

Snakes at sea: diving performance of free-ranging sea kraits

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Abstract. Evolutionary transitions from terrestrial to marine life pose massive physiological challenges. Marine mammals and birds exhibit major adaptations of cardiovascular and respiratory physiology to increase the depths to which they can dive, and the time for which they can remain underwater. Marine reptiles have attracted far less attention in this respect, but we would expect ectotherms to outperform endotherms in several dive performances because ectothermy reduces oxygen demand. We surgically implanted dive-loggers in amphibious sea snakes (sea kraits, *Laticauda laticaudata* and *L. saintgironsi*) in the lagoon of New Caledonia, and recorded dive performance (e.g., depths, durations and post-dive intervals) for two free-ranging animals over periods of 8 and 11 weeks. During foraging excursions the snakes spent > 80% of their time underwater, diving > to 80 m and for periods of > 130 min. Inter-dive intervals were brief, typically < 45 sec, suggesting that dives were aerobic. Dive patterns in these animals differ in major respects from those of previously-studied marine endotherms, turtles and pelagic sea snakes.

1 INTRODUCTION

Evolutionary transitions in habitat use provide exceptionally powerful opportunities to understand the selective pressures operating on morphology, physiology and behaviour, especially if the novel habitat poses physical challenges different from those experienced in the ancestral habitat type. For example, aquatic life exerts major selection on attributes such as the ability to move efficiently through water, to remain underwater for long periods without needing to surface to breathe, and to dive to considerable depths (Kooyman, 1989). The morphological, physiological and behavioural attributes that facilitate such tasks are very different from those required in the day-to-day lives of most terrestrial organisms. Accordingly, lineages of terrestrial vertebrates that have evolved to exploit marine habitats provide many striking examples of adaptation to aquatic life (Boyd, 1997; Kooyman, 1989).

Some of the most clearcut examples of adaptation to marine life involve modifications of endothermic vertebrates (whales, seals, penguins, etc.) related to diving performance (Butler and Jones, 1997; Boyd, 1997). Notably, compared to their terrestrial homologues, diving endotherms are able to store large amounts of oxygen via abundant haemoglobin and myoglobin, and increased blood volume. They also reduce oxygen needs while diving by reliance on anaerobic metabolism, peripheral vasoconstriction, bradycardia, and decreased body temperature (Butler and Jones, 1997; Boyd, 1997). Likewise, cardiovascular

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adjustments and reinforcement of body cavities reduce susceptibility to the high hydrostatic pressures encountered at depth.

Despite these adaptations, air-breathing vertebrates are highly constrained in dive duration and depth. Prolonged dives inevitably increase plasma CO₂ levels and reduce oxygen stores; the resultant shift to anaerobic metabolism increases lactic acid concentration which in turn forces the animal to spend even longer periods of time resting at the surface after dives, breathing to purge its physiological debt (Butler and Jones, 1997). Although such issues are universal for air-breathers, they should apply with much less force to ectotherms than to endotherms. Indeed, Pough's seminal (1980) review of the advantages of ectothermy identified the exploitation of underwater niches as a key adaptive zone available to ectotherms. First, the low metabolic rates of ectotherms (comparatively to endotherms) reduce oxygen needs, so that a given oxygen store can support the animal's activities for a much longer period. Second, at least in the tropics, because water temperatures are so high, thermal exchanges between animals and the surrounding water are not a limiting factor on snake metabolism. Accordingly, ectotherms escape the body-shape constraints associated with endothermy, and can exhibit high ratios of surface area to volume that in turn allow for high rates of oxygen uptake underwater across the body surface (Avolio et al., 2006).

These contrasts suggest that all else being equal, marine ectotherms should outperform endotherms in several aspects of dive performance. Hence, we expect to see that marine reptiles should exhibit longer, and potentially deeper dives, more leisurely rates of ascent and/or descent, and shorter post-dive intervals, than would be possible for marine endotherms. Available data are not adequate to test this prediction, because studies have focused strongly on endotherms whereas marine reptiles have attracted far less attention. The most detailed studies come from work with marine turtles (Eckert et al., 1989; Sakamoto et al., 1993; Southwood et al., 1999; Hochscheid and Wilson, 1999; Hochscheid et al., 1999, 2005; Hays et al., 2004; James et al. 2005). Surprisingly, marine turtles display maximum dive-depth and dive-duration values within the range of those observed in mammals and birds (Schreer and Kovacs, 1997). They are able to remain under water for long time periods when environmental temperatures are low (Butler and Jones, 1982), but animals in this situation are in torpor and virtually motionless. Similarly extended submergences have been recorded in inactive individuals not only in other species of reptiles (Andersen, 1961; Wood and Moberly, 1970; Wood and Johansen, 1974; Ultsh et al., 1999) but also in mammals (hippopotamus, Pocock, 1918 in Parker, 1935). Therefore, such dive durations cannot be compared directly with those of actively foraging endothermic vertebrates (i.e., foraging diving must be clearly distinguished from torpor). Thus, for comparison with active aquatic endotherms, we need data on free-ranging ectothermic animals in the course of their daily foraging activities.

