall (1982). Surgery was performed in a sterile environment after anaesthetizing snakes with isoflurane (Abbott Laboratories, Abbott Park, IL, USA). The incision was made just posterior to the stomach, and on the left side to avoid the

Table 1 *Laticauda* spp. Morphology and tag characteristics of *Laticauda* sea kraits that undertook foraging trips from Signal Islet, New Caledonia

	<i>laticaudata</i>	<i>saintgironsi</i>	<i>saintgironsi</i>
Snake ID	1428	1680	2177
Year	2006	2006	2010
Sex	Female	Female	Female
Snout-vent length (cm)	110	105	91
Total length (cm)	120	114	100
Body mass (g)	350	390	247
VHF-t	SI-2	SI-2	SI-2
Length (cm)	3.3	3.3	3.3
Diameter (cm)	1.1	1.1	1.1
Mass (g)	9	9	9
TDR	LTD-1110	LTD-1110	G5
Length (cm)	3.2	3.2	3.1
Diameter (cm)	1.1	1.1	0.8
Mass (g)	2	2	2.7
D resolution (m)	±1	±1	±0.1
T resolution (°C)	±0.1	±0.1	±0.05
D sampling interval (s)	450	225 450	5
T sampling interval (s)	450	225 450	60

Snakes were equipped with a temperature-depth recorder (TDR) together with a radio-transmitter (VHF-t). TDR models were LTD-1110 (Lotek Wireless Inc., New Market, ON, Canada) and G5 (Cefas Technology Ltd., Lowestoft, UK). VHF-t models were SI-2 (Holohil Systems Ltd., Carp, ON, Canada).

D, depth; T, temperature.

major midventral vein and the lung. The radio-transmitter was inserted with whip antenna fitted under the skin towards the tail. The incision was sutured with resorbable thread. Surgery lasted 45 min and snakes recovered < 5 min later. Snakes were then kept in calico bags and released after 48 h of careful monitoring.

Released snakes were tracked daily with a directional antenna and a LAQ12 receiver (AVM Instrument Co., Ltd., Colfax, CA, USA) for 5 weeks and then opportunistically during successive island visits thereafter. Snakes hid under rocks for 31 ± 7 days after release (during which time they sloughed their skins) before going to sea. Four snakes were recaptured 2 to 3 months after release, and the tags were retrieved through surgery. Tag data showed that three of these animals underwent foraging trips, while one snake remained on land for the entire period following post-surgery release. Two snakes were not relocated and therefore not recaptured.

Data analysis

The beginning and end of each trip at sea were detected by sudden shifts in thermal profiles. Diel thermal variation is much greater when the snakes are on land than when they are in the ocean (Brischoux, Bonnet & Shine, 2009a). We defined 'a trip at sea' as a period of such dampened thermal variation that included more than one dive (to eliminate any short non-foraging excursions into the tidal zone, such as those which occur in *L. laticaudata* when it is on land: Bonnet *et al.*, 2009).

Dives were analysed using MultiTrace (Jensen Software Systems, Laboe, Germany). Because of differences in resolution between data loggers (Table 1), the threshold for dive detection was set at 2 m and 0.2 m for snakes followed in 2006 and 2010, respectively. For snakes from 2006, we only calculated the maximum depth reached during each dive because sampling interval of the depth sensor was too long (225 or 450 s) to enable accurate estimation of other dive parameters (Table 1). In 2010, however, sampling interval was short (5 s) and we therefore calculated several dive parameters for the snake studied that year.

For every dive, we calculated maximum dive depth, dive duration and post-dive interval (the period spent on the surface between the end of one dive and the onset of the next). Descent duration and descent rate (m s^{-1}) were calculated between the surface and the beginning of the time that the snake spent moving along the lagoon bottom. Ascent duration and ascent rate (m s^{-1}) were calculated between the end of this substrate-based phase and the return to the surface. We defined the substrate phase as starting and ending when the vertical transit rate of the snake was $>0 \text{ m s}^{-1}$.

Dives were visually categorized according to their dive shape in MultiTrace. They were sorted into flat-bottomed dives and other-shaped dives (U- or V-shaped), categories commonly used in studies on other air-breathing vertebrates (Cook *et al.*, 2012). The perception of a dive's shape may vary according to the time scale at which it is observed. Thus, shape was determined with the visualization window of MultiTrace showing 2 h and with depth scale set to display 0–25 m, except for dives $<10 \text{ m}$, where the range of display was 0–10 m. We also examined the extent to which snakes returned to the same maximum depth during consecutive dives. Consecutive dives that returned to the same depth zone were called intra-depth zone dives (Tremblay & Cherel, 2000). Depth zone was defined as the maximum depth of the current dive $\pm 10\%$ of the maximum depth reached during the preceding dive.

For all snakes, we calculated (with MultiTrace) the mean snake temperature recorded during each dive. Due to their small size and elongate morphology (high surface area relative to volume), we assumed that the resistance of snakes to temperature change (thermal inertia) was low and the heat generated by muscular activity was negligible. Thus, intraperitoneal temperature serves as a good proxy for ambient sea water temperature.

Statistics

Statistics were only calculated on data from the one snake studied in 2010 (snake 2177) because it was the only individual for which we could calculate detailed dive parameters, due to logger sampling frequency (Table 1). Using simple polynomial and exponential regressions, we studied the influence of maximum dive depth on snake temperature and dive duration, and the influence of dive duration on post-dive interval. For the latter, we excluded all post-dive intervals $>3.3 \text{ min}$ (8% of post-dive intervals). This threshold was based on an abrupt break in the distribution of post-dive intervals around this value. Prolonged periods at the ocean surface (up to 2.3 h)

were likely not related to post-dive recovery and pre-dive preparation of aerobic dives, but to other activities (Tremblay, Cook & Cherel, 2005). However, the exact nature of these activities is not clear. Data are graphically presented as means \pm standard deviation per class, but all regressions were fitted on the raw data. In the text, results are reported as mean \pm standard deviation.

Results

Activity budgets

Between release and recapture, all three snakes alternated trips at sea with bouts on land (Fig. 1). During this period, they carried out 1 to 5 trips at sea. Mean trip length was 3.3 ± 2.1 days (range: 0.6–6.0 days) in *L. laticaudata* and 6.6 ± 3.6 days (range: 2.0–10.2 days) in *L. saintgironsi* (Table 2). Phases on land between foraging trips lasted 12.6 ± 15.1 days (range: 0.7–33.9 days) in *L. laticaudata* and 5.4 ± 2.3 days (range: 3.0–7.8 days) in *L. saintgironsi*.

Aquatic thermal environment

On land, mean snake temperature was $29.3 \pm 1.1^\circ\text{C}$ and $27.4 \pm 1.5^\circ\text{C}$ in *L. laticaudata* and *L. saintgironsi*, respectively. At-sea mean snake temperature was $26.2 \pm 0.5^\circ\text{C}$ and $28.9 \pm 0.9^\circ\text{C}$ in *L. saintgironsi* and *L. laticaudata*, respectively. Temperatures of snakes at sea were less variable than on land (Fig. 1). At sea, temperatures ranged between 25 and 28°C in the two *L. saintgironsi*, but were higher ($27\text{--}31^\circ\text{C}$) in the one *L. laticaudata* (Fig. 2). On some days, snake diving activity had a strong thermal effect (Fig. 1c, Fig. 3). On other days, temperature showed only minor variation (amplitude $\approx 0.5^\circ\text{C}$). Thus, snake temperature varied at a range of temporal scales. In snake 2177 for example, temperature remained within a 3°C range over 10 days (trip), 0.5°C over 12 h (diurnal oscillation) and 1°C over $\approx 10 \text{ min}$ (within a single dive).

