



Why does the only 'planktonic tetrapod' dive? Determinants of diving behaviour in a marine ectotherm



Timothée R. Cook^{a, b, *}, François Brischox^c

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

^b Percy FitzPatrick Institute, University of Cape Town, Cape Town, South Africa

^c Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique – University of La Rochelle, Chizé – La Rochelle, France

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Marine tetrapods represent powerful models for studying how evolutionary transitions shape the life history traits, physiology and behaviour of animals. Whereas adaptations to diving are driven primarily by the need to secure underwater food, diving in the pelagic sea snake, *Hydrophis (Pelamis) platurus*, seems less foraging-dependent. Indeed, this reptile captures fish while floating at the sea surface. Despite knowledge about its surface ecology, its underwater behaviour remains mostly unknown. Yet, study of this life phase is a key to understanding how and why this snake dives. In this study, we reanalysed published data on its diving behaviour. The pelagic sea snake spends 95% of its time underwater, where it can dive to 50 m and stay for 3.5 h without breathing. Dives are S-shaped, with a long phase of gradual ascent during which the snake is neutrally buoyant. Snake lungs deflate slowly during this phase at a rate that increases with water temperature, and thus metabolism. Dive duration is linked to inferred lung volume at the start of the dive, suggesting aerobic diving. We propose that pelagic sea snakes dive for multiple reasons, but primarily to avoid sea surface turbulence. Underwater, they can reduce metabolism by targeting cooler water layers. By hovering in the water column, they reduce energy expenditure and escape both surface and bottom predators, while more easily locating their own prey from underneath. Some marine turtles occasionally display S-shaped dives, but the role of such dives remains under debate. We suggest the study of sea snakes can help interpret diving behaviour in other lineages of marine reptiles.

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Evolutionary transitions between contrasted habitats provide powerful frameworks for understanding how organismal traits respond to habitat-related pressures (Little, 1990). Accordingly, secondarily marine vertebrates (marine tetrapods) represent textbook examples for understanding how marine environments have shaped the life history traits, physiology and behaviour of these species as compared to terrestrial vertebrates (Mazin & de Buffrénil, 2001). For example, marine life has exerted strong selective pressures on the ability of these organisms to remain submerged underwater for long periods of time, and most of these animals display breath-holding abilities remarkably longer than their terrestrial counterparts (Kooyman, 1989).

The study of such organisms can also help us understand the evolutionary motor that led to these transitions (Pyenson, Kelley, &

Parham, 2014). Although marine tetrapods display contrasted degrees of emancipation from their ancestral terrestrial environments (e.g. amphibious pinnipeds versus entirely marine cetaceans or flying seabirds versus flightless penguins), all of these species use the marine environment for foraging, thereby suggesting that the transition to marine life has been linked to the occupation of rich and presumably vacant foraging niches (Vermeij & Dudley, 2000). Accordingly, adaptations to marine life include traits that help these species forage successfully, such as the ability to dive. This may entail the capacity to move efficiently through water (thus to pursue and capture fast-moving prey), to remain underwater for long periods without needing to breathe (extending time spent in contact with prey), or to dive to considerable depths (increasing the range of available foraging space) (Kooyman, 1989). Overall, to successfully forage in the marine environment, diving marine tetrapods have evolved a suite of traits that ultimately led to efficient diving behaviour, enabling the search and capture of prey either within the water column (pelagic diving) or near the seafloor (benthic diving).

In this context, studying species that diverge from the widespread pattern of 'diving equals foraging' is critical for

* Correspondence: T. R. Cook, Institute of Ecology and Environmental Sciences, Department of Evolutionary Ecology, Evolutionary Ecophysiology Team, University Pierre et Marie Curie, Bâtiment A–7^{ème} étage, 7 quai St Bernard, 75252 Paris, France.

E-mail address: timothee.cook@gmail.com (T. R. Cook).

understanding other facets of the evolution of diving behaviour. Although many marine tetrapods dive to locate and capture prey, some can also remain underwater for reasons other than prey capture. Such exceptions include resting, where individuals are inactive or sleeping underwater, sometimes for extended durations and at considerable depth. This is the case in some species of marine turtles (Houghton et al., 2008), pinnipeds (Mitani et al., 2010) and cetaceans (Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008). Diving without foraging is also used to escape predators (Wirsing, Heithaus, & Dill, 2007), for communication between individuals (Tyack, 1998) or for transit between food patches (e.g. porpoising in penguins and dolphins; Wilson & Wilson, 1990) and migration (Block et al., 2011).

Species that forage exclusively at the sea surface but that none the less spend the rest of their time submerged at depth would offer a rare opportunity to shed light on the evolution of diving behaviour that is independent from foraging. The viviparous yellow-bellied sea snake, *Hydrophis (Pelamis) platurus* (Hydrophiinae), also known as the pelagic sea snake, represents one such rare opportunity. *Hydrophis platurus* is the only pelagic species of sea snake and the only 'planktonic' species of marine tetrapod: it drifts passively with surface and subsurface currents, spending its entire life cycle at sea (Heatwole, 1999). As a consequence, it is widely distributed, covering the entire tropical Indo-Pacific basin (Heatwole, 1999), and has one of the largest global distributions of any species of squamate reptile. Another remarkable feature of this species is its very unusual life history, insofar as it spends most of its day-to-day life floating in the water column 20–50 m deep (Rubinoff, Graham, & Motta, 1986). Submergence time is interrupted by surfacing events, which can be brief to air-breathe or longer to forage (Rubinoff et al. 1986). This species has a remarkable foraging strategy among marine tetrapods: it ambushes small larval fish that are concentrated under debris on oceanic labile features such as slicks or drift lines, doing 'float-and-wait' foraging at the oceanic surface (Brischox & Lillywhite, 2011; Dunson & Ehlert, 1971; Rubinoff et al., 1986). To our knowledge, *H. platurus* is the only marine tetrapod foraging specifically at the ocean surface, but spending a considerable proportion of its time budget submerged, thereby offering a unique opportunity to explore the determinants of diving independently from foraging.

In the late 1980s, a series of three articles on *H. platurus* attempted for the first time to describe their diving behaviour and physiology (Graham, Gee, Motta, & Rubinoff, 1987; Rubinoff et al., 1986; Rubinoff, Graham, & Motta, 1988). These articles, on snakes from the Gulf of Panama, featured unprecedented field studies and laboratory experiments that have not been equalled in complexity or repeated since. They made two important points. First, diving captive snakes are neutrally buoyant at depth, suggesting that, upon diving, they modulate the volume of respiratory air necessary to attain neutral buoyancy near the bottom of the dive (Graham et al., 1987). Second, free-ranging *H. platurus*, fitted with ultrasonic pressure transmitters, display dive profiles that are 'S-shaped', a term referring to the sinusoidal shape dives have when looked at from a 90° angle. In particular, S-shaped dives are pelagic dives characterized by an extended gradual ascent phase (Rubinoff et al., 1986). Since then, S-shaped dives have rarely been recorded in other marine tetrapods, except in four species of turtles, in which they occur occasionally and seem linked to activities other than foraging (e.g. Hochscheid, Godley, Broderick, & Wilson, 1999; Minamikawa, Naito, & Uchida, 1997; Sperling, Grigg, & Limpus, 2010; Storch, 2003). Hence, S-shaped dives are widespread in *H. platurus*, but unusual in other marine tetrapods, and the function of such dives remains unclear (Graham et al., 1987; Hochscheid, 2014).