The recent development of miniature data loggers (Time-Depth Recorders, TDRs) has the potential to enormously facilitate such studies. Such units have clarified dive patterns in marine turtles (Eckert et al., 1989; Sakamoto et al., 1993; Southwood et al., 1999; Hochscheid and Wilson, 1999; Hochscheid et al., 1999, 2005; Hays et al., 2004; James et al., 2005) but as yet, have not been applied to the wide array of marine reptiles belonging to other lineages. Snakes are of particular interest in this regard, because aquatic habits have evolved independently in at least 4 separate phylogenetic lineages of these elongate animals (Heatwole, 1999). Two of those origins, in particular, have resulted in familial-level radiations of sea snakes: the Hydrophiidae (or "true sea snakes") and Laticaudidae (or "sea kraits"). The only sea snake from either lineage previously studied in detail with respect to

dive performance is a hydrophiid, the pelagic *Pelamis platurus* (Rubinoff et al., 1986). Although pioneering, these authors relied on externally-mounted transmitters that generated substantial drag on swimming snakes and had very limited memory. Furthermore, *P. platurus* displays unusual diving behaviour, in that it apparently dives to avoid surface currents rather than to feed, unlike all other sea snake species.

In this study, we investigated the diving behaviour of two species of sea kraits. The aim was to implant for the first time Time-Depth Recorders (TDRs) surgically on sea snakes in order to provide novel quantitative data on time-budget and diving behaviour.

2 MATERIAL AND METHODS

2.1 Study site and species

Fieldwork was conducted from December 2005 to March 2006 on Signal Island, a 6-hectare islet in the southwest lagoon of New Caledonia, 15 km west of Nouméa and 10 km from the external reef barrier ($22^{\circ}17'46''$ S; $166^{\circ}17'35''$ E, Fig. 1). Sea-kraits are large (up to 1.5 metre) venomous snakes that forage in the ocean, mostly on anguilliform fishes, and return to land to digest their prey, mate, slough their skins, and lay their eggs (Heatwole, 1999; Shetty and Shine, 2002a). Two species of sea kraits are broadly sympatric in New Caledonia: *Laticauda saintgiroisi* (Cogger and Heatwole, 2006; formerly regarded as part of the wide-ranging *L. colubrina* Schneider 1799) and *L. laticaudata* (Linné 1758, [Saint Girois, 1964; Ineich and Laboute, 2002]).

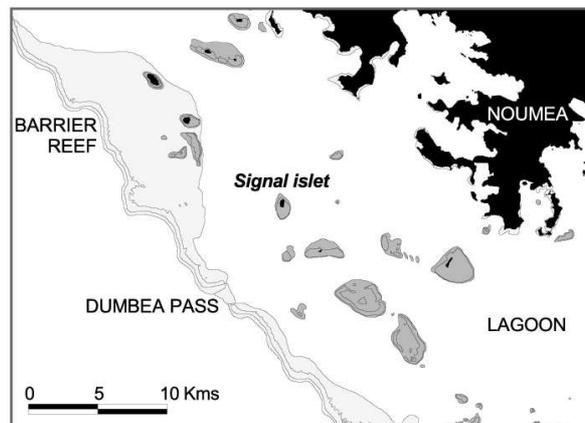


FIG. 1 - Study area. Signal Island is situated in the SW lagoon of New Caledonia ($22^{\circ}17'46''$ S; $166^{\circ}17'35''$ E). Black areas indicate emergent land (mainland and islands); grey areas represent coral reef flats. The barrier reef and other fringing reefs are represented by the light grey areas.

2.2 Devices

A total of five sea kraits (1 male and 2 female *L. laticaudata*; 2 female *L. saintgironsi*) were captured on Signal Island and fitted with Time-Depth Recorders (TDR LTD-1110 dataloggers, Lotek Wireless Inc., Canada). As this was the first attempt to describe diving behaviour in sea snakes, we were unable to predict the parameters needed to program TDRs with the optimal sampling interval. For example, it was impossible to know how long it would take to the snakes to recover from surgery and undertake a new fishing trip, or when the snakes would be recaptured after fishing trips. We therefore programmed the TDRs to record data with a variable sampling interval: when the 32kb tag memory was filled, the sampling interval doubled, decreasing precision of diving parameters but retaining information on mean dive depth and duration of foraging trips and periods on land. Depth and temperature reading resolution was ± 1 m and ± 0.1 °C, respectively.