Diving behaviour: dive depth, duration and recovery

While at sea, snakes dived continuously (Fig. 1). Dive depth ranged between 0.3 and 82.6 m (Figs. 1, 2, Table 2), but 98.8% of dives were $<30 \text{ m}$ deep. Average maximum dive depth was $10.7 \pm 7.0 \text{ m}$ ($n = 1850$).

L. saintgironsi (snake 1680) dived up to 82.6 m. The long dive duration associated with this dive (123.7 min) could be an artefact of combining successive dives, if the sampling rate of the logger was too low to capture brief periods at the surface. Based on a mean vertical transit rate of $0.1\text{--}0.2 \text{ m s}^{-1}$ (Table 3), however, it appears unlikely that the logger would have failed to sample snake ascent or descent between dives in the 80 m depth zone. Furthermore, we did record relatively long dives (to 37.8 min) also in a snake foraging in shallower water, and where records were obtained every 5 s (Tables 1, 2).

At sea, snake 2177 spent 21.2% of its time at sea at the surface, 10.0% in descent, 57.9% at the bottom of the lagoon and 10.9% in ascent. Mean dive depth was $8.4 \pm 4 \text{ m}$ (0.3–22.6 m). Dives lasted on average $9.0 \pm 5.7 \text{ min}$ (0.2–37.8 min)

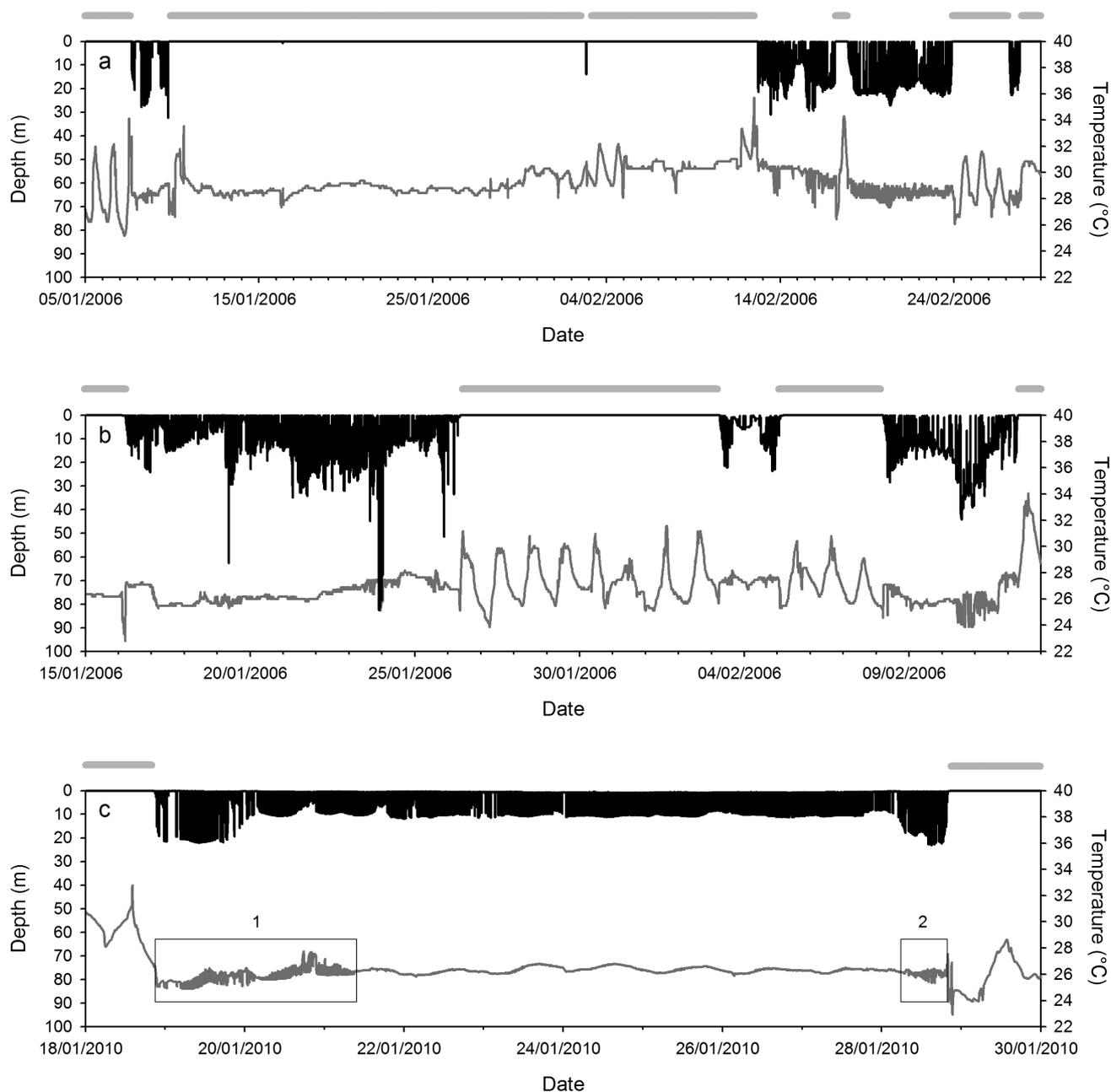


Figure 1 *Laticauda* spp. Time-depth profiles (black lines) and time-temperature profiles (grey lines) recorded by three sea kraits. (a) *L. laticaudata* (snake 1428), (b) *L. saintgironsi* (snake 1680) and (c) *L. saintgironsi* (snake 2177). In snake 2177, rectangles 1 and 2 show when diving activity had an effect on snake temperature. Between rectangles, temperature variation was linked to the effect of the diurnal oscillation. Thick horizontal grey lines above each graph represent periods when the snake is on land. The second trip of snake 1428 lasting 0.1 day (on 2 February 2006) was not considered as a foraging trip as it comprised only one dive.

and mean post-dive interval was 2.4 ± 7.9 min (0.02–140.4 min; Fig. 4). Dive duration increased linearly with maximum dive depth (Fig. 5a). Post-dive interval ≤ 3.3 min increased with dive duration and levelled out at ≈ 1.3 min for dives lasting ≈ 12.5 min (Fig. 5b).

Diving behaviour: dive shape and diurnal cycle

In snake 2177, dives exhibited a variety of shapes: flat-bottomed, U-shaped or V-shaped (Fig. 3). Flat-bottomed

Table 2 *Laticauda* spp. General foraging parameters of three individuals studied on Signal Islet, New Caledonia

	<i>laticaudata</i>	<i>saintgironsi</i>	<i>saintgironsi</i>
Snake ID	1428	1680	2177
Total trips at sea	4	3	1
Min. trip duration (day)	0.6	2.0	–
Max. trip duration (day)	6.0	10.2	–
Mean trip duration (day)	3.3 ± 2.1	5.4 ± 3.5	10
Total dives recorded	162	434	1254
Min. dives per trip	10	24	–
Max. dives per trip	62	351	–
Mean dives per trip	40.2 ± 21.1	144.7 ± 146.6	1254
Min. dive depth (m)	4.4	2.1	0.3
Max. dive depth (m)	32.4	82.6	22.6
Mean dive depth (m)	19.1 ± 5	14.3 ± 10	8.4 ± 4
Min. dive duration (min)	–	–	0.2
Max. dive duration (min)	–	–	37.8
Mean dive duration (min)	–	–	9.0 ± 5.7

Dive durations are not presented in snakes 1428 and 1680 because of high logger sampling interval in these individuals (see Table 1).

dives and other-shaped dives (U- and V-shaped combined) comprised 69.1% and 30.9% of dives, respectively. Dives were sometimes skewed, that is, with the descent slower than the ascent (left-skewed) or the ascent slower than the descent (right-skewed), resulting in asymmetrical dive shapes (Fig. 6). Flat-bottomed dives were predominantly non-skewed (90%), whereas U-shaped dives were mostly right-skewed (52%).