Recent advances in the study of diving behaviour and physiology allow us to go significantly further in the analysis and

interpretation of the data collected by Rubinoff et al. (1986; 1988). The aim of this study was to explore potential functions of the S-shaped dives discovered by these authors. To do this, we re-analysed time–depth data from Rubinoff et al. (1986; 1988) using up-to-date analytical and conceptual approaches (Ropert-Coudert & Wilson, 2005). Specifically, we aimed to describe the diving behaviour and model the diving physiology of *H. platurus* in order to understand the determinants of diving in a species that forages exclusively at the sea surface. In this paper we also review the occurrence of S-shaped dives in other marine tetrapods and discuss the general implications of this enigmatic behaviour.

METHODS

Data Collection

Rubinoff et al. (1986) published dive profiles of 15 *H. platurus* individuals recorded with ultrasonic pressure transmitters deployed on snakes over a period of ca. 3–29 h each in the Gulf of Panama (8°25'N, 79°02'W) between 1983 and 1985. These authors extracted maximum dive depth and dive duration, and did some preliminary analyses of dive parameters. Unfortunately, the data have since been lost (J. B. Graham, personal communication) and profiles published in this paper provide the only available source for the original data set. Time–depth data were therefore retrieved from published dive profiles using Plot Digitizer 1.9. Graphic resolution of the profile of one snake (snake G; Rubinoff et al., 1986), which made only short and shallow dives, was too low to allow accurate data capture; this profile was therefore discarded. We tested the precision of data capture by comparing values determined by Rubinoff et al. (1986) with our method. We found a difference in individual maximum dive depth of 0.8 ± 1.8 m and in maximum dive duration of 3.9 ± 4.4 min, suggesting we accurately retrieved data from profiles.

Dive Parameters

Dive profiles were split into two categories: S-shaped dives and V-shaped dives. S-shaped dives were divided into four phases according to the terminology in Rubinoff et al. (1986) (Fig. 1). (1) Descent corresponded to the commuting between sea surface and maximum dive depth. (2) Bounce ascent corresponded to the quick ascent immediately following maximum dive depth (Rubinoff et al., 1986). This phase is hereafter called 'first ascent' for consistency with the literature on marine turtles (see Discussion). (3) Gradual ascent corresponded to the slow, long ascent following the first ascent. We assumed snakes were neutrally buoyant throughout the entire gradual ascent and that any decrease in depth that occurred during this phase was linked to loss of respiratory volume through consumption of pulmonary O₂ and cutaneous release of CO₂ and N₂ (Graham et al., 1987). (4) Final ascent corresponded to the quick ascent to the sea surface following the gradual ascent. Dive duration was defined as the period between submergence and emergence of the snake. Postdive interval was defined as the surface period following the dive and preceding the next dive and dedicated to breathing, and sometimes to foraging. V-shaped dives comprised a descent to maximum dive depth followed by an ascent (Fig. 1).

Gradual ascent is the phase in which the snake spends the most time during the dive cycle. We tested the extent to which snakes returned to the same depth of gradual ascent during consecutive dives. Consecutive dives that returned to the same depth zone were called intradepth zone dives (Tremblay & Cherel, 2000). We calculated two intradepth zone dives. In the first, depth zone was defined as the depth of the start of gradual ascent of the current

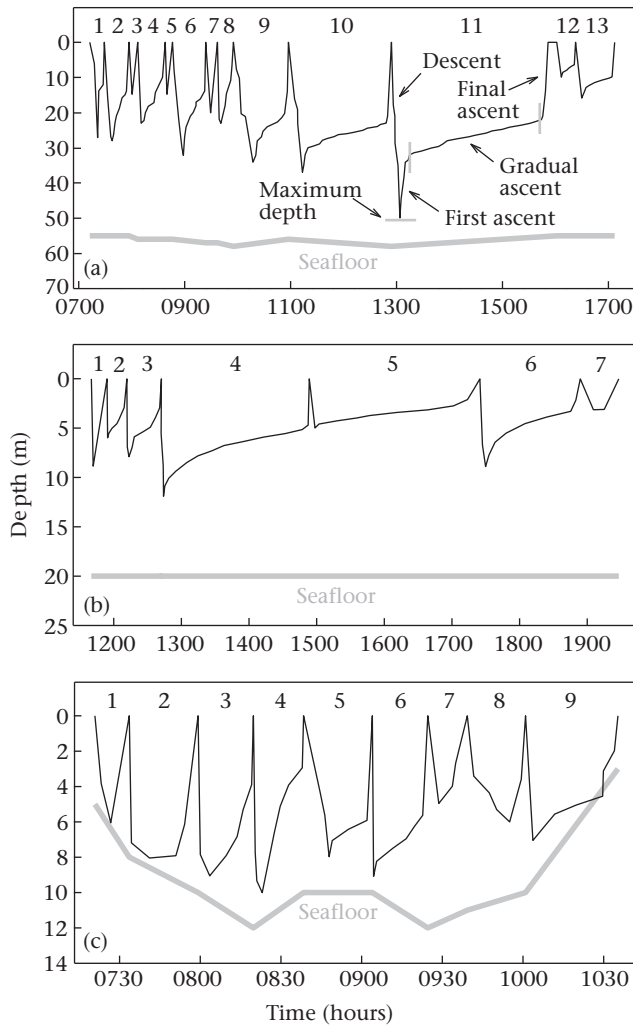


Figure 1. Examples of dive profiles of *H. platurus* (the seafloor is the thick grey line). (a) Example of pelagic dives and illustration of the different phases of the S-shaped dive in dive number 11. Dives number 3, 5 and 7 are V-shaped. (b) Example of pelagic dives. In dive number 5, the snake began the phase of gradual ascent at the depth at which it ended gradual ascent in dive number 4. (c) Example of benthic dives. Dive 2 is the only U-shaped dive in the data set and was considered as a V-shaped dive for convenience.

dive $\pm 10\%$ of the depth of the start of gradual ascent during the preceding dive. In the second, depth zone was defined as the depth of the start of gradual ascent of the current dive $\pm 10\%$ of the depth of the end of the gradual ascent phase reached during the preceding dive.

Environmental Variables

Of the 15 snakes for which dive profiles were recorded, five also had their position monitored at sea during the entire time of recording (Rubinoff et al., 1988). We superposed their tracks on the British Admiralty Nautical Chart 1929 Gulf of Panama (corrected up to date) and extracted depth of seafloor beneath dives using times of day which were annotated to the tracks. Owing to the natural imprecision of estimated bathymetry at this geographical scale, dives were considered as benthic when maximum dive depth was ± 5 m of seafloor depth (Cook et al., 2012). All other dives reached a maximum depth < 5 m to the depth of the seafloor and were considered as pelagic.

