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First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration

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We used Satellite Relay Data Loggers to obtain the first dive profiles for critically endangered leatherback turtles outside the nesting season. As individuals moved from the Caribbean out into the Atlantic, key aspects of their diving behaviour changed markedly, in line with theoretical predictions for how dive duration should vary with foraging success. In particular, in the Atlantic, where foraging success is expected to be higher, dives became much longer than in the Caribbean. The deepest-ever dive profile recorded for a reptile was obtained in the oceanic Atlantic, with a 54-min dive to 626 m on 26 August 2002. However, dives were typically much shallower (generally <200 m) and shorter (<40 min). These results highlight the suitability of this species for testing models of dive performance.

Air-breathing marine vertebrates exist in an environment where their prey abundance varies over a number of spatial and temporal scales, some of which are quasipredictable. Across species, individuals might be expected to show behavioural adaptations to exploit their prey optimally. However, uncovering these adaptations is often difficult, except in cases where animals occur close to shore and near the surface, facilitating direct observation (Sims & Quayle 1998), where they repeatedly come ashore at haul out sites (often breeding locations), allowing the deployment and recovery of data loggers (Boyd 1997), or where mortality in commercial fisheries allows the recovery of data storage tags (Metcalfe & Arnold 1997). Obtaining behavioural information when animals are in remote locations far from land is far more difficult, and consequently the diving behaviour of many species remains unexplored throughout much of their lives. An important goal is therefore to obtain dive profiles and other behavioural information from diving animals in remote locations where data loggers cannot be recovered, for example, during long-distance migration.

Furthermore, in many cases (e.g. pinnipeds, penguins and turtles) breeding sites are selected on the basis of their suitability for reproduction rather than foraging, so there are strong reasons to suspect that the diving behaviour at breeding areas may not reflect that exhibited elsewhere. Theoretical predictions suggest that the pattern of diving, and most importantly the extent to which animals use their aerobic dive limit (ADL), may be dictated by the foraging success on dives (Thompson & Fedak 2001). It has been suggested that if prey are more readily available, increasing foraging success, then a diver should extend the dive and consequently approach closer to its ADL (Thompson & Fedak 2001). Conversely, when foraging success is poor, then the diver should curtail that dive and surface well before it approaches its ADL. However, testing these predictions has been hampered by the problems with relaying dive data from animals in remote locations far from their breeding sites.

The Argos satellite system, which is the most widely used technique for tracking animals over extended time and space scales, has a limited bandwidth for data transmission (Fedak et al. 2002). Consequently, when using this system, it is impossible to transmit all the dive

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data that are routinely collected by time depth recorders (TDRs), that is, depth values collected every few seconds. Instead, reduction of dive data on board the transmitter is required before transmission. The standard data reduction technique is to record the time spent in preselected depth intervals (depth 'bins') over preselected intervals (typically a few hours; e.g. Godley et al. 2002). However, although this information can reveal the pattern of depth utilization, the association of the duration versus depth of individual dives is lost.

Leatherback turtles, *Dermochelys coriacea*, are a particularly good species for investigating temporal patterns in diving, because they move long distances between tropical nesting beaches and oceanic foraging zones (Morreale et al. 1996; Eckert 1998; Hughes et al. 1998). It is axiomatic that these movements are associated with the turtles moving from a nesting area where food is scarce to distant areas where food is more abundant, and hence their postnesting movements are ideal for testing theoretical predictions for how dive duration varies with foraging success. We used satellite transmitters incorporating on-board data processing, which allowed individual dive profiles to be obtained from animals in remote locations. We used these transmitters to obtain information about the pattern of diving for leatherback turtles both while they were close to nesting sites in the Caribbean and as they travelled out into the Atlantic Ocean at the end of the nesting season. In this way, we tested the general prediction associated with improved foraging success that, as animals travelled away from their breeding sites, their dive durations should increase.