Overall, the dive parameters of snake 2177 depended on dive shape (Table 3, Supporting Information Appendix S1). Flat-bottomed dives were deeper and longer-lasting than other dives, and were followed by longer post-dive intervals, and more prolonged periods of descent, bottom and ascent phases. Vertical transit rates of flat-bottomed dives were faster than in other dives.

Diel timing also affected dive parameters of snake 2177 (Table 3, Fig. 7, Supporting Information Appendix S1, S2 and S3). Dives were deeper and longer during the daytime, whereas post-dive intervals were longer at night. Vertical transit rates of flat-bottomed dives were faster during the day than during the night. Dives that returned to the same depth zone (intra-depth zone dives; see Materials and methods) during the day and the night comprised 89.2 and 73.6%, respectively, of flat-bottomed dives, and 21.1 and 18.1% of other dives (diurnal period: $z = 4.9$, $P < 0.0001$; dive shape: $z = 15.3$, $P < 0.0001$; maximum dive depth: $z = -0.6$, $P = 0.574$; d.f. = 1,1248). Flat-bottomed dives occurred throughout the 24 h cycle, but were more frequent during the daytime (Supporting Information Appendix S2). Other dive types occurred predominantly in the late afternoon and early evening (Supporting Information Appendix S3).

Discussion

Bio-logging in free-ranging sea snakes

Our sample size was small due to the need to first test the bio-logging approach on snakes, but also because of the dif-

iculty of recapturing snakes after release (two snakes were never recaptured). A researcher can never be certain of recapturing a specific snake because sea kraits sometimes move to different islands within the lagoon (Bonnet *et al.*, 2015); and it is not logistically feasible for researchers to stay on islets for weeks on end. Also, equipment failure is a significant risk. Our sample size was further reduced by the fact that one of four snakes remained on land throughout the post-surgery period, possibly as a result of tag implantation. Tag deployment might have also influenced behaviour of snakes which did go to sea. Future studies will be necessary to assess this potential effect, for example, by comparing foraging trip durations between equipped with bio-loggers compared with snakes which are simply marked, as is now routinely done for seabirds (Phillips *et al.*, 2003).

Link between ectothermy and foraging behaviour in *Laticauda* snakes

Both species of *Laticauda* dived almost continuously during their time at sea. In *L. saintgironsi*, vertical transit rates were about tenfold slower ($\approx 0.05\text{--}0.2\text{ m s}^{-1}$) than those of most diving endotherms (e.g. Beck, Bowen & Iverson, 2000; Lovvorn *et al.*, 2004; Watwood *et al.*, 2006; Cook *et al.*, 2010). This 'leisurely' diving behaviour was associated with long dive durations when compared with diving endotherms of comparable body mass (Brischoux *et al.*, 2008) and to a low catch per unit effort (CPUE). The CPUE of breeding diving birds, for example, varies between 1 and 4 g fish min^{-1} of active time spent at sea (Enstipp *et al.*, 2006). In *L. saintgironsi*, for a mean trip duration of 6.6 days and a mean capture rate of 1.27 fish (83.3 g) per trip (see below 'Energy budgets of *Laticauda* snakes'), CPUE is 0.0044 g fish min^{-1} of time spent at sea (excluding surface time), 1000 times less than in seabirds. These differences in foraging parameters are not due simply to the smaller body size of *Laticauda* snakes versus endotherms; instead, they reflect the snake's low energy needs because of lower temperature-specific metabolic rate (on average $\approx 10\%$ that seen in resting endothermic tetrapods: Pough, 1980), and lower body temperatures (Brischoux *et al.*, 2008).

Because *Laticauda* snakes are benthic foragers, they need to spend as much time as possible near the seafloor, in potential contact with the prey. As a result, dives to deeper substrates are more costly in time: there was a positive relationship between dive depth and duration in *L. saintgironsi* (Fig. 5a). Deep dives last longer because of the need for prolonged vertical commuting phases (from the surface to the seafloor and back), which increase overall dive duration. For shallow dives, it is less clear why snakes do not extend the duration of time they spend on the seafloor. In *Pelamis platurus*, the pelagic yellow-bellied sea snake, dive duration is linked to dive depth because snakes adjust the volume of air in their lung to the depth they target in order to reach neutral buoyancy at depth, and thus reduce oxygen consumption (Cook & Brischoux, 2014). Similarly, *Laticauda* snakes might use respiration-mediated buoyancy control in order to reduce costs of excessive buoyancy at shallow depths.