Temperature at the depth of the start of gradual ascent was extracted using Plot Digitizer 1.9 from depth–temperature profiles

recorded by Rubinoff et al. (1986) between the surface and 60 m deep in the Gulf of Panama during the study periods. The study comprised two periods. (1) The ‘wet’ season is a period characterized by warm sea water between 28°C near the surface and 25°C at 40 m with a strong thermocline around 50 m deep. (2) The ‘dry’ season is a period characterized by the disappearance of thermal stratification and with cooler water temperatures (upwelling) varying between 25°C near the surface and 16°C at 50 m.

For time of day, the 24 h cycle was divided into day and night periods. The low latitude of the Gulf of Panama means that the times of sunrise and sunset vary little throughout the year. Thus, the day period was defined as beginning at 0530 and ending at 1900 hours.

Snake Morphology

The body mass (BM) and total length (TL) of snakes were available in Rubinoff et al. (1986) (mean TL = 67.9 ± 4.9 cm; mean BM = 0.139 ± 0.027 kg). We calculated a body condition index using residual scores from the linear regression between TL and BM (both variables were log-transformed for linearity, Bonnet & Naulleau, 1995).

The body volume of snakes (excluding the lung) was calculated after measuring preserved snakes (Brischoux & Shine, 2011). The individual mean diameter of snakes (excluding the lung) was calculated by measuring the horizontal diameter of preserved snakes at nine different points along the snake’s body axis. It was assumed that preserved snakes had a totally collapsed lung during measurements. Snake volume was inferred from snake diameter using the formula for the volume of a cylinder. Using measured snout–vent length SVL (cm), mean snake diameter SDIA (cm) can be calculated as: $\text{SDIA} = 0.034 (\text{SVL}) - 0.465$ ($R^2 = 0.84$, $P < 0.001$). Only TL was available from live snakes measured in Rubinoff et al. (1986). We therefore used measurements made on preserved snakes (Brischoux & Shine, 2011) and live snakes (Brischoux & Lillywhite, 2013) to estimate mean tail length as ca. 11.2% of TL (cm) and $\text{SVL} = \text{TL} - \text{tail length}$. Mean SDIA and body volume were thus calculated as 1.56 ± 0.15 cm and 117.0 ± 28.7 ml, respectively.

The lung of *H. platurus* runs from the neck to the vent, where it is attached to the inner body wall (Graham, Gee, & Robison, 1975). Lung length was therefore calculated as snake SVL minus head length. Head length represents ca. 6% of SVL (Brischoux & Lillywhite, 2013). Thus, mean lung length was calculated as 56.2 ± 4.1 cm. Although the lung is divided into three parts (tracheal, vascular and saccular lung; Graham et al. 1975; Seymour, Spragg, & Hartman, 1981), we approximated its shape to that of a cylinder. Lung volume at sea level (and thus lung diameter) to achieve neutral buoyancy within the diving range of snakes was derived from a formula for calculating the force of buoyancy on a snake underwater (see below).

Modelling of Lung Volume and Depth of Neutral Buoyancy

The formula for calculating the force of buoyancy F_{UP} (N) as a function of depth on a diving snake was adapted from Wilson, Hustler, Ryan, Burger, and Nöldeke (1992) as:

$$F_{\text{UP}} = \rho g \left(\frac{p_s V_{\text{LS}}}{p_s + \rho g d} + V_{\text{T}} \right) - gm$$

where ρ is sea water density (1021 kg/m^3) in the Gulf of Panama (Fofonoff & Millard, 1983), g is gravitational acceleration (9.807 m/s^2) at sea level, p_s is standard atmospheric pressure (101 325 Pa) at sea level, V_{LS} is lung volume (m^3) at sea level, V_{T} is body volume (m^3) (lung excluded), m is body mass (kg) and d is current

dive depth (m). We derived the V_{LS} for different depths of neutral buoyancy (where $F_{UP} = 0$) from this equation.

Statistics

We tested the effect of dive shape (with maximum dive depth as covariate) on dive parameters, the effect of light intensity on dive depth and duration, the effect of season on the depth of the start of gradual ascent and on water temperature at the start of gradual ascent, and the effect of season on dive duration (with the depth of the start of gradual ascent as covariate) and on lung volume loss and lung volume loss rate during gradual ascent (with gradual ascent duration as covariate). Dive data are typically pseudoreplicated, an individual making several successive dives (repeated measures). Snake identity ($N = 14$) was therefore fitted as a random effect, except when testing the effect of light level and season, because of the modest number of snakes tracked at night ($N = 6$) and during the dry season ($N = 4$). For this, we used generalized linear mixed models in R 3.0.3 (R Development Core Team, 2008). The significance of factors was obtained after performing an ANOVA on the models. We tested the effect of seafloor depth on dive category (benthic or pelagic) and the effect of dive shape on dive category using logistic regressions (no random effect, see above) in R 3.0.3. All graphs and regressions were plotted with SigmaPlot 10.0 (Systat Software Inc., Chicago, IL, U.S.A.). Data are graphically presented as means \pm SD per class, but all regressions were fitted on the raw data.

RESULTS

General Diving Behaviour

The 14 snakes produced a total of 177 dives. Snakes dived up to 50 m, with an average dive depth of 14 ± 8.7 m (Fig. 2a). The five tracked snakes dived over seafloors 31.5 ± 21.8 m deep (range 3–59 m, $N = 72$ dives; Fig. 2b). Dives were long, lasting up to 213.5 min. There was a positive relationship between dive duration and maximum dive depth (Fig. 2c) and between dive duration and the depth of the start of gradual ascent ($R^2 = 0.37$, $P < 0.0001$, $y = 3.63x + 10.87$). Postdive intervals were short (Fig. 2d) and there was no relationship between postdive interval and dive duration ($R^2 = 0.02$, $P = 0.112$).

S-shaped dives were by far the most frequent (84.7%) compared to V-shaped dives (15.3%). S-shaped dives reached greater depths and lasted longer than V-shaped dives (Table 1). Descents and ascents of V-shaped dives lasted longer and had slower vertical rates than in S-shaped dives (Table 1).

In S-shaped dives, the horizontal water layer comprising the first ascent phase was 3.2 ± 3.3 m thick on average. Gradual ascents were long (Fig. 3a), constituting 65.7% of the snake's time budget (Fig. 4). The speed of gradual ascent was the slowest of all vertical transit rates (0.002 ± 0.002 m/s). The horizontal water layer comprising the gradual ascent phase was only 3.3 ± 2.7 m thick (Fig. 3b). Intradepth zone dives represented 32.4% (the depth of the start of gradual ascent of the current dive $\pm 10\%$ of the depth of the start of gradual ascent during the preceding dive) and 9.7% (the depth of the start of gradual ascent of the current dive $\pm 10\%$ of the depth of the end of the gradual ascent phase reached during the preceding dive) of dives. Average depth of the end of gradual ascent was 8.5 ± 5.2 m.