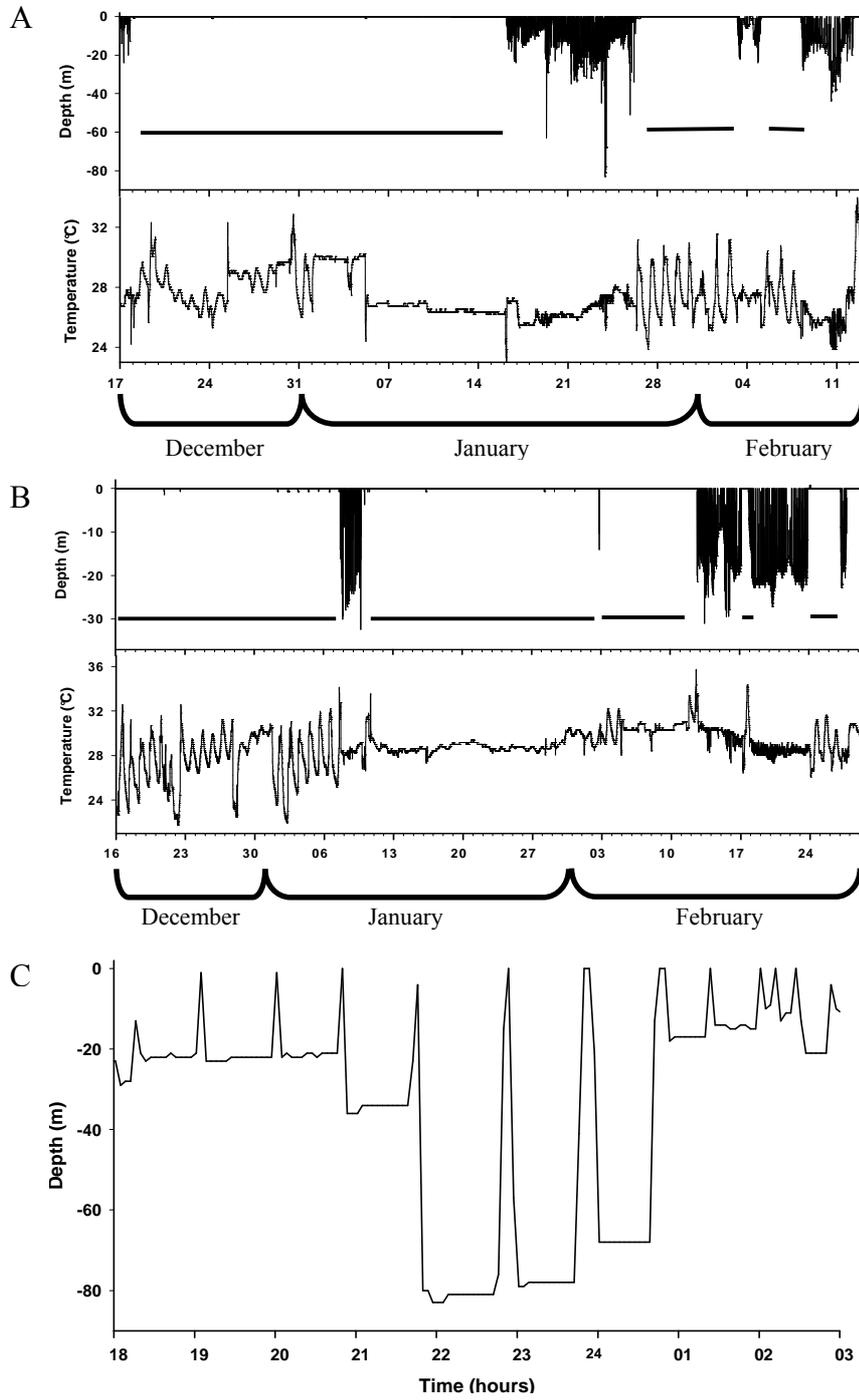
To facilitate relocation and recovery we also implanted a small radio-transmitter (SI 2; Holohil Systems Ltd., Canada) in each snake. The combined mass of the data-logger (11mm \times 32mm, 2g) and transmitter (11mm \times 33mm, 9g, with a 20 cm whip antenna) corresponded to 2 to 5% of the snake's body mass, in accordance with Kenward's (1987) recommendations. For comparison, we note that the transmitters used by Rubinoff et al. (1986) were slightly larger than our own (based on linear dimensions, they probably weighed about 6 to 8% of snake mass).