METHODS

Instrument Deployment

To record the movements and diving behaviour of leatherback turtles after the end of the nesting season, in July 2002 we attached satellite transmitters (Satellite Relay Data Loggers (SRDLs), Sea Mammal Research Unit, St Andrews, U.K.) to three leatherback turtles (turtles 1–3) nesting at Levera beach on the north shore of Grenada (12.2°N, 61.6°W). Transmitters were held in place on the carapace by a flexible harness that was individually sized to each turtle. This soft-harness system has facilitated long-term tracking of leatherbacks (Hughes et al. 1998). The transmitters are the same size as ones that we have put on much smaller green turtles, *Chelonia mydas* (Hays et al. 2002). The weight of the transmitter in air is 0.7 kg, and the weight of adult leatherback turtles is 400–600 kg, so the relative size of the transmitter is tiny. We know from observations where we have trialled the harness with internesting turtles (i.e. ones that we resight within a single season) that the harness has no discernible effect: turtles with a harness return to nest and show no ill effects. The harness is attached within a few minutes as the turtle returns to the sea after nesting, so she is not restrained at all. The harness is individually sized to each turtle, so it fits snugly without constraining the animal. One of the key conservation goals is ultimately to record the movements of turtles over their entire 2- or 3-year remigration period, that is, until they return to the Caribbean to nest again, so the harness is designed not to fall off. Rather, we hope that it stays on until the turtle's next nesting season when it will be removed. The work was conducted with the permission and collaboration of the Grenadian Ministry of Agriculture, Forestry, Land and Fisheries and because of the strong conservation implications was partly funded by the Marine Conservation Society of the U.K.

To record the diving behaviour of a fourth turtle (turtle 4) over 20 days (two internesting intervals between emergences on to the beach to lay three successive clutches) within the nesting season, we attached a TDR (LTD_1100, LOTEK Marine Technologies, St John's, Newfoundland, Canada) to a nesting female. This TDR was tiny (weight 5 g in air), so it was simply wired on to one of the standard metal flipper tags that were attached to each rear flipper as part of the routine conservation work with leatherback turtles on Grenada.

Deriving Turtle Movements from the Satellite Data

SRDLs were located with the Argos system (http://www.argosinc.com/). Each Argos location is provided with a measure of its accuracy, called the location class. Location classes A, B and 0 are the least accurate, and classes 1, 2 and 3 are the most accurate (e.g. Hays et al. 2001). For turtles 1 and 2, there were insufficient locations of classes 1, 2 and 3 to reconstruct the movements within the Caribbean. We therefore analysed all locations, regardless of their class, and filtered out locations that required a high speed of travel (>9 km/h was selected as an objective cutoff to filter out locations that visibly appeared highly erroneous, i.e. that lay outside the pattern of previous and subsequent locations). This filter removed 25 of 152 locations for these two turtles. We did not apply this filtering criterion if two locations were separated by less than 2 h and 30 km. We also removed four locations that necessitated course reversals. For turtle 3, there were sufficient high-quality locations (classes 1–3) to reconstruct the movements using these locations only. Once turtles were outside the Caribbean and in the Atlantic (i.e. when they moved east of the island of Martinique), movements were reconstructed using only locations of classes 1, 2 and 3.

Deriving Turtle Diving Behaviour from Satellite Data

Each SRDL included a pressure sensor, which was used to measure the depth to an accuracy of 0.33 m every 4 s. These depth values were analysed by bespoke software on board the SRDL before transmission. Individual dives were recorded when the depth exceeded 10 m. The start of these dives was defined by the time that the saltwater switch on the SRDL perceived that the transmitter was submerged, and the end of the dive was defined when either the saltwater switch recorded the transmitter breaking the surface, or the depth became less than 2 m.