Body Size

The influence of individual snake body size or condition on diving performance was assessed through linear regressions ($N = 14$). There was no effect of snake body mass, total length or body condition index on maximum individual maximum dive

depth, mean individual maximum dive depth, maximum individual dive duration or mean individual dive duration (all $P > 0.26$).

Bathymetry, Water Temperature and Diurnal Cycle

The difference between seafloor depth and maximum dive depth was on average 16.6 ± 15.7 m (maximum 46 m). Pelagic dives (68%)

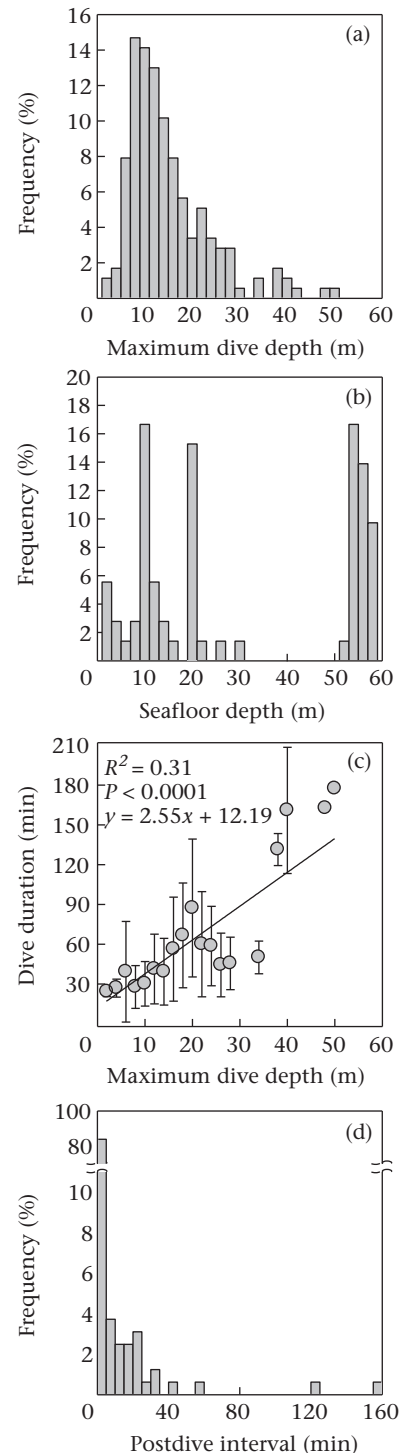


Figure 2. General dive parameters of *H. platurus*. (a) Frequency distribution of maximum dive depth. (b) Frequency distribution of seafloor depth beneath dives. (c) Dive duration as a function of maximum dive depth. (d) Frequency distribution of postdive interval.

Table 1
Comparison of dive parameters of S-shaped dives ($N = 149$) and V-shaped dives ($N = 27$) carried out by yellow-bellied sea snakes

Parameter	S-shaped		V-shaped		F	P
	Mean	Max.	Mean	Max.		
Maximum dive depth (m)	14.8±9	50	9.6±5.5	26	$F_{1,161}=12.30$	<0.0001
Dive duration (min)	52.8±39.8	213.5	19.9±13.6	70.2	$F_{1,154}=36.45$	<0.0001
Descent duration (min)	5.5±4.2	25.2	10.1±10.1	43.2	$F_{1,160}=17.78$	<0.0001
Descent rate (m/s)	0.068±0.068	0.529	0.049±0.061	0.246	$F_{1,160}=2.78$	0.097
First ascent duration (min)	5.9±3.9	21.1	—	—	—	—
First ascent rate (m/s)	0.013±0.016	0.109	—	—	—	—
Depth of start of gradual ascent (m)	11.6±6.8	33.9	—	—	—	—
Gradual ascent duration (min)	36.9±36.4	187	—	—	—	—
Gradual ascent rate (m/s)	0.002±0.002	0.014	—	—	—	—
Depth of end of gradual ascent (m)	8.4±5.2	27	—	—	—	—
Final ascent duration (min)	4.8±3.2	18.6	9.9±5.6	27	$F_{1,154}=36.39$	<0.001
Final ascent rate (m/s)	0.04±0.034	0.213	0.026±0.031	0.167	$F_{1,154}=6.22$	0.01
Postdive interval (min)	3.2±14.6	152.4	8.4±24.0	119.6	$F_{1,144}=3.27$	0.072

and benthic dives (32%) occurred over a seafloor of 42.1 ± 18.3 m (difference with maximum dive depth: 24.2 ± 13.2 m) and 8.7 ± 4 m (difference with maximum dive depth: 0.4 ± 3.9 m), respectively ($z = 3.39$, $P < 0.001$). There was a trend for dive category to influence dive shape, with S-shaped dives constituting 77% and 56% of pelagic and benthic dives, respectively ($z = 1.71$, $P = 0.08$).

The effect of season on diving behaviour was studied for S-shaped dives of four and 10 snakes during the dry and wet season, respectively ($N = 149$ dives). There was an effect of season on the depth of the start of gradual ascent ($F_{1,147} = 16.59$, $P < 0.0001$; Fig. 5a). Season also had an influence on water temperature at the start of gradual ascent ($F_{1,147} = 3001.7$, $P < 0.0001$; Fig. 5b). Finally, there was an effect of season on dive duration (interaction between dive duration and the depth of the start of gradual ascent: $F_{1,139} = 4.25$, $P = 0.041$; Fig. 5c).

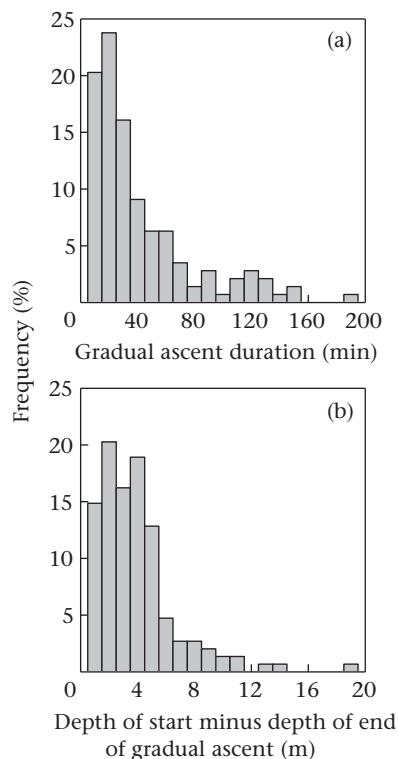


Figure 3. Gradual ascent in S-shaped dives of *H. platurus*. (a) Frequency distribution of gradual ascent duration. (b) Frequency distribution of the depth of the start minus the depth of the end of gradual ascent.

Diving frequency during daytime (5.3 dives/h) was double that at night (2.7 dives/h). Dives were shallower during the day (13.5 ± 8.2 m) than at night (17.7 ± 11.4 m; $F_{1,168} = 4.48$, $P = 0.036$). Dives were also shorter during the day (42.5 ± 34.3 min) than at night (90.3 ± 47.4 min; $F_{1,168} = 28.14$, $P < 0.0001$). Time of day had a significant effect on dive duration during daytime (Fig. 6a), in concordance with the frequency distribution of postdive intervals as a function of time of day (Fig. 6b).