2.3 Surgery

Snakes were captured by hand while crossing the beach. There are no buildings on Signal Island, so surgery was conducted under shelter on a sterilized beachside table. Snakes were anaesthetised using isoflurane gas (Abbott Laboratories, Illinois, USA) administered through a mask; induction of anaesthesia required ~ 10 min. Surgical instruments were heat-sterilized and the animal's skin was disinfected with Bétadine[®]. Loggers and transmitters were cleaned with bleach and dried with sterile cloth prior to insertion. Snakes were incised laterally on the left side (to avoid a major midventral vein, and the lung which lies towards the right side of the body). The incision was made with surgical scissors just posterior to the stomach and the transmitter inserted first (the whip antenna was inserted under the skin towards the tail). The TDR was placed posterior to transmitter, with the pressure sensor facing the animal's tail. The 3-cm long incision was stitched with resorbable surgical thread (4 stitches per incision), and again disinfected with Bétadine[®]. Total duration of each operation was ~ 45 min. Snakes usually recovered from anaesthesia within 5 min of the cessation of surgery, and were then kept in calico bags and released after 48 hours of careful monitoring.

2.4 Tracking

We tracked the snakes with a directional antenna and an AVM LAQ12 receiver daily or more often during a 5-week period immediately following release, and then during a 2-week period 15 days later, in order to monitor behaviour and determine if and when snakes left the islet to forage at sea. Immediately after release, snakes stayed hidden under rocks or in bird burrows for a mean period of 27 ± 7 days. After sloughing (direct observation of two snakes), the snakes began to alternate foraging trips at sea with periods on land (fig. 2A,B).



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FIG. 2 - Examples of depth and temperature recordings by implanted data-loggers (A) for *L. saintgironsi* and (B) for *L. laticaudata*. Horizontal black lines correspond to time spent on land. Plot (C) provides a detailed view of deep dives for *L. saintgironsi* during the night between the 23rd and the 24th of January 2006. Interestingly, this profile is virtually the inverse of that seen in aquatic endotherms - if read upside-down, it resembles a classical endotherm dive profile, with short dives and long recovery periods.

Three of the five snakes were recaptured 2 to 3 months after release, but one of these animals had remained on land for the entire intervening period. The remaining snakes (1 female *L. laticaudata* and 1 female *L. saintgironsi*) underwent foraging trips (confirmed by their absence from the islet, and by finding food inside one of these snakes when it returned) and hence provided useful data for the current analysis.

2.5 Data analysis

Most of our data had a long (450 sec) sampling interval, but we obtained more detailed (one sample per 225 sec) data on a 10-day foraging excursion by the female *L. saintgironsi*. Dive parameters for this fishing trip were analysed using Multitrace (Jensen Software Systems) to calculate dive depths, dive durations, and post dive intervals (PDIs) for all dives. Ascent and descent rates were calculated only for a single dive that presented enough data points during the ascent and the descent. Data from all other sampled fishing trips were used for trip duration estimates and time-at-depth analyses. Below, mean values are given \pm standard deviations.

3 Results

3.1 Duration of aquatic and terrestrial activity phases

Post-recovery, fishing trips alternated with periods on land (Fig. 2A,B,C). Overall, foraging trips lasted an average of 3.70 ± 3.31 days (range 0.05-10.14 days) and periods on land averaged 7.04 ± 8.25 days (range 0.64-24.00 days). While at sea, the two sea-kraits spent little time at the sea-surface (Fig. 3). Overall, during their aquatic life the snakes averaged 19% of time on the sea surface.

3.2 Depth profiles

Foraging snakes used a wide range of dive-depths, from 1 to 83 m. Of the two snakes studied, the *L. saintgironsi* tended to use both shallower and deeper water than did the *L. laticaudata*, which used intermediate depths (Fig. 3).