Once a dive was completed, onboard software examined the dive profile and determined the time and depth of the five most significant points of inflection during the dive. The time and depth of these five points, along with the time of the end of the dive and dive duration, were then transmitted. This onboard data reduction meant that a large number of dive profiles could be obtained despite the limited bandwidth of the Argos satellite system, and it allowed, for the first time, the dive profiles of leatherback turtles to be obtained outside the breeding season. Each dive entered a buffer within the SRDL so that these data would be randomly transmitted for the next 10 days. In this way, the specific dive profiles obtained via the Argos system were not weighted by the surfacing behaviour of the turtle immediately subsequent to each dive. A dive number accompanied the depth and time data for each dive, so that it was possible to estimate the number of dive profiles that were not received.

In addition to relaying individual dive profiles, the SRDL also summarized the dive information into 6-h summary periods. Included in the parameters determined for each summary period were the following: percentage of time spent hauled out (i.e. saltwater switch was dry for longer than 10 min); percentage of time spent shallower than 10 m; percentage of time spent deeper than 10 m; mean depth of dives to over 10 m; mean dive duration for dives to over 10 m; maximum depth. Each SRDL also relayed diagnostic data concerning the total number of transmissions that had been made, the performance of the saltwater switch that was used to synchronize transmissions with surfacing events and the maximum depth attained. Consequently, the maximum depth attained for each tracked individual continued to be received, regardless of the rate at which other dive information was received.

The TDR recorded depth every 26 s or 52 s with a resolution of 30 cm. We used dive analysis software (MultiTrace, Jensen Software Systems, Laboe, Germany) to record the depth and duration of individual dives, defining a dive as any submergence deeper than 10 m. In this way, the dive data from the TDRs and SRDLs were directly comparable.

Determining Local Time of Sunrise and Sunset

Both location and dive data obtained from the SRDLs were in Greenwich Mean Time (GMT). However, two of the three satellite-tracked animals moved large distances, so when expressed in GMT, the times of sunrise and sunset at each turtle's location would change. We therefore used Telonics Satellite Predictor Software (Telonics Inc., Mesa, Arizona) to determine the time in GMT of sunrise and sunset at different dates and locations, defining sunrise and sunset as the time when the sun was at zero degrees elevation. Knowing the date of each Argos location, we then established an empirical relation for each turtle between the day of the year and the times of sunrise and sunset at the turtle's location. We used these relations to determine the time of sunrise and sunset for each day that at least one dive profile was obtained. To reduce the computations for times and sunrise and sunset, only one location was selected for each turtle per week, always selecting the highest-quality location available (generally location class 1 or 2). If we obtained fewer locations per week than one, we selected all locations. We obtained summary dive information for one 6-h period that was always at night (0000–0600 hours GMT) and one 6-h period that was always during the day (1200–1800 hours GMT), with the two remaining 6-h periods straddling dawn and dusk.

RESULTS

Movements and Overall Data Volume

SRDLs were attached to three turtles, and all three initially moved northwards from Grenada. However, only two turtles (turtles 1 and 3) were tracked as they moved out into the Atlantic, with the third track ending prematurely when the transmitter was removed close to a neighbouring island of St Vincent (Fig. 1).

Turtle 1 headed northwest into the Caribbean before turning northeast and passing between the islands of Martinique and Dominica and then heading out into the Atlantic. The first location to the east of Martinique was obtained on 17 July, 12 days after the transmitter was attached. The turtle then continued to head eastwards (Figs 1, 2).

Turtle 2 moved northwards and then eastwards, arriving within 10 km of the north shore of the island of St Vincent on 15 July. On 20 July, 12.5 days after the turtle had been last seen on Grenada, the saltwater switch on the transmitter indicated that the transmitter came out of the water, following which locations were obtained inland on the east coast of St Vincent (Fig. 1). We continued to receive locations on land for several months, during which time the saltwater switch confirmed that this transmitter remained out of the water. A visit to the island of St Vincent during July 2002 confirmed that, in the village where the transmitter was located, leatherback turtles are on occasion taken for consumption, although we were unable to get confirmation of the fate of the satellite-tracked individual.