Lung Volume and Depth of Neutral Buoyancy

For *H. platurus* to achieve neutral buoyancy within their diving range in the Gulf of Panama, inferred volume of the snake's lung at sea level should vary between 18.8 ml (neutral buoyancy just below the sea surface) and 111.8 ml (neutral buoyancy at 50 m; Fig. 7a). However, we assumed snakes were only capable of being neutrally buoyant within the range of depths at which they had carried out a gradual ascent, i.e. between their minimum depth of the end of gradual ascent and their maximum depth of the start of gradual ascent. Hence, inferred lung volume (and diameter) of snakes varied between 21.6 ml (0.7 cm) for neutral buoyancy at 1.5 m deep (assumed minimum snake lung volume) and 81.8 ml (1.4 cm) for neutral buoyancy at 33.9 m (assumed maximum snake lung volume; Fig. 7b). Mean inferred lung volume at sea level at the start of the gradual ascent phase was 40.5 ± 12.7 ml.

For snakes to remain neutrally buoyant during the slow gradual ascent of S-shaped dives, they must constantly lose some fraction of pulmonary volume. Total loss of lung volume during gradual ascent (5.9 ± 4.5 ml) increased logarithmically with gradual ascent duration and tended to level out at ca. 18 ml after 200 min (Fig. 8a).

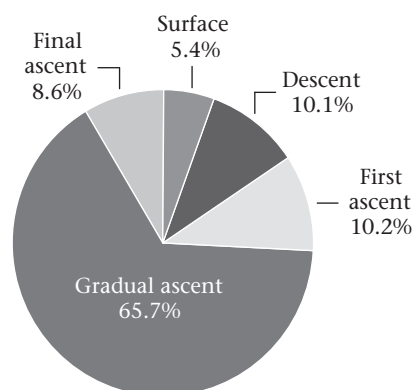


Figure 4. At-sea time budget of *H. platurus* carrying out S-shaped dives.

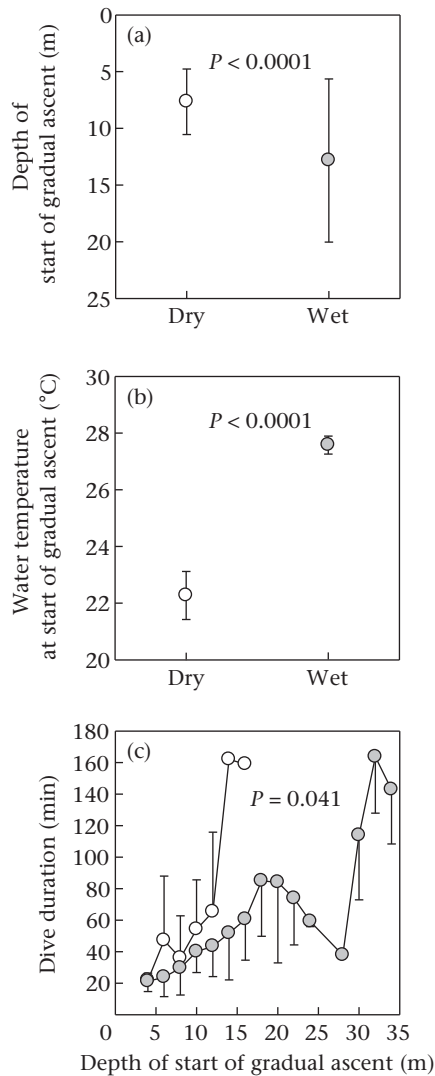


Figure 5. Influence of season on diving behaviour of *H. platurus* carrying out S-shaped dives. (a) Effect of season on water temperature at the start of gradual ascent. (b) Influence of season on the depth of the start of gradual ascent. The wet season corresponds to warm and stratified waters (thermocline at 50 m) and the dry season corresponds to cooler, unstratified waters (upwelling). (c) Dive duration as a function of the depth of the start of gradual ascent (wet season: grey circles are means – SD; dry season: white circles are means + SD).

Correlatively, rate of lung volume loss (0.2 ± 0.2 ml/min) decayed exponentially with gradual ascent duration and levelled out at ca. 0.1 ml/min after 200 min (Fig. 8b). During gradual ascent, season had a significant positive effect on loss of lung volume ($F_{1,140} = 7.64$, $P < 0.01$; Fig. 8c), and a close to significant negative effect on the rate of loss of lung volume ($F_{1,140} = 3.47$, $P = 0.064$; Fig. 8d).

DISCUSSION

The detailed analysis of the diving behaviour of *H. platurus* in the Gulf of Panama allowed a precise description and quantification of dive parameters, which were then linked to physiological and environmental variables. Dives were predominantly S-shaped (85%) lasting ca. 55 min on average (up to 3.5 h). Surface periods of these dives were usually short (<3 min), but could last up to 2.5 h. Dives were mainly pelagic (70%) and relatively shallow, reaching a mean maximum depth of ca. 15 m, over seafloors up to 60 m deep. They were longer at night than during the daytime and snakes

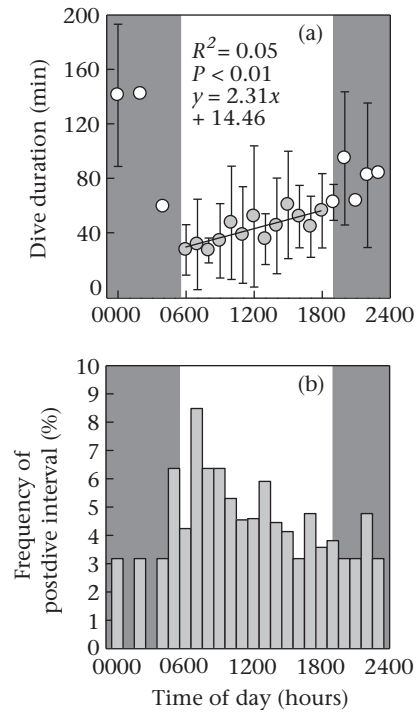


Figure 6. Influence of time of day on diving behaviour of *H. platurus* (night period in dark grey). (a) Dive duration and (b) frequency distribution of postdive interval as a function of time of day. Frequency was calculated for each hour as the mean of individual counts of postdive interval divided by the sum of all hourly means in the day.

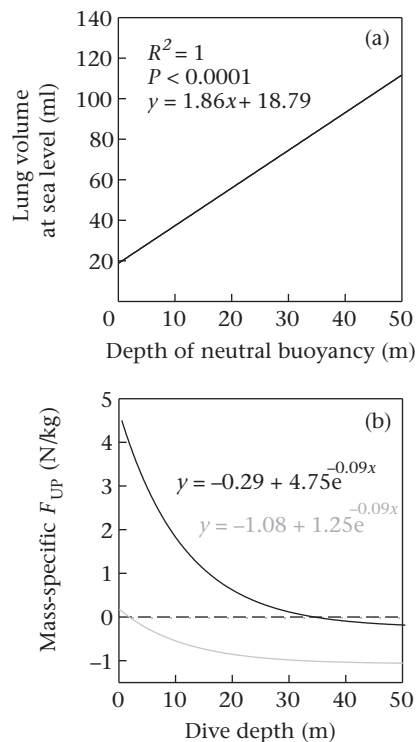


Figure 7. Influence of lung volume on buoyancy in *H. platurus*. (a) Relationship between lung volume and depth of neutral buoyancy (assuming snakes are neutrally buoyant throughout their diving range). (b) Mass-specific force of buoyancy (F_{UP}) on snakes as a function of dive depth for a snake diving with minimum lung volume (21.6 ml; grey line) and for a snake diving with maximum lung volume (81.8 ml; black line; all $R^2 = 0.99$, $P < 0.0001$).