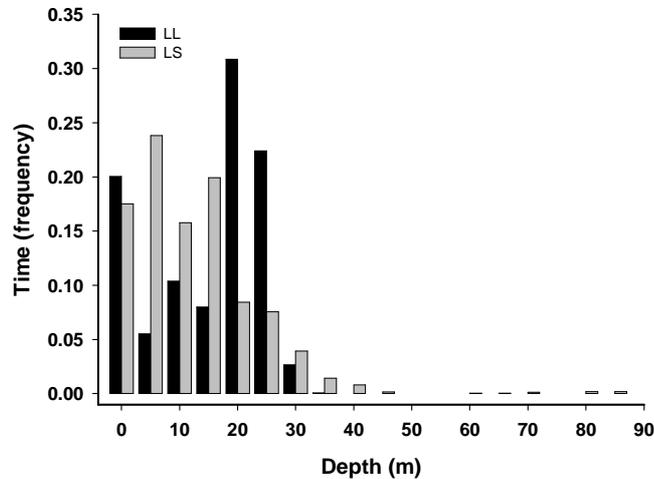


FIG. 3 - Distribution of the time-at-depth profiles for two species of sea-kraits. Black and grey bars represent *Laticauda saintgironsi* and *L. laticaudata* respectively. Maximum dive depth was 83 m for *L. saintgironsi* and 32 m for *L. laticaudata*.

3.3 Detailed analysis of foraging trip by *L. saintgironsi*

During this 10-day trip, the snake dove 833 times (84.1 ± 18.1 dives/day). Those dives occurred both during the day (525 dives, ~ 4 dives/hour) and at night (308 dives, ~ 3 dives/hour; $\chi^2=56.53, df=1, p<0.001$). Overall dive depth averaged 12 ± 8 m, with a range of 1 to 83 m. Most dives were < 30 m (Fig. 3), and during the course of a single dive the snake tended to remain at the same depth throughout its foraging period (Fig. 2C). Mean depths were similar for diurnal dives (12 ± 7 m) versus nocturnal dives (12 ± 10 m; t-test, $p=0.32$). Dive duration averaged 16 ± 12 min (range 4 to 138 min) and averaged slightly longer by night than by day (20 ± 16 vs. 14 ± 10 ; t-test, $p<0.001$). Periods spent at the sea surface between dives were remarkably brief, averaging 0.7 ± 4 min (< 225 sec to 68 min) and affected only slightly by time of day (diurnal mean 0.5 ± 2.5 , nocturnal mean 1 ± 6 min; t-test, $p=0.04$). Ascent and descent rates calculated on one dive were relatively slow and gradual (0.26 m/sec for both rates).

The duration of the post-dive interval was not correlated with prior dive duration (Fig. 4A), but we detected a weak but statistically significant correlation between dive duration and dive depth ($F=115.9, df=1.8, r^2=0.12, p<0.001$, Fig. 4B). The temperature range experienced by the snake during a dive tended to decrease with depth, but the trend was not statistically significant ($F=1.19, df=1, r^2=0.08, p=0.29$, Fig. 5).

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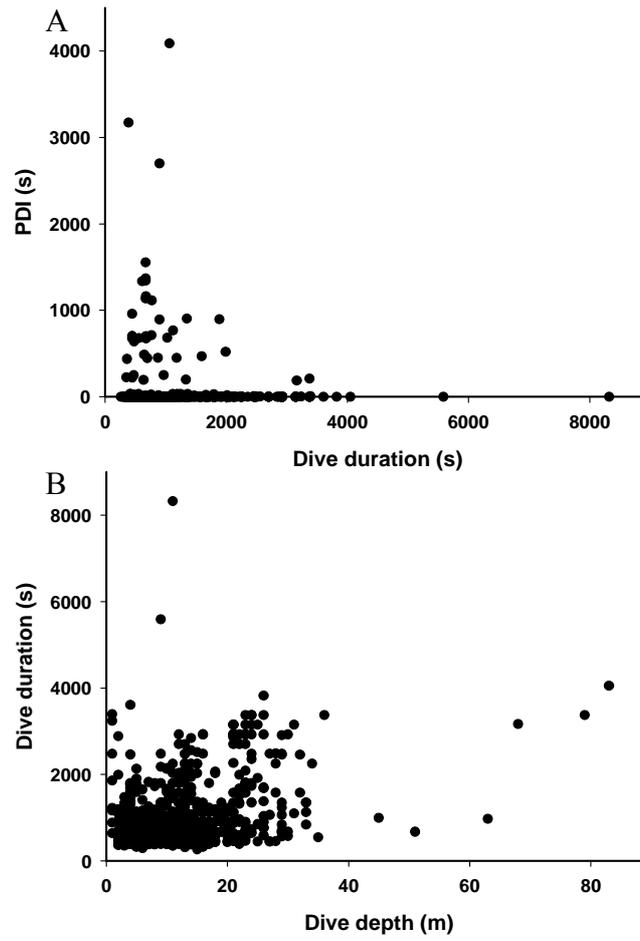


FIG. 4 - (A) Post dive interval (PDI) in relation to dive duration, and (B) dive duration in relation to dive depth for the sea krait *L. saintgironsi*.