After leaving Levera beach, turtle 3 moved northwards and was successively located near the islands of St Vincent and St Lucia before passing between St Lucia and Martinique into the Atlantic. The first location to the east of Martinique was obtained on 8 August. Following this date, the turtle continued to move eastwards and then southwards in the Atlantic (Figs 1, 2).

For the two turtles tracked as they moved out into the Atlantic, the amount of data supplied from each transmitter changed with time. Both SRDLs initially provided 10–30 individual dive profiles each day (e.g. Fig. 3). However, as the tracking continued, this rate of data supply diminished, so that by the end of October 2002, an average of fewer than two dive profiles were obtained for each day. By the end of October 2002, we had nevertheless received a total of 1091 and 782 individual dive profiles for turtles 1 and 3, respectively. Diagnostic data transmitted from each SRDL indicated that this reduction in data supply was at least partly caused by the failure of the

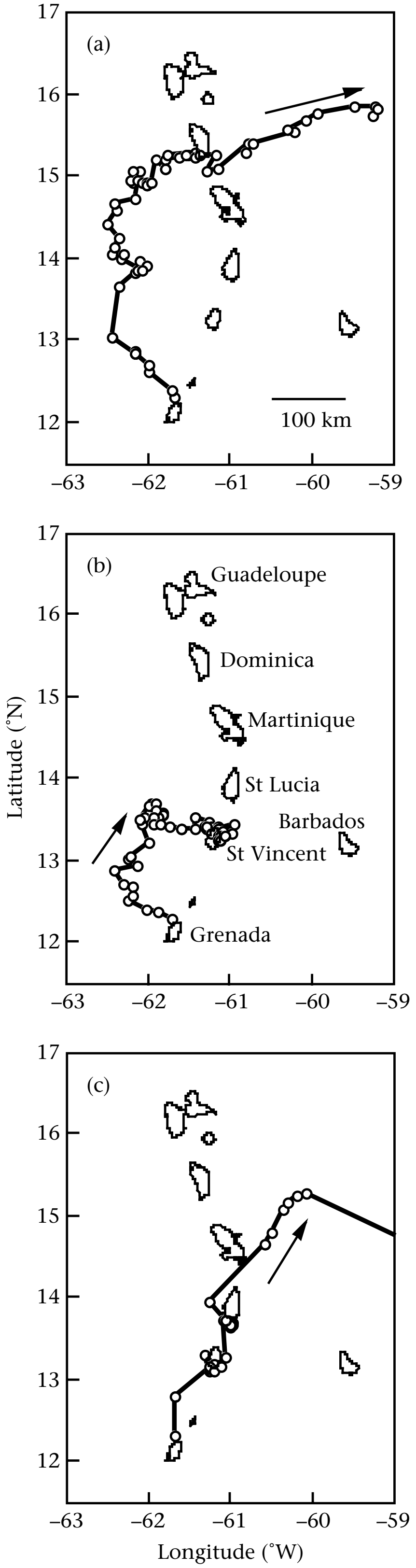

Figure 1. The initial movements of three leatherback turtles tracked by satellite. (a–c) Turtles 1–3, respectively. The tracks are shown up until the animals entered the Atlantic (turtles 1 and 3) or the transmitter was removed (turtle 2). Arrows indicate direction of travel.

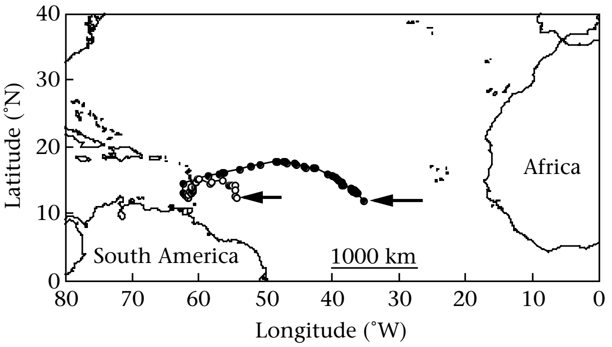

Figure 2. The long-distance movements of two turtles equipped with SRDLs. ●: Locations of turtle 1 obtained between 5 July (when the transmitter was attached) and 15 October. This turtle entered the Atlantic on 17 July. ○: Locations of turtle 3 obtained between 10 July (when the transmitter was attached) and 15 October. This turtle entered the Atlantic on 8 August. Arrows indicate the position of each turtle on 15 October.

saltwater switch that is designed to synchronize transmissions with the turtle surfacing. The diminished data supply meant that the end of October 2002 was a logical cutoff date for the analysis of dive behaviour associated with the postnesting movement into the Atlantic.