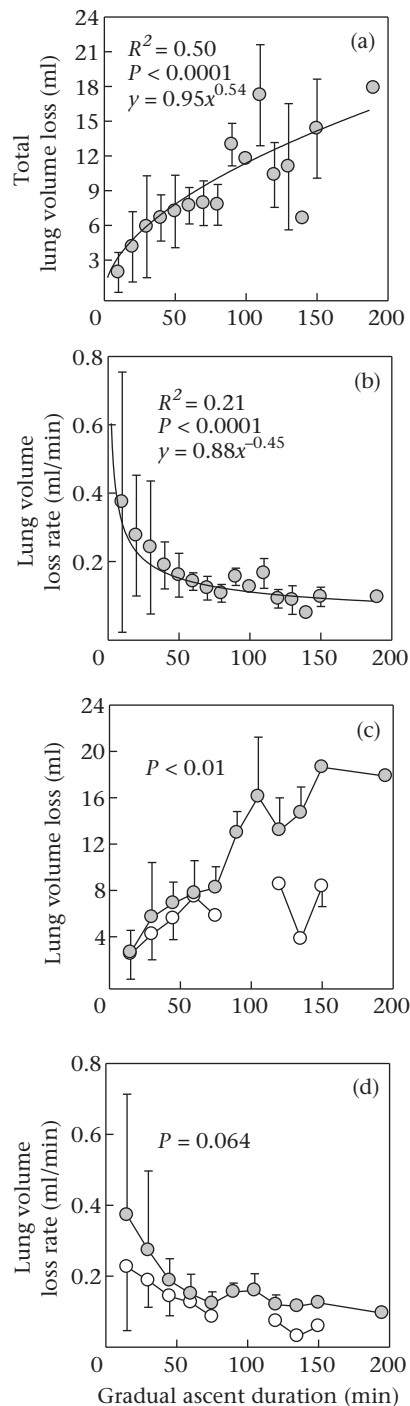


Figure 8. Influence of gradual ascent duration on lung volume in S-shaped dives of *H. platurus*. (a) Total lung volume loss during gradual ascent and (b) lung volume loss rate as a function of gradual ascent duration. (c) Lung volume loss and (d) lung volume loss rate as a function of gradual ascent duration for the wet season (warm water, grey circles are means + SD) and the dry season (cooler water, white circles are means – SD).

surfaced mostly between 0500 and 1300 hours (52% of surfacing events). Snakes targeted greater depths when the water was warm than they did during the cooler, upwelling season. They achieved neutral buoyancy in the 35 m depth zone with a maximally inflated lung volume of 82 ml. During the gradual ascent phase, snakes lost on average 6 ml of lung gas (15% of initial volume) at an average rate of 0.2 ml/min. This rate increased when sea water was warmer.

These results not only shed light on the ecology and physiology of *H. platurus*, but they also provide insights into understanding how and why this pelagic sea snake dives.

Lung Volume, Water Temperature and Dive Duration

Nearly 70% of the snake's time at sea corresponded to underwater gradual ascent, suggesting this is a key phase to understanding the evolutionary pressures driving the dive cycle of this species. Gradual ascent was slow (7 m/h), lasting on average ca. 40 min. In view of the high energetic costs of maintaining depth for such a long time in the absence of neutral buoyancy (particularly in such a small animal; Schmidt-Nielsen, 1972), it is most likely that snakes were neutrally buoyant during this whole phase. This suggests that one of the important roles of the gradual ascent phase is to reduce energy expenditure. For snakes to remain positively buoyant during ascent there must be a corresponding pulmonary deflation. This deflation is linked to the pulmonary removal of O_2 and N_2 during extended diving and the concomitant cutaneous release of CO_2 and N_2 (Graham et al., 1987). Gradual ascents corresponded to strictly positive ascents of snakes, i.e. there were (with rare exceptions) no moments of descent during these phases. In other words, snakes were regularly readjusting their depth in order to reach neutral buoyancy. Remarkably, gradual ascent occurred inside a thin horizontal layer of water only 3 m thick on average, suggesting acute senses in snakes for judging vertical body acceleration, allowing for quick compensation. For dives deeper than the depth of neutral buoyancy corresponding to a maximally inflated snake lung (ca. >35 m), snakes risk sinking or increasing energy expenditure to maintain depth or to ascend. Snakes could also use the seafloor to rest, as in some marine turtles (Hays et al., 2000; Hochscheid et al., 1999; Houghton, Broderick, Godley, Metcalfe, & Hays, 2002). However, dive profiles did not suggest this was the case in *H. platurus*, as benthic dives were not flat-bottomed. It is clear that, because of pulmonary deflation, resting on the seafloor would eventually lead to the snake becoming negatively buoyant, subsequently increasing the locomotor costs of ascent. Benthic dives comprised more V-shaped dives than did pelagic dives. We hypothesize that infrequent V-shaped dives may represent S-shaped dives that were aborted because of the proximity of the seafloor (Fig. 1c) and the associated costs of buoyancy regulation or even of predation.

Body size did not influence diving performance, which is consistent with findings in other studies on diving ectotherms (Brischoux, Bonnet, Cook, & Shine, 2008). In diving endotherms, mass-specific metabolic rate decreases with body size, explaining why larger species or individuals of diving birds and mammals can dive for longer, therefore potentially deeper than smaller ones (Cook, Lescroël, Cherel, Kato, & Bost, 2013). In diving reptiles, however, metabolism is comparatively low and this relationship is not established. In addition, in *H. platurus*, aquatic cutaneous exchange is responsible for an O_2 uptake of up to 33% of pulmonary O_2 uptake, a CO_2 excretion of 94% of pulmonary O_2 uptake and a substantial loss of N_2 to water. Such an adaptation should supplement a submerged snake with O_2 , while preventing respiratory acidosis and caisson disease (Graham et al. 1975; Lillywhite & Donald, 1989). Furthermore, by utilizing the intracardiac right–left shunt of its single ventricle, this species is thought to be able to efficiently manage its lung O_2 consumption (Graham, 1974). Despite such adaptations, it is likely that dive duration is limited by the amount of pulmonary O_2 and thus by pulmonary volume. Indeed, the positive relationship between maximum dive depth and dive duration can be explained not only by an increase in vertical commuting duration with maximum depth of dive, but also

by snakes diving with larger pulmonary air reserves in order to reach neutral buoyancy at greater depths.