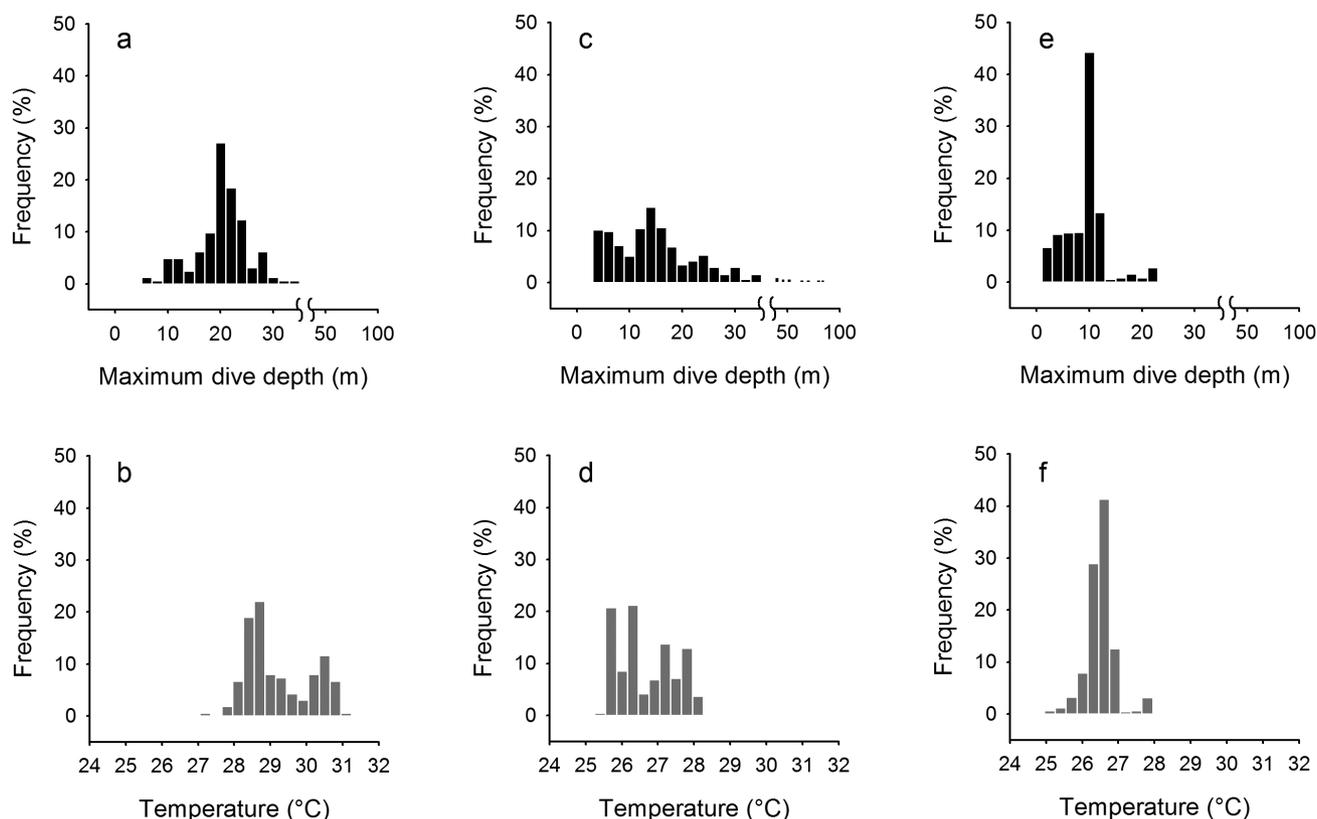


Figure 2 *Laticauda* spp. Distribution of maximum dive depth (black bars) and mean snake temperature during the dive (grey bars) recorded for three sea kraits. (a, b) *L. laticaudata* (snake 1428), (c, d) *L. saintgironsi* (snake 1680) and (e, f) *L. saintgironsi* (snake 2177).

Because of their short post-dive recovery duration, it is likely that most dives were aerobic, which converges with previous conclusions for other free-diving sea snake species based on dive times (Heatwole, 1975), measures of blood lactate (Seymour, 1979) and heart rates (Heatwole, Seymour & Webster, 1979). Interestingly, there was a positive relationship in *L. saintgironsi* between dive duration and post-dive interval for dives <10 min long (Fig. 5b). No such relationship was found in *P. platurus* (Cook & Brischoux, 2014), possibly because this species displays strong aquatic cutaneous exchange, excreting CO₂ into water at rates up to 94% of standard O₂ consumption (Graham, 1974). As in *Laticauda* snakes, oxygen reserves in *P. platurus* are mostly found in the lung, with relatively little oxygen stored in the blood or in the muscles (Rubinoff *et al.*, 1986). Hence, when surfacing, *P. platurus* need in theory only to exhale and inhale once to entirely replenish their oxygen stores (irrespective of the duration of the preceding dive), thus explaining the extremely short post-dive intervals in this species. Reflecting their amphibious lifestyle, *Laticauda* snakes have lower rates of aquatic cutaneous gas exchange than do *P. platurus* (Heatwole & Seymour, 1978). Hence, in *Laticauda* snakes, the increase of post-dive intervals with dive duration could result from the need to offload CO₂ at the surface (requiring multiple respiratory

cycles). In *L. saintgironsi*, post-dive intervals stabilized at ≈1.4 min for dives >10 min (Fig. 5b), suggesting that snakes gain no benefit in terms of recovery beyond this threshold. A minority (8%) of periods spent at the surface were long (3.3–140 min), and their role is unclear. They might represent recovery from diving in cases where the snake engaged in vigorous underwater activity (perhaps in an attempt to capture a fish or to escape from a predator) and thus, had to rely on anaerobic metabolism which requires a sustained period for recovery (Seymour, 1979; Pough, 1980).

The apparent inability of these ectothermic predators to sustain vigorous activity via aerobic metabolism may have important implications for foraging strategies in *L. laticaudata* and *L. saintgironsi*. Underwater observations suggest that prey is located by slow and careful exploration of the seafloor, with snakes moving along the substrate and tongue-flicking in an apparent search for fish scent. When a fish is detected, snake behaviour shifts suddenly to active chasing. Fish usually escape by fast swimming from one shelter to the next, with the snake in hot pursuit (X. Bonnet, pers. obs.). As soon as they have ingested a fish (occasionally, more than one), the snakes return to their home islet or, in some cases, to the nearest islet. Once on land, higher temperatures accelerate digestion. Although snake temperatures were,

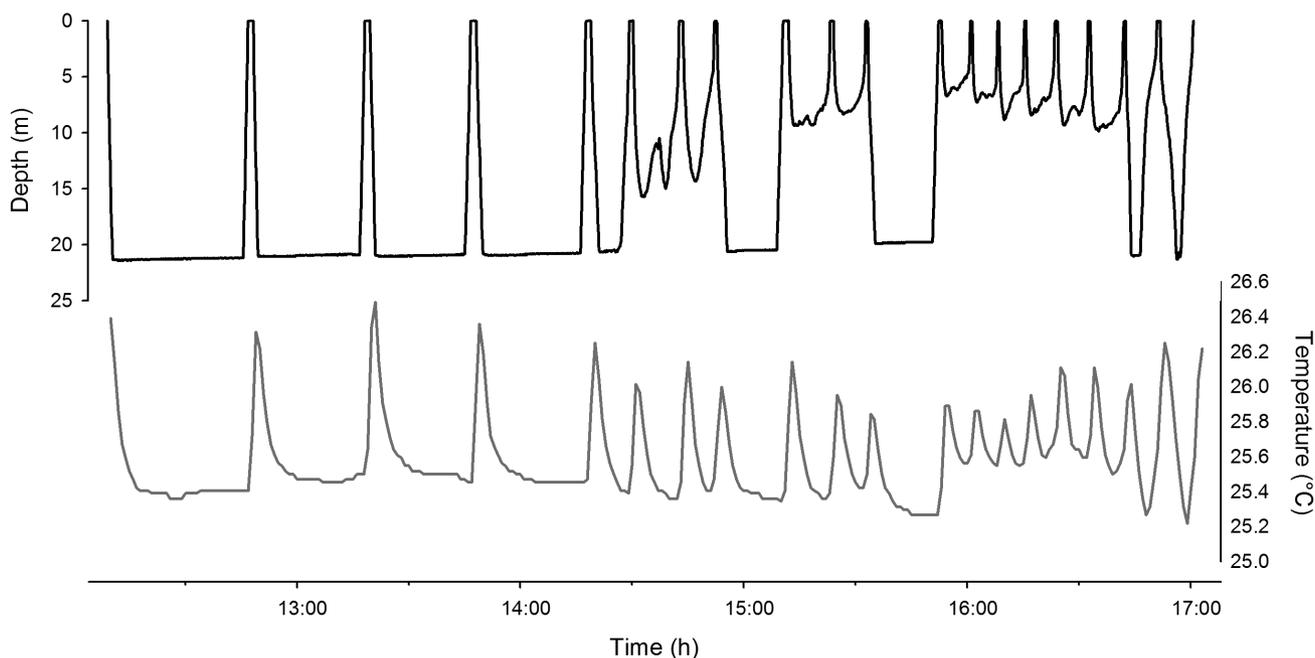


Figure 3 *Laticauda saintgironsi* ($n = 1$). Example of close-up of dive and temperature profiles recorded in snake 2177 over a 5-h period on 19 January 2010. Over the 10-day trip, temperature decreased as a function of dive depth in this snake ($y = -0.04x + 26.65$, $R^2 = 0.19$, $P < 0.0001$, $n = 1254$).