Diving Behaviour

On average, all four turtles spent 55–70% of their time conducting dives deeper than 10 m. Most of these dives were relatively shallow, with only occasional dives recorded deeper than 200 m (Fig. 4). For example, when diving, the percentage of time spent on dives to 10–110 m was 71, 87, 81 and 94% for turtles 1–4, respectively, but for all four individuals less than 1.5% of all the diving time was spent on dives to deeper than 200 m. The maximum depths attained were 640, 300, 510 and 316 m for turtles 1–4, respectively. The deepest dive for which the actual profile was obtained was a 54-min dive to 626 m on 26 August 2002, performed by turtle 1 (Fig. 5).

The two turtles that were tracked moving out into the Atlantic (turtles 1 and 3) tended to dive slightly deeper (Fig. 4a, c) than did those turtles for which data were collected only from within the Caribbean (turtle 2) or within internesting intervals (turtle 4) (Fig. 4b, d). This difference in diving performance was more marked for dive duration; modal durations of dives were 30–35 min and 20–25 min, respectively, for the two turtles (turtles 1 and 3) that moved out into the Atlantic, but only 10–15 min and 5–10 min, respectively, for the two turtles for which data were recorded only within the Caribbean (turtles 2 and 4). There was a highly significant difference between the mean depth of dives recorded in the Caribbean ($N = 2548$ dives for four individuals, $\overline{X} \pm \mathrm{SD} = 51.7 \pm 39.9$ m) and those recorded in the Atlantic ($N = 1190$ dives for two individuals, 76.7 ± 65.3; t test: $t_{1616} = 12.2$, $P < 0.0001$). Similarly, the mean duration of dives in the Caribbean (10.95 ± 6.13 min) was significantly shorter than those recorded in the Atlantic (25.87 ± 8.27 min; $t_{1820} = 55.5$, $P < 0.0001$).