Estimating respiratory volume is difficult in air-breathing vertebrates, particularly when the respiratory system is inflated or deflated voluntarily to extend dive duration or for buoyancy control (Cook, Lescroël, Tremblay, & Bost, 2008; Cook, Kato, Tanaka, Ropert-Coudert, & Bost, 2010). Our estimate of a maximally inflated lung volume was 82 ml, or 588 ml/kg, representing 41% of snake body volume (body + lung). Coincidentally, this value, estimated indirectly using the deepest depth of the start of gradual ascent, was similar to the volume (81 ml) found independently by Heatwole and Seymour (1975) using traditional anatomical investigation methods. The lung volume of snakes can be very large and may represent up to 30–53% of the body volume of snakes (body + lung; Lillywhite, 2014). Although there is consistency in the lung morphology of marine snakes, *H. platurus* is thought to have one of the largest relative lung volumes in sea snakes (Heatwole & Seymour, 1975), which is logical in a species that also uses its lung for advanced buoyancy adjustment.

It is possible to model maximum aerobic dive duration in *H. platurus* with a maximally inflated lung. We assumed that a maximally inflated lung contains 21% O₂ (17 ml of O₂), that a 139 g snake holds an additional 1 ml of O₂ in its blood and that it has negligible levels of muscle O₂ (Rubinoff et al., 1986). We also assumed that *H. platurus* has a field metabolic rate of 0.083 mlO₂/g/h at 30 °C (Rubinoff et al., 1986). By applying a Q₁₀ factor of 2, we estimated a field metabolic rate of 0.048 mlO₂/g/h and 0.072 mlO₂/g/h at 22 °C and 28 °C, respectively (average water temperatures experienced by snakes in the Gulf of Panama during the dry and wet season, respectively). Maximum aerobic dive duration was thus calculated as 2 h 45 min and 1 h 50 min at 22 °C and 28 °C, respectively. However, with a concomitant cutaneous O₂ uptake of 33% of field metabolic rate, snakes would also have absorbed at the end of their maximum aerobic dive duration the equivalent in O₂ of an additional submergence time of 55 min and 33 min in 22 °C and 28 °C waters, respectively. By adding these two values (i.e. 2 h 45 min + 55 min), it is possible for snakes diving in 22 °C waters to reach the maximum dive duration recorded in the Gulf of Panama (3 h 33 min). This finding differs from the estimate by Graham et al. (1987) of a maximum aerobic dive duration of 45 min at 25 °C, and is due to the difference in estimated pulmonary volume at sea level necessary for being neutrally buoyant in the 30–35 m depth zone between our study (ca. 80 ml) and their own (ca. 30 ml). See Heatwole and Seymour (1975) for similar differences between Graham (1974) and their own measurements.

Our model is limited by several assumptions which we were unable to verify, in particular that pulmonary O₂ was indeed 21% of lung volume upon diving, that it was entirely exhausted during the dive and that the metabolic rate of submerged snakes was constant. Yet, the remarkable similitude between our estimates of relative lung volume and the independent measurements of Heatwole and Seymour (1975) suggest that our model should not generate spurious patterns. Our model indicates that *H. platurus* can extend dive duration substantially by increasing its pulmonary air reserves upon diving and that dive duration is also dependent upon metabolism, which itself depends on water temperature. This is illustrated by the significant effect of season (cold or warm water) on dive duration, the significant effect of season on volume of pulmonary deflation and the nearly significant effect of season on rate of pulmonary deflation.

Why Does *H. platurus* Dive?

The link between lung volume, water temperature and dive duration raises questions about the drivers of dive cycle

management in *H. platurus*. Snakes might decide to dive deeper to target layers of water that are colder than near the surface, hence reducing metabolism and, as a consequence, energy expenditure and speed of physiological processes, such as digestion. This would have been possible during the wet season, despite high stratification of the warm waters, providing a difference in temperature of 3 °C between the surface and the beginning of the thermocline at 50 m. During the dry season, water temperature decreased quickly with depth (6 °C difference between the surface and 25 m), offering an even wider range of thermal environments over a smaller range of depth. However, any dive below 25 m would have exposed snakes to their lower thermal threshold (<19 °C), under which they cease feeding, display strongly reduced movement capacities and may even die (Dunson & Ehlert, 1971; Graham, Rubinoff, & Hecht, 1971). Accordingly, snake dives were shallow during the dry season, when deeper waters were cold. Frequently, snakes targeted the same depth zone of gradual ascent, dive after dive, a behaviour that could represent the selection of a specific water layer, perhaps because of its thermal characteristics.

Although temperature appears important, it is certainly not the only factor influencing behaviour. Another clue to understanding why *H. platurus* dives is to examine what it does when it is on the sea surface. There are two main reasons why snakes need to surface: to replenish O₂ reserves and to feed. (1) The majority of postdive intervals were very short and were therefore not related to feeding activity. Instead, they probably corresponded to postdive and pre-dive respiratory activity. This should be quick in a species that has little CO₂ to offload because of cutaneous excretion during the dive. Furthermore, the absence of significant haemoglobin and myoglobin O₂ stores means that snakes only need the surface time necessary to renew their pulmonary O₂ reserves. Most likely, many surface periods corresponded simply to a rapid turnover of pulmonary gases, i.e. the snake exhaling and inhaling once before submerging again (see Brischox, Bonnet, Cook, & Shine, 2007 for sea krait species). (2) *Hydrophis platurus* are surface feeders that ambush small and larval fish concentrated under floating debris at the sea surface (Dunson & Ehlert, 1971; Rubinoff et al., 1986). A previous study has demonstrated that the probability of finding foraging *H. platurus* at the sea surface on a slick was significantly higher when flotsam was abundant, and when solar irradiance was high: two parameters that should help snakes detect a potential food patch from below, while floating in the water column (Brischox & Lillywhite, 2011). We hypothesize that only surface periods longer than 5 min allowed sufficient time for foraging activity; these represented only 10% of surfacing events. Accordingly, 100% of these long surfacing events occurred during the daytime, which is consistent with the foraging activity of a visual predator. Hence, following the hypothesis of Brischox and Lillywhite (2011), submergence in *H. platurus* during the day may enhance the detection of foraging patches. Probably as important as light intensity and water turbidity is depth of the snake itself. At the sea surface, the snake's vantage point is very limited, with swell obscuring the horizon even further. However, underwater its field of view is expanded and the deeper it dives, the greater the area of sea surface it can observe (up to a certain depth), hence increasing probability of slick or prey detection.

During the tracking of the snakes at sea, Rubinoff et al. (1986) observed surfacing events as short as 1 s, particularly during rough seas, which lends support to the idea that *H. platurus* only need one breathing cycle to replenish almost fully their O₂ reserves. These observations also suggest that submergence in this species could be influenced by the need to escape from unstable conditions at the sea surface, as suggested for the loggerhead turtle, *Caretta caretta* (Minamikawa et al., 2000; Sakamoto, Naito, Uchida, & Kureha, 1990) or for animals that are not air breathing, such as

jellyfish (Houghton, Doyle, Davenport, & Hays, 2006). The pitching and rolling caused by wave action may be uncomfortable or even costly for snakes if they have to make an effort to maintain a stable trim. Interestingly, snakes surfaced more frequently in the morning, which is when sea conditions are generally calmer (Ueyama & Deser, 2008). Swell also disrupts the formation of slicks or drift lines (which are associated with snake feeding) that occur as the result of Langmuir circulation, internal waves or convergent currents (Barstow, 1983). Hence, surfacing during the daytime and when the sea is calmer (more usually in the morning) has several advantages.