Table 3 *Laticauda saintgironsi* ($n = 1$). Summary of dive parameters of snake 2177, as a function of dive shape and day versus night ($n = 1254$ dives)

	Flat-bottomed				U- and V-shaped combined			
	Day		Night		Day		Night	
	Mean	Max.	Mean	Max.	Mean	Max.	Mean	Max.
Max. dive depth (m)	10.5 ± 3.3	22.6	9.0 ± 3.0	21.2	6.1 ± 4.3	21.9	4.2 ± 2.3	16.7
Dive duration (min)	11.9 ± 5.7	37.8	10.1 ± 4.7	25.5	4.7 ± 2.7	12.3	3.5 ± 2.0	9.9
Post-dive interval (min)	1.2 ± 0.5	5.3	5.4 ± 12.5	90.5	0.5 ± 0.4	2.2	2.4 ± 10.0	140.4
Descent duration (min)	1.1 ± 0.6	5.6	1.3 ± 0.8	6.5	1.2 ± 1.0	4.9	1.1 ± 0.6	3.3
Bottom duration (min)	9.9 ± 5.7	34.9	8.0 ± 4.7	23.9	1.4 ± 1.7	6.5	0.5 ± 1.1	6.4
Ascent duration (min)	1.0 ± 0.6	6.9	0.9 ± 0.5	5.6	2.1 ± 1.4	6.3	1.9 ± 1.2	6.1
Descent rate (m s ⁻¹)	0.18 ± 0.05	0.41	0.14 ± 0.05	0.43	0.10 ± 0.04	0.27	0.07 ± 0.03	0.24
Ascent rate (m s ⁻¹)	0.20 ± 0.04	0.29	0.18 ± 0.05	0.28	0.05 ± 0.02	0.12	0.04 ± 0.02	0.12

on average, only slightly higher on land than at sea, they often reached 32°C (or more) for a few hours every day (Fig. 1). Thus, bouts on land may be crucial for physiological processes such as digestion and also vitellogenesis (Brischoux & Bonnet, 2009). Furthermore, it is likely easier to digest when resting than when swimming. The presence of a bulky prey in the stomach may also reduce locomotor (swimming) abilities, impeding escape from predators (e.g. see Brischoux, Bonnet & Shine, 2011b).

Link between foraging behaviour and prey ecology in *Laticauda* snakes

Dietary analyses show that *L. laticaudata* specializes on anguilliform fish living in burrows in soft-bottom substrate

(like seagrass beds, mud flats or sand), whereas *L. saintgironsi* specializes on eels that live in crevices in hard-bottom substrate like coral, rubble or rock (Brischoux *et al.*, 2007a; Brischoux, Bonnet & Shine, 2009b; Brischoux *et al.*, 2011a). Based on the rate of prey digestion by the snake, Brischoux *et al.* (2007a) estimated that prey can be ingested up to 23 km and 38 km away from the home islet in *L. laticaudata* and *L. saintgironsi*, respectively. The shorter range of *L. laticaudata* can be explained by the vastness of the area covered by the soft-bottom substrate of the lagoon (Andréfouët & Torres-Pulliza, 2004). In contrast, the foraging habitat of *L. saintgironsi* (isolated coral patches, reef flats and the barrier reef) is more patchily distributed, requiring longer trips. The mean trip duration of each species is consistent with this idea (Table 2). Also, the waters prospected by

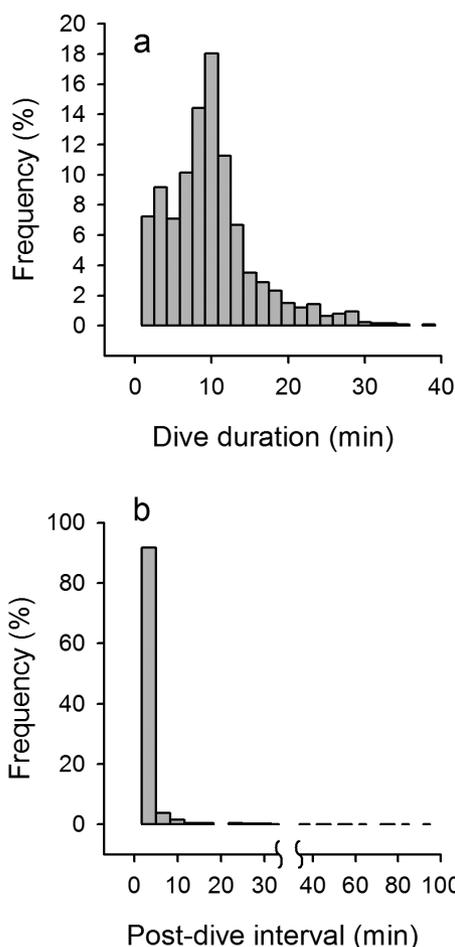


Figure 4 *Laticauda saintgironsi* ($n = 1$). Distribution of (a) dive duration and (b) post-dive interval in snake 2177.

L. laticaudata are warmer than those used by *L. saintgironsi* (Fig. 2), and the maximum dive depth of 83 m recorded in *L. saintgironsi* (Fig. 1b) could only have occurred (in view of the bathymetry of the lagoon) over the outer edge of the barrier reef, a typical hard-bottom habitat. Underwater observations of snakes in the vicinity of the islet show only *L. saintgironsi* foraging in the coral matrix, whereas *L. laticaudata* are observed swimming straight out beyond the reef flat (Brischoux & Bonnet, 2009).

The detailed dive profiles of *L. saintgironsi* allow further exploration of snake foraging strategies, although they originate from one individual (snake 2177) and generalizations to the population level should be considered carefully. Most dives by *L. saintgironsi* were flat-bottomed ($\approx 70\%$). Overall, 83% of these were dives that returned to the same depth zone (intra-depth zone dives; see Materials and methods), suggesting consecutive diving to a relatively even seafloor. Such dives could represent diving over more open habitat, perhaps even soft-bottom substrate. Other dives, mainly U-shaped and to a lesser extent V-shaped, displayed a small proportion of intra-

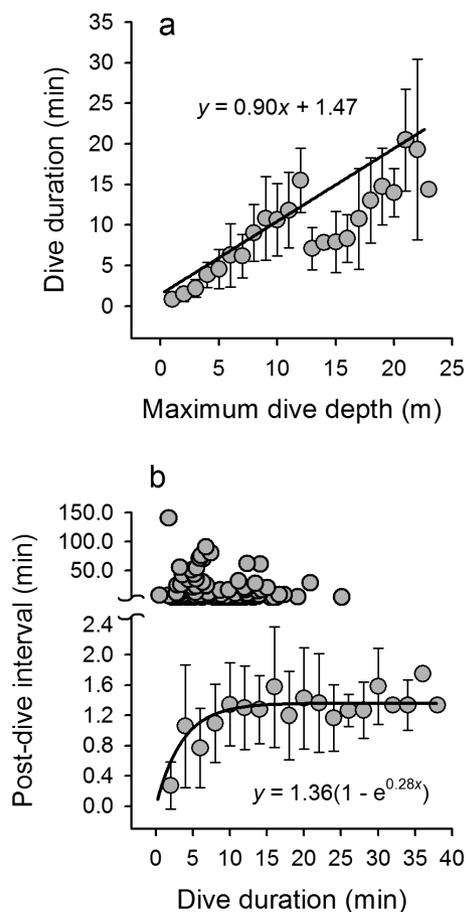


Figure 5 *Laticauda saintgironsi* ($n = 1$). (a) Maximum dive depth as a function of dive duration ($R^2 = 0.40$, $P < 0.0001$, $n = 1254$) and (b) dive duration as a function of post-dive interval ($R^2 = 0.20$, $P < 0.0001$, $n = 1150$) in snake 2177. In b, the regression was plotted for post-dive intervals ≤ 3.3 min (see 'Statistics' in Materials and methods).