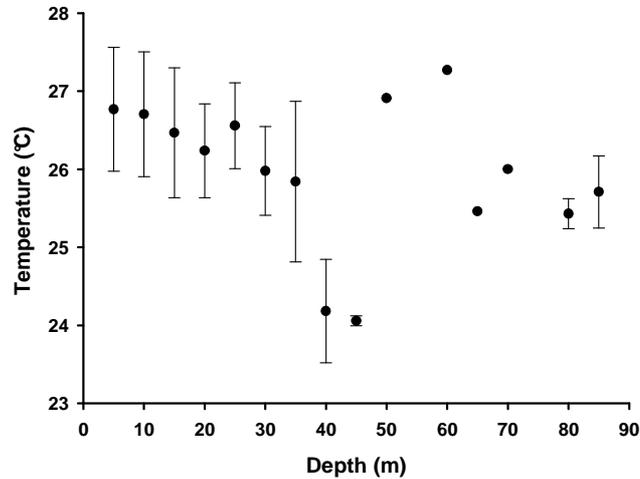


FIG. 5 - Body temperature (mean \pm SD) in relation to dive depth experienced by the sea krait *L. saintgironsi*.

3.4 Diving performance relative to previously-studied species

The extensive data available for marine endotherms and turtles provide an interesting comparison with our results for sea kraits. Perhaps the most consistent pattern emerging from the published literature is the relationship between body mass and maximum dive duration: larger animals can stay underwater for longer (Schreer and Kovacs, 1997; Halsey et al., 2006; Fig. 6A). As predicted (see Introduction), ectotherms exhibit greater maximal dive durations than do endotherms of comparable body mass. Maximum dive depths on the other hand, are similar to the depths reached by foraging sea birds (fig 6B).

All of the sea snakes for which we have data (present study, Heatwole, 1975; Rubinoff et al., 1986; Fig. 6A,B) exhibit dive durations unachievable by endotherms < 100 kg (Fig. 6A). For most of these species, dive duration data were obtained by direct observations, and probably do not represent physiologically maximal dive durations for the species involved (Heatwole 1975). Nevertheless, for the two species for which we have continuous recording over a large number of dives, the superiority in dive performance over endotherms is spectacular: both *Pelamis platurus* (mean 137 g, Rubinoff et al. 1986) and *Laticauda saintgironsi* (390 g, present study), exhibited dive durations unachievable by endotherms < 600 kg (Fig. 6A).

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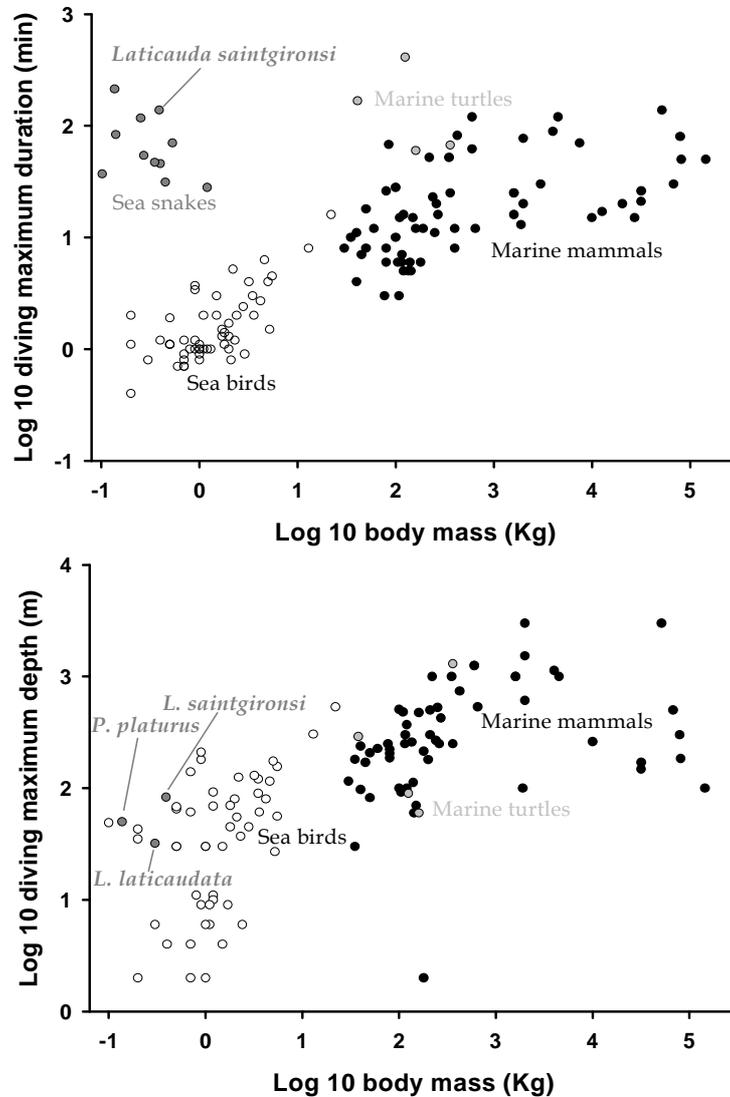