In summary, *H. platurus* can be called 'surfacers', rather than 'divers', a term coined by Kooyman (1989) to refer to those species, such as marine turtles, that spend more time submerged than at the surface or out of the water. The natural habitat of *H. platurus* is under water, where they spend an imposing 95% of their time. They could stay submerged to avoid unfavourable surface and subsurface sea conditions while at the same time benefiting from the reduction in energy expenditure gained from the decrease in locomotor activity during neutral buoyancy. Diving deeper allows for longer dives because of the associated larger O₂ reserves and this strategy should be preferred when snakes wish to avoid surfacing too frequently, such as during rough seas, or at night when there is little to no feeding activity. One cannot rule out that diving may also serve as an antipredator response to aerial predators or to marine predators that use the contrast between the animal's silhouette at the sea surface and the lighter sky above to locate their prey from underneath (although this seems unlikely when snakes forage on slicks among floating debris, see Lillywhite, Solorzano, Sheehy, Ingley, & Sasa, 2010 for pictures). Gradual ascent phases could also help this species detect and move towards oceanic slicks: processes that are unlikely to be random and passive (Brischoux & Lillywhite, 2011). Under water, snakes can reduce energy expenditure further by lowering metabolism through the targeting of colder water layers, such as during the night, when they dive deeper. Surfacing in *H. platurus* appears driven mainly by the imperatives of replenishing O₂ reserves and feeding, and examination of surface durations suggests that the latter behaviour is not frequent. A third reason for surfacing, and not a minor one, could be for drinking freshwater. *Hydrophis platurus* dehydrate at sea and may spend up to 6–7 months in a dehydrated state because of seasonal droughts (Lillywhite, Sheehy, Brischoux, & Grech, 2014). They are suspected of rehydrating by drinking the freshwater that accumulates at the sea surface during the heavy rains of the wet season (Lillywhite et al., 2014). We hypothesize that surfacing events should mirror this strong physiological constraint and thus be more frequent during the wet season. Here, 75% of postdive intervals longer than 5 min occurred during the wet season. However, the sample size was low and further studies will be necessary to quantify the relative contribution of different behaviours to surface periods. Clearly, the different reasons cited above for diving or for surfacing in *H. platurus* need not be mutually exclusive.

Review of 'S Diving' in other Divers

It is impossible not to draw a parallel with the diving behaviour of some marine turtles. Marine turtles are also typical 'surfacers', spending up to 90% of their time submerged (Hochscheid, Bentivegna, Hamza, & Hays, 2010). S-shaped dives have also been recorded in some turtle species: in the green turtle, *Chelonia mydas* (Hatase, Sato, Yamaguchi, Takahashi, & Tsukamoto, 2006; Hays et al., 2001; Hays, Metcalfe, Walne, & Wilson, 2004; Hochscheid, Bentivegna, Bradai, & Hays, 2007; Hochscheid et al., 1999; Rice & Balazs, 2008; Salmon, Jones, & Horch, 2004; Seminoff, Jones, &

Marshall, 2006; Thomson, Heithaus, & Dill, 2011), the loggerhead turtle (Fossette, Schofield, Lilley, Gleiss, & Hays, 2012; Houghton et al., 2002; Minamikawa et al., 1997, 2000; Thomson et al., 2011), the hawksbill turtle, *Eretmochelys imbricata* (Storch, 2003), and the flatback turtle, *Natator depressus* (Sperling et al., 2010). The function of S-shaped dives remains unclear (Hays et al., 2001; Hochscheid, 2014), but we believe that the gradual ascent phase of such dives serves the same resting function as in *H. platurus*, with neutrally buoyant turtles reducing energetic expenditure by hovering effortlessly in the water column, while escaping sea conditions above, or predation at the surface or near the seafloor. Thus, turtles, despite low cutaneous exchange, must experience progressive lung deflation with gradual ascent, probably because of consumption of pulmonary O₂ and accumulation in the blood of some of the CO₂ that does not return to the lungs. To counter this, they adjust continuously to the depth of neutral buoyancy by infrequent, but regular flipper beating (Hays et al., 2004). Whether they are resting on the bottom or in mid-water, turtles may be dormant (Houghton et al., 2008), as the greater occurrence of S-shaped dives at night in migrating green turtles suggests (Rice & Balazs, 2008). Similarly, it is likely that *H. platurus* are sometimes asleep (particularly at night) during gradual ascent and that they also readjust depth automatically through gentle but regular movements of their body.

The comparison with turtles is all the more interesting in that the two groups have different foraging modes (as do different species of turtles among themselves): *H. platurus* forage on the surface, whereas adult turtles forage almost exclusively benthically or in the water column. This strengthens the idea that S-shaped dives in both groups serve a common purpose that is not necessarily related to food. In this regard, the function of the maximum depth of the dive, which is deeper than the depth of the start of gradual ascent, remains 'enigmatic', in the words of Hays et al. (2001). This phase varies considerably in depth, from a few metres to four times the depth of the start of gradual ascent (Rice & Balazs, 2008). In *H. platurus*, it is thought to represent snakes overshooting the targeted depth and then reascending slowly to enter the gradual ascent phase at the perfect depth of neutral buoyancy (Graham et al., 1987). It is difficult to believe that it serves the same function in all turtles, considering the extent by which animals may sometimes overshoot neutral buoyancy. It might represent some exploratory behaviour, animals searching for the seafloor, for food (Rice & Balazs, 2008) or for a favourable thermal environment. However, the reasons why animals would search for the seafloor are not clear (particularly if there is a predation risk associated with staying near the bottom) and the feeding hypothesis, as explained above, contradicts the occurrence of S-shaped dives in species with different foraging modes.

Conclusion

The detailed analysis of the diving behaviour of *H. platurus* has shown how this exclusively marine species of tetrapod manages its dive cycle and the influence environmental parameters have upon its diving and surfacing behaviours. This has opened the door to a better understanding of the adaptations developed by this species. Interestingly, there is an important parallel in behaviour between *H. platurus* and several species of marine turtles. Adaptations in both these lineages of reptiles reflect a response to pressures of the marine environment experienced during the evolutionary transition from terrestrial to oceanic life. Unfortunately, the behaviour of sea snakes at sea is still inadequately known compared to that of marine turtles (Ropert-Coudert, Beaulieu, Hanuise, & Kato, 2010), despite being a highly diversified group comprising four families and ca. 90 species (Murphy, 2012; Sanders, Lee, Mumpuni, Bertozzi, & Rasmussen, 2013). We suggest behavioural studies can help fill

this gap, contributing at the same time to our understanding of other taxa.

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