depth zone dives (19%). They could represent diving over a substrate with uneven bathymetry (like coral) and thus, be associated to this species' foraging habitat. Remarkably, $\approx 47\%$ of U-shaped dives were right-skewed (and the remaining mostly non-skewed, Fig. 6). Plausibly, snakes often dive to the bottom of vertical structures or coral heads and then ascend slowly beside them, hunting for prey. It is not clear why U-shaped dives in *L. saintgironsi* would occur mostly in the late afternoon, around dusk and throughout the night (Supporting Information Appendix S3); prey activity rhythms need to be investigated. Interestingly, the longest surface periods occurred exclusively at night, after flat-bottomed as well as U- or V-shaped dives (Fig. 7). If these represent post-dive recovery behaviour, they could be the consequence of a sustained locomotor activity (see 'Link between ectothermy and foraging behaviour in *Laticauda* snakes'), as occurs during active hunting. Day-night differences in dive parameters were not clear-cut in U- and V-shaped dives,

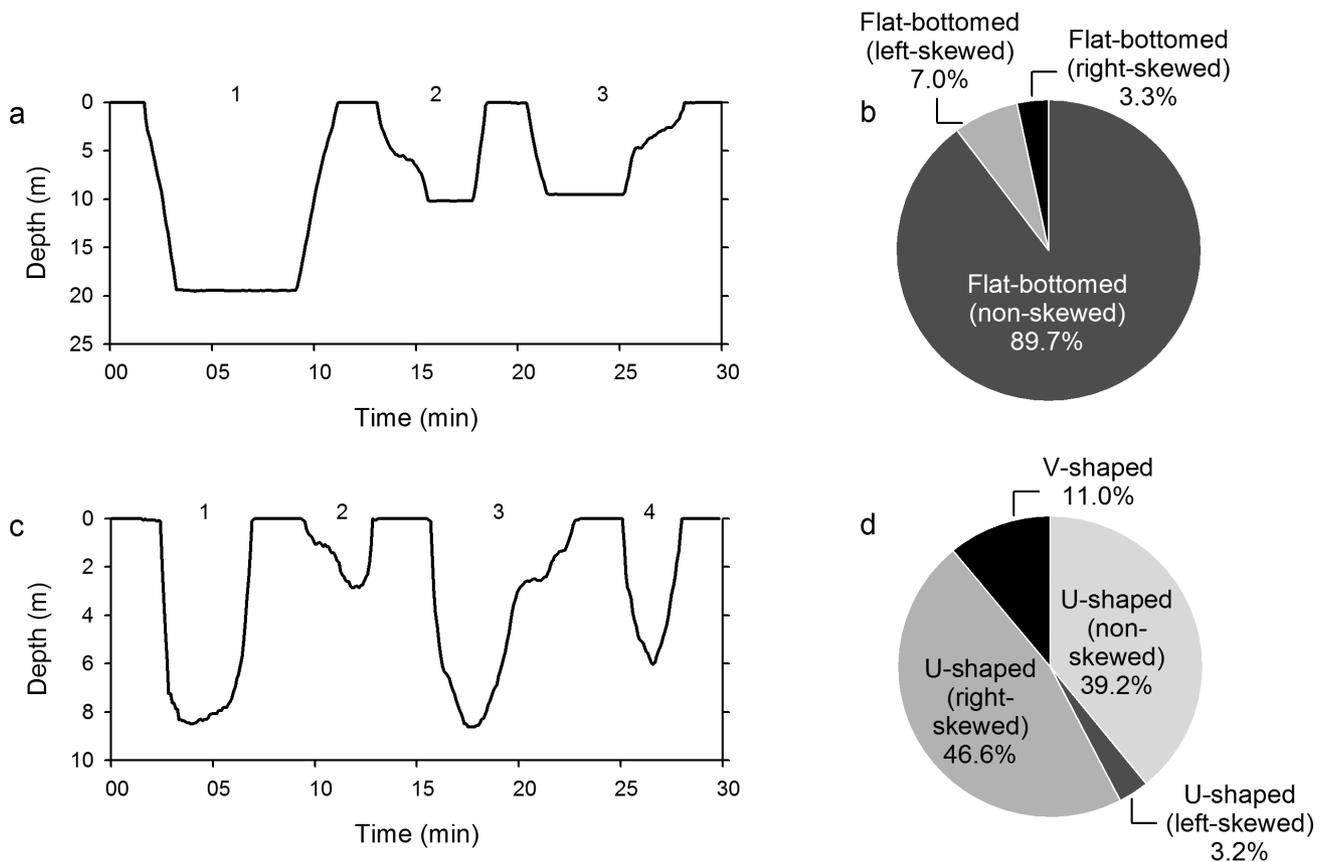


Figure 6 *Laticauda saintgironsi* ($n = 1$). Shapes of dives carried out by snake 2177. (a, b) Flat-bottomed dives ($\approx 70\%$) comprised non-skewed flat-bottomed dives (dive 1), left-skewed flat-bottomed dives (dive 2) and right-skewed flat-bottomed dives (dive 3). (c, d) Other dives ($\approx 30\%$) comprised non-skewed U-shaped dives (dive 1), left-skewed U-shaped dives (dive 2), right-skewed U-shaped dives (dive 3) and V-shaped dives (dive 4). Examples of shapes are actual dives recorded by *L. saintgironsi*.

possibly because of the scarcity of such dives during the daytime (Supporting Information Appendix S3). In flat-bottomed dives, dives were deeper during the day (Supporting Information Appendix S2), perhaps because this is when snakes commute over deep, open habitat, between shallow and rocky feeding habitats.

Energy budgets of *Laticauda* snakes

Our sea kraits displayed high activity rates, diving continuously and combining bouts of travelling with bouts of hunting behaviour. It usually takes a snake several days to secure a single prey and then several additional days to return to land to digest it. This seems to be an inefficient foraging behaviour, compared with diving endotherms (see above), but the magnitude of such inefficiency depends upon the field metabolic rate of sea kraits. We propose a simple energetic model in order to explore this question. Using their activity budgets, the energy expenditure of snakes was calculated as $28.6 \text{ kJ kg}^{-1} \text{ day}^{-1}$ and $23.2 \text{ kJ kg}^{-1} \text{ day}^{-1}$ on land, and $230.4 \text{ kJ kg}^{-1} \text{ day}^{-1}$

and $244.9 \text{ kJ kg}^{-1} \text{ day}^{-1}$ at sea, in *L. laticaudata* and *L. saintgironsi*, respectively (Supporting Information Appendix S4).

Even if they are approximate, our estimates suggest some general conclusions about the metabolic rate of free-ranging *Laticauda* snakes. At-sea metabolic rate was 8.0 times and 10.5 times greater than on-land metabolic rate in *L. laticaudata* and *L. saintgironsi*, respectively. These snakes are slothful on land, but almost continuously active in the water. By contrast, many terrestrial snakes rely upon ambush predation, and activity levels (and thus, their metabolic rates) while foraging may be close to baseline resting levels (Secor & Nagy, 1994). Overall field metabolic expenditure was very low compared with marine endotherms. Expenditure estimates for breeding diving seabirds vary between 1260 and $1780 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (Enstipp *et al.*, 2006), about 10–20 times greater than our estimates of overall field metabolic rate for *Laticauda* snakes. Thus, as is true in a range of situations worldwide, ectothermy allows animals to exploit trophic niches in ways that are very different from those of sympatric endotherms;