FIG. 6 - Allometric relationship between body mass and maximum dive duration (A) and maximum dive depth (B) in several species of air-breathing diving vertebrates. For sea birds (open circles), marine mammals (black circles) and marine turtles (light grey circles), data on body mass (kg), maximum dive duration (min) and maximum dive depth (m) were gathered from Schreer and Kovacs 1997. We updated the data on marine turtles with recent studies (Dermochelys coriacea Southwood et al. 1999, Caretta caretta Hochscheid et al. 2005, Chelonia mydas Hays et al. 2004). For sea snakes (dark grey circles), we used data from the present study (depth and duration for *L. saintgironsi*, depth only for *L. laticaudata*) and the data available in the literature (duration and depth for *Pelamis platurus*, Rubinoff et al. 1986; duration only for nine other species of sea snakes, Heatwole 1975).

4 Discussion

4.1 The method

Despite a limited sample size in terms of numbers of individual animals, our study provides the most extensive data set available in terms of numbers of dives and detail of depths, durations and post-dive intervals for free-ranging sea snakes. Indeed, a total of 833 dives over 10 days were recorded for *L. saintgironsi* alone. Recent technological developments allow detailed monitoring of such traits in free-ranging animals, in circumstances that provide much more detail than is possible with visual observation alone (e.g., Heatwole 1975) and that minimize experimental artefacts associated with earlier technologies (e.g., Rubinoff et al. 1986). Intraperitoneal implantation of devices (radio-transmitters and temperature loggers) is now routinely used to study the ecology of terrestrial snakes (Reinert and Cundall, 1982), and clearly can work well with aquatic species also.

Implantation of TDRs in sea-kraits enabled us to gather the first automatically recorded data on the diving behaviour and activity budget of sea snakes. Concurrent data on depth and temperature allowed us to robustly distinguish time spent at sea *versus* on land. The devices were deployed for periods of 2 to 3 months, and recaptured snakes appeared healthy and unaffected by the experimental procedures. Nevertheless, our implanted snakes spent a long time on land post-surgery, as did the closely related species *L. colubrina* after being exposed to similar procedures (mean 22.8 days, Shetty & Shine 2002b). After sloughing, however, the snakes resumed their usual activities. After recovery, durations of time spent at sea *versus* on land were consistent with previous data based on radio-tracking (Shetty & Shine 2002b) and from mark-recapture (unpublished data). This similarity suggests that TDR implantation used in did not affect negatively sea-snake behaviour. Similarly, the recapture of one individual with food in its stomach suggests that feeding was not impeded by the presence of the TDR in the body cavity.

4.2 Diving behaviour of sea kraits

In respect of variables that can be directly compared between our study and earlier work on diving in sea snakes, there are both important similarities and differences. For the variable most extensively documented (dive duration), all sea snakes so far studied show consistent dive performance, massively greater than achievable by endothermic marine animals (Fig. 6A). The tight clustering of sea snake data in Figure 6A is especially impressive in that the species involved belong to three separate lineages that have independently made the transition from terrestrial to aquatic habits (acrochordids, hydrophiids, laticaudids). Although data for other variables are less extensive, sea snakes also appear to exhibit relatively similar abilities in terms of maximal dive depths (Fig. 6B).

One extensive data series from a dive-logger paints a clear picture of a foraging trip by a laticaudid sea snake, and shows several novel patterns (Figs. 2A,C, 4). First, the snake was active very consistently over a prolonged period, in strong contrast to the episodic (and often, infrequent) activity of foraging terrestrial snakes (Greene, 1997; Shine et al., 2004). Indeed, sea kraits appear to be extremely active animals, spending weeks at a time in dive after dive, 24 hours a day, without any resting period. Interestingly, a hydrophiid sea snake using a very different prey resource (*Emydocephalus annulatus* foraging for fish eggs) also shows

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virtually non-stop motion during each foraging bout (Shine et al., 2004); the low cost of aquatic locomotion (due to buoyancy) may facilitate such continued activity.