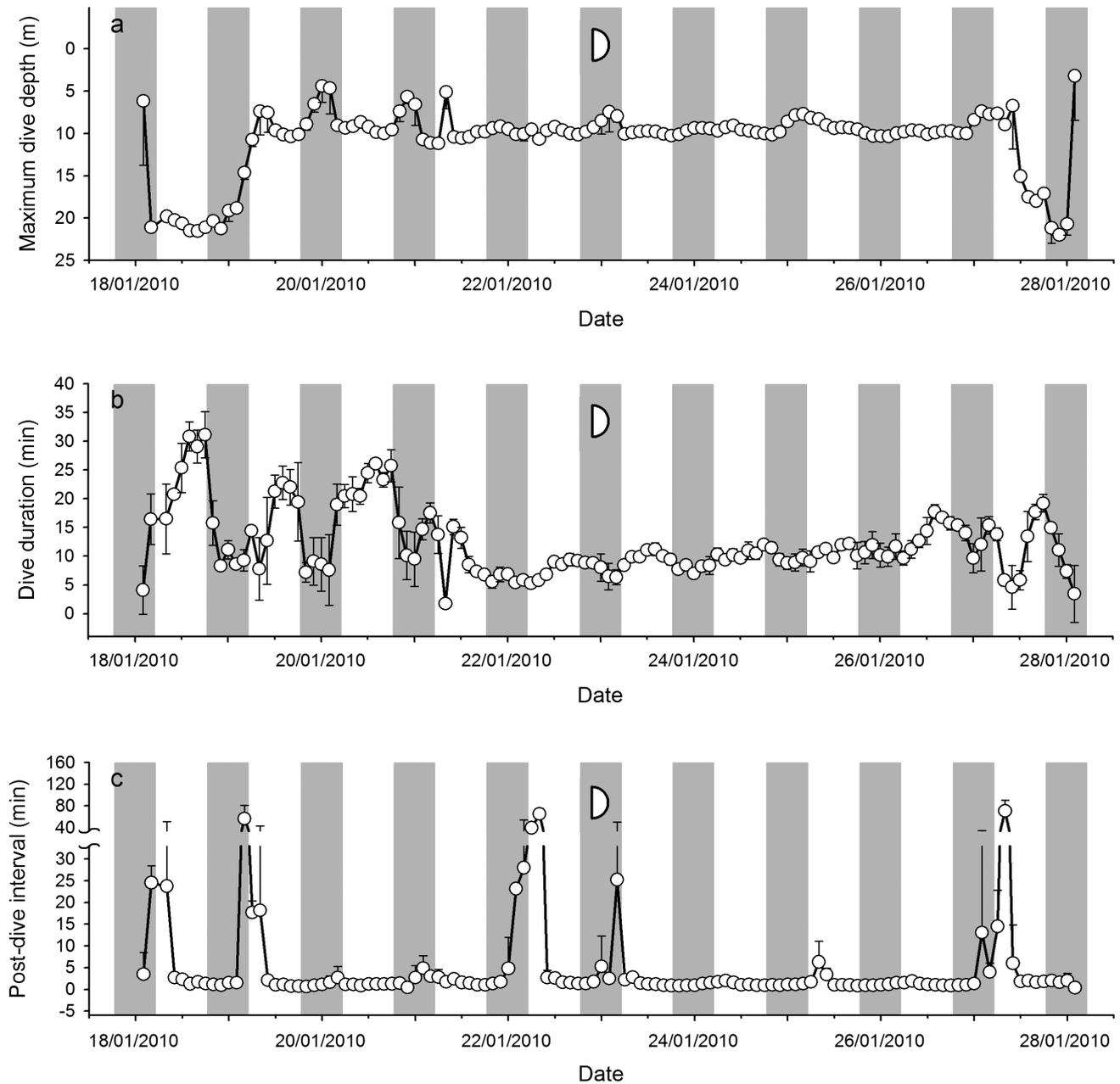


Figure 7 *Laticauda saintgironsi* ($n = 1$). Influence of time on dive parameters of flat-bottomed dives ($\approx 70\%$ of dives) in snake 2177. The panels show variation in (a) maximum dive depth, (b) dive duration and (c) post-dive interval over the study period. Night period is shown in grey. Date of first moon quarter is represented by a white half circle.

and allows populations to thrive on rates of energy intake vastly lower than are required for their endothermic competitors (Pough, 1980).

Acknowledgements

We warmly thank Amélie and Bruno Mège as well as Christophe and Monique Bonnet for their help. We also thank

Akiko Kato for preliminary dive analyses. Thanks to Eric Potut (Scaphca), Richard Farman (Aquarium des Lagons) and the programme Zoneco. The DENV (Province Sud, New Caledonia) provided logistical support. Funding was provided by the CNRS (France), the DENV and the Australian Research Council. The study was carried out under permits 6024-179/DRN/ENV, 6024-3601/DRN/ENV, 503/DENV/SMER and 3431-2011/ARR/DENV issued by the DENV.