Second, a typical dive involved a gradual ascent and descent separated by a relatively long period (> 55 % of total dive duration) during which the snake remained at an approximately constant depth (Fig. 2C). Our visual observations of foraging *L. saintgironsi* show that these periods are devoted to moving along the coral substrate, exploring holes in the matrix and tongue-flicking in an apparent search for prey items (anguilliform fishes). The bathymetry of the New Caledonian lagoon accords well with this interpretation, because the range of depths in sites near Signal Islet is similar to the depths at which our study organisms spent most of their time during foraging trips (SHOM website, <http://www.shom.fr>).

Third, post-dive intervals were remarkably brief (typically, < 45 sec) and unrelated to duration of the prior dive (Fig. 4A), showing that even these prolonged dives were sustainable without resorting to anaerobic metabolism. Fourth, the leisurely rates of ascent and descent (ca. 32% of the snakes' maximum swimming speed of 0.8 m.s⁻¹, Shine et al., 2003) accord with the lack of any strong physiological constraint on dive duration. This poses a strong contrast to the rapid ascent and descent rates of endothermic marine animals; for example, mean swimming speeds were 71% of maximum swimming speeds in Adélie penguins (Yoda et al., 1999), 45% in king penguins (Culik et al., 1996), 82% in California sea lions (Feldkamp, 1987) and 67% in New Zealand sea lions (Crocker et al., 2001). Interestingly, New Zealand sea lions accelerate (mean descent speed 148% of mean surface swimming speed) during ascent and descent to decrease transit time and thus increase bottom time or depth. The great lability in metabolic rates conferred by ectothermy means that sea kraits can achieve the same result (increased dive duration and thus, time available to explore the bottom) by adopting low swimming speeds that reduce rates of oxygen consumption.

4.3 Comparison with previous studies

The only detailed data on snakes with which we can compare our results come from Rubinoff et al.'s (1986) pioneering study of the pelagic sea snake *Pelamis platurus* in deep oceanic waters of the Gulf of Panama. Using externally-attached ultrasonic transmitters, these authors quantified dive times and depths. Despite broad similarities in some aspects (maximum dive depths and durations, post-dive intervals), several differences are apparent also. Most notably, *P. platurus* dove near-vertically (typically to around 15 m) and then immediately began ascending very slowly (ascent many times slower than descent: Rubinoff et al., 1986), whereas *L. saintgironsi* dove slowly, remained at a constant depth while foraging, then ascended at about the same rate as it had descended (Fig. 2C). This difference presumably relates to the different functions of diving in the two species. *Pelamis platurus* feeds only at the sea surface, and dives primarily to avoid surface currents and thereby control its position; slow ascent may allow the snake to locate potential feeding sites (slicks, etc.) and move up into them (Rubinoff et al., 1986). In contrast, *L. saintgironsi* searches actively for its anguilliform prey among the coral matrix (Heatwole, 1999; Reed et al., 2002; Ineich et al. unpublished), and spends most of the dive cruising close to the sea bottom in chemosensory exploration of crevices that might contain eels (pers. obs.). In this respect, the dive profiles of laticaudids are likely to be more typical of other sea snakes (many of which take fishes from the coral matrix) than is the "quick dive-slow ascent" pattern documented for Rubinoff et al. (1986) for *P. platurus*. Similarly, the purely benthic U-shaped dives of *L.*

saintgironsi and *L. laticaudata* compared to the pelagic dives of *P. platurus* reflect the need for the former species to reach the sea floor whereas the latter taxon needs to dive only deep enough to avoid surface currents.

Previous studies on dive performance in marine mammals and birds have emphasised the magnitude of physiological challenges faced by these animals, and the degree to which multiple adaptive shifts have enhanced performance compared to their terrestrial counterparts (Kooyman, 1989; Boyd, 1997). Analysis of dive performance in sea snakes generates a very different perspective. First, these animals do not show such dramatic modifications associated with aquatic life. Except for an increase in lung volume and in skin oxygen absorption abilities, they broadly resemble their terrestrial relatives (Heatwole and Seymour, 1975; Graham, 1974; Belkin, 1963). Nonetheless, these snakes massively outperform endotherms in terms of dive performance, with a 150 - 400g snake able to dive for at least as long as a 600 kg elephant seal (Fig. 6A). These comparisons strongly support the hypothesis that ectothermy preadapts reptiles to exploit underwater resources in tropical oceans, because reduced or lack of access to oxygen poses much less of a physiological challenge to these animals than it does to endothermic taxa attempting to utilise the same environments.

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