References

- Andréfouët, S. & Torres-Pulliza, D. (2004). *Atlas des récifs coralliens de Nouvelle-Calédonie*. Nouméa: IFRECOR Nouvelle-Calédonie.
- Beck, C.A., Bowen, W.D. & Iverson, S.J. (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J. Exp. Biol.* **203**, 2323–2330.
- Bonnet, X. (2012). Long term field study of sea kraits in New Caledonia: fundamental and conservation issues. *Integr. Comp. Biol.* **52**, 281–295.
- Bonnet, X., Brischoux, F., Pearson, D. & Rivalan, P. (2009). Beach rock as a keystone habitat for amphibious sea snakes. *Environ. Conserv. J.* **36**, 62–70.
- Bonnet, X., Brischoux, F., Pinaud, D., Michel, C.L., Clobert, J., Shine, R. & Fauvel, T. (2015). Spatial variation in age structure among colonies of a marine snake: the influence of ectothermy. *J. Anim. Ecol.* (Online DOI: 10.1111/1365-2656.12358).
- Brischoux, F. & Bonnet, X. (2009). Life history of sea kraits in New Caledonia. *Mém. Mus. Nat. His. Nat.* **198**, 133–147.
- Brischoux, F., Bonnet, X. & Shine, R. (2007a). Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. *Mar. Ecol. Prog. Ser.* **350**, 145–151.
- Brischoux, F., Bonnet, X., Cook, T.R. & Shine, R. (2007b). *Snakes at sea: diving performances of free-ranging sea kraits*. Proceedings of the 11th Annual Meeting on Health, Science & Technology. Tours: Tours University.
- Brischoux, F., Bonnet, X., Cook, T.R. & Shine, R. (2008). Allometry of diving capacities: ectothermy versus endothermy. *J. Evol. Biol.* **21**, 324–329.
- Brischoux, F., Bonnet, X. & Shine, R. (2009a). Kleptothermy, an additional category of thermoregulation and a possible example in sea kraits (*Laticauda laticaudata*, Serpentes). *Biol. Lett.* **5**, 729–731.
- Brischoux, F., Bonnet, X. & Shine, R. (2009b). Determinants of dietary specialization: a comparison of sympatric species of sea snakes. *Oikos* **118**, 145–151.
- Brischoux, F., Bonnet, X., Cherel, Y. & Shine, R. (2011a). Isotopic signatures, foraging habitats and trophic relationships between fish and sea snakes on the coral reefs of New Caledonia. *Coral Reefs* **30**, 15–165.
- Brischoux, F., Bonnet, X. & Shine, R. (2011b). Conflicts between reproduction and feeding in amphibious snakes (sea kraits, *Laticauda* spp.). *Aust. Ecol.* **36**, 46–52.
- Brischoux, F., Tingley, R., Shine, R. & Lillywhite, H.B. (2012). Salinity influences the distribution of marine snakes: implications for evolutionary transitions to marine life. *Ecography* **35**, 1–10.
- Cook, T.R. & Brischoux, F. (2014). Why does the only ‘planktonic tetrapod’ dive? Determinants of diving behaviour in a marine ectotherm. *Anim. Behav.* **98**, 113–123.
- Cook, T.R., Kato, A., Tanaka, H., Ropert-Coudert, Y. & Bost, C.-A. (2010). Buoyancy under control: underwater locomotor performance in a deep diving seabird suggests respiratory strategies for reducing foraging effort. *PLoS ONE* **5**, e9839.
- Cook, T.R., Hamann, M., Pichegru, L., Bonadonna, F., Grémillet, D. & Ryan, P.G. (2012). GPS and time-depth loggers reveal underwater foraging plasticity in a flying diver, the Cape Cormorant. *Mar. Biol.* **159**, 379–387.
- Dunson, W.A. (1975). *The biology of sea snakes*. Baltimore: University Park Press.
- Enstipp, M.R., Daunt, F., Wanless, S., Humphreys, E.M., Hamer, K.C., Benvenuti, S. & Grémillet, D. (2006). Foraging energetics of North Sea birds confronted with fluctuating prey availability. In *Top predators in marine ecosystems: their role in monitoring and management*: 191–210. Boyd, S., Wanless, S. & Camphuysen, C.J. (Eds). Cambridge: Cambridge University Press.
- Goiran, C. & Shine, R. (2013). Decline in seasnake abundance on a protected coral-reef system in the New Caledonian lagoon. *Coral Reefs* **32**, 281–284.
- Graham, J.B. (1974). Aquatic respiration in the sea snake *Pelamis platurus*. *Respir. Physiol.* **21**, 1–7.
- Heatwole, H. (1975). Voluntary submergence times of marine snakes. *Mar. Biol.* **32**, 205–213.
- Heatwole, H. (1999). *Sea snakes*. Sydney: University of New South Wales Press.
- Heatwole, H. & Seymour, R.S. (1978). Cutaneous oxygen uptake in three groups of aquatic snakes. *Aust. J. Zool.* **26**, 481–486.
- Heatwole, H., Seymour, R.S. & Webster, M.E.D. (1979). Heart rates of sea snakes diving in the sea. *Comp. Biochem. Physiol.* **62**, 453–456.
- Ineich, I., Bonnet, X., Brischoux, F., Kulbicki, M., Séret, B. & Shine, R. (2007). Anguilliform fishes and sea kraits: neglected predators in coral reef ecosystems. *Mar. Biol.* **151**, 793–802.
- Kenward, R. (1987). *Wildlife radio tagging. Equipment, field techniques and data analysis*. London: Academic Press.
- Lillywhite, H.B., Sheehy, C.M. & Zaidan, F. (2008). Pitviper scavenging at the intertidal zone: an evolutionary scenario for invasion of the sea. *Bioscience* **58**, 947–955.
- Lovvorn, J.R., Watanuki, Y., Kato, A., Naito, Y. & Liggins, G.A. (2004). Stroke patterns and regulation of swim speed and energy cost in free-ranging Brünnich’s guillemots. *J. Exp. Biol.* **207**, 4679–4695.
- Lukoschek, V., Beger, M., Ceccarelli, D., Richards, Z. & Pratchett, M. (2013). Enigmatic declines of Australia’s sea snakes from a biodiversity hotspot. *Biol. Conserv.* **166**, 191–202.
- Murphy, J.C. (2012). Marine invasions by non-sea snakes, with thoughts on terrestrial-aquatic-marine transitions. *Integr. Comp. Biol.* **52**, 217–227.
- Nguyen, C., Nguyen, T., Moore, A., Montoya, A., Rasmussen, A., Broad, K., Harold, V. & Takacs, Z. (2014).

- Hidden catch: sea snake exploitation in the Gulf of Thailand. *Conserv. Biol.* **28**, 1677–1687.
- Phillips, R.A., Xavier, J.C., Croxall, J.P. & Burger, A.E. (2003). Effects of satellite transmitters on albatrosses and petrels. *Auk* **120**, 1082–1090.
- Pough, F.H. (1980). The advantages of ectothermy for tetrapods. *Am. Nat.* **115**, 92–112.
- Reed, R.N., Shine, R., Shetty, S. & Cogger, H. (2002). Sea kraits (Squamata: *Laticauda* spp.) as a useful bioassay for assessing local diversity of eels (Muraenidae, Congridae) in the western Pacific Ocean. *Copeia* **4**, 1098–1101.
- Reinert, K.H. & Cundall, D. (1982). An improved surgical implantation method for radio-tracking snakes. *Copeia* **1982**, 702–705.
- Ropert-Coudert, Y. & Wilson, R.P. (2005). Trends and perspectives in animal-attached remote sensing. *Front. Ecol. Environ.* **3**, 437–444.
- Ropert-Coudert, Y., Beaulieu, M., Hanuise, N. & Kato, A. (2009). Diving into the world of biologging. *Endanger Species Res.* **10**, 21–27.
- Rubinoff, I., Graham, J.B. & Motta, J. (1986). Diving of the sea snake *Pelamis platurus* in the Gulf of Panama I. Dive depth and duration. *Mar. Biol.* **91**, 181–191.
- Rubinoff, I., Graham, J.B. & Motta, J. (1988). Diving of the sea snake *Pelamis platurus* in the Gulf of Panama II. Horizontal movement patterns. *Mar. Biol.* **97**, 157–163.
- Saint Girons, H. (1964). Notes sur l'écologie et la structure des populations des Laticaudinae (Serpentes: Hydrophiidae) en Nouvelle-Calédonie. *Terre et la Vie* **111**, 185–214.
- Secor, S.M. & Nagy, K.A. (1994). Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* **75**, 1600–1614.
- Seymour, R.S. (1979). Blood lactate in free-diving sea snakes. *Copeia* **3**, 494–497.
- Shetty, S. & Shine, R. (2002). Activity patterns of yellow-lipped sea kraits (*Laticauda colubrina*) on a Fijian island. *Copeia* **2002**, 77–85.
- Shine, R. & Shetty, S. (2001). The influence of natural selection and sexual selection on the tails of sea-snakes (*Laticauda colubrina*). *Biol. J. Linn. Soc.* **74**, 121–129.
- Tremblay, Y. & Cherel, Y. (2000). Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar. Ecol. Prog. Ser.* **204**, 257–267.
- Tremblay, Y., Cook, T.R. & Cherel, Y. (2005). Time budget and diving behaviour of chick-rearing Crozet shags. *Canad. J. Zool. (Lond.)* **83**, 971–982.
- Vermeij, G.J. & Dudley, R. (2000). Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biol. J. Linn. Soc.* **70**, 541–554.
- Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T. & Tyack, P.L. (2006). Deep-diving foraging behavior of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* **75**, 814–825.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. *Laticauda saintgironsi* ($n = 1$). Statistics of general linear models testing the effect of diurnal period (day vs. night), dive shape (flat-bottomed vs. U- and V-shaped combined) and maximum dive depth on eight dive parameters of snake 2177.

Appendix S2. *Laticauda saintgironsi* ($n = 1$). Summary of the influence of the diurnal cycle on dive parameters of flat-bottomed dives ($\approx 70\%$ of dives) in snake 2177 over the study period. The panels show the effects of time of day on (a) frequency distribution of dives, (b) dive depth, (c) dive duration, (d) post-dive interval, (e) descent rate and (f) ascent rate. Night period is shown in grey.

Appendix S3. *Laticauda saintgironsi* ($n = 1$). Summary of the influence of diurnal cycle on dive parameters of U- and V-shaped dives ($\approx 30\%$ of dives) in snake 2177 over the study period. The panels show effects of time of day on (a) frequency distribution of dives, (b) dive depth, (c) dive duration, (d) post-dive interval, (e) descent rate and (f) ascent rate. Night period is shown in grey.

Appendix S4. Building an energy-budget for *Laticauda* snakes based on their activity-budgets.