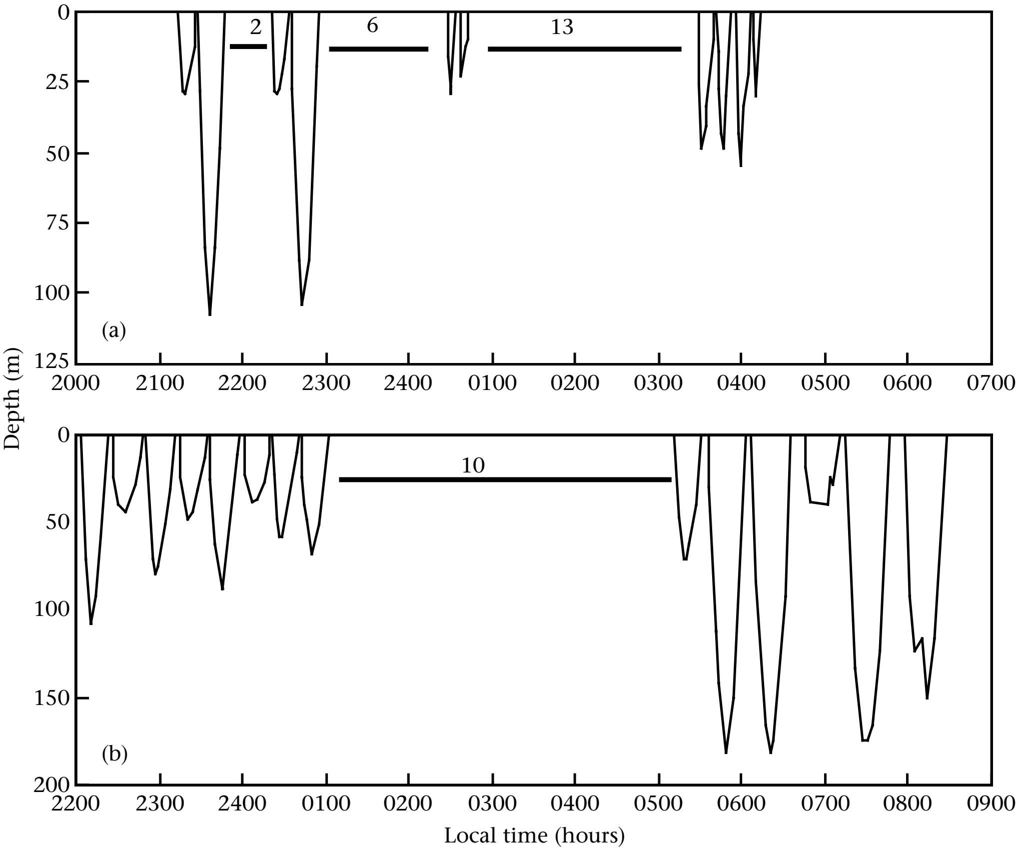

Figure 3. Two examples of the dive profiles received from the SRDLs. Both parts show 11 h of data. The numbers between patches of dive profiles indicate the number of dive profiles that were 'missed' because of the limited bandwidth available within the Argos system. (a) Data from turtle 1 collected on 15 and 16 July 2002. (b) Data from turtle 1 collected on 19 and 20 July 2002.

The duration of dives tended to increase with dive depth (Fig. 6). However, any single depth-versus-duration relation masked clear spatiotemporal patterns in this relation. Dives to the same depth became longer when turtles moved out into the Atlantic (Fig. 7). For example, for turtle 1 (Fig. 7a), the average duration of dives to 55 m was 13.9 min when inside the Caribbean and 28.6 min in the Atlantic, and for turtle 3 (Fig. 7c), the mean duration of dives to 55 m increased from 18.9 to 25.3 min. This increase in the duration of dives to corresponding depths in the Atlantic compared to the Caribbean was highly significant for both turtles (paired t tests: $t_{18} = 19.8$ and $t_{16} = 9.6$, respectively, $P < 0.0001$).

When all the dives were pooled, this pattern for longer dives in the Atlantic was evident as an increase in dive duration as the year progressed (Fig. 8). When previous information on the depth and duration of leatherback turtles' dives during the internesting period is examined (Eckert et al. 1989), this change in dive duration is reiterated (Fig. 8).

Diel Patterns

For the SRDL-equipped turtles, we used the individual dive profiles as a proxy for the proportion of time spent diving over the 24-h cycle, and then converted these proxy values into absolute units using the mean percentage of time spent diving supplied in the 6-h summaries. The two turtles tracked as they moved into the Atlantic showed clear diel patterns in their diving behaviour. The time spent diving to greater than 10 m showed a systematic variation with the time of the day, increasing in the middle of the night and decreasing in the middle of the day (Fig. 9). The diel pattern in the time spent diving was maintained for extended periods. For example, for these two turtles, summary statistics for individual 6-h periods showed that almost every night, around 85% of the time was spent diving to deeper than 10 m, but in the day, the time spent diving was generally less but also much more variable (Fig. 10).

Changes in dive depth accompanied these changes in the time spent diving. The general pattern was for dives to be consistently shallow at night (mean depth = 50–70 m). For both turtles 1 and 3, deeper dives were then recorded around dawn and dusk. For example, the mean dive depth for dives starting between 0500 and 0600 hours local time was around 130 and 100 m for turtles 1 and 3, respectively (Fig. 9b, c).

Analysis of the summary dive statistics for individual 6-h periods revealed that the mean depth of dives was generally shallower than 150 m and the maximum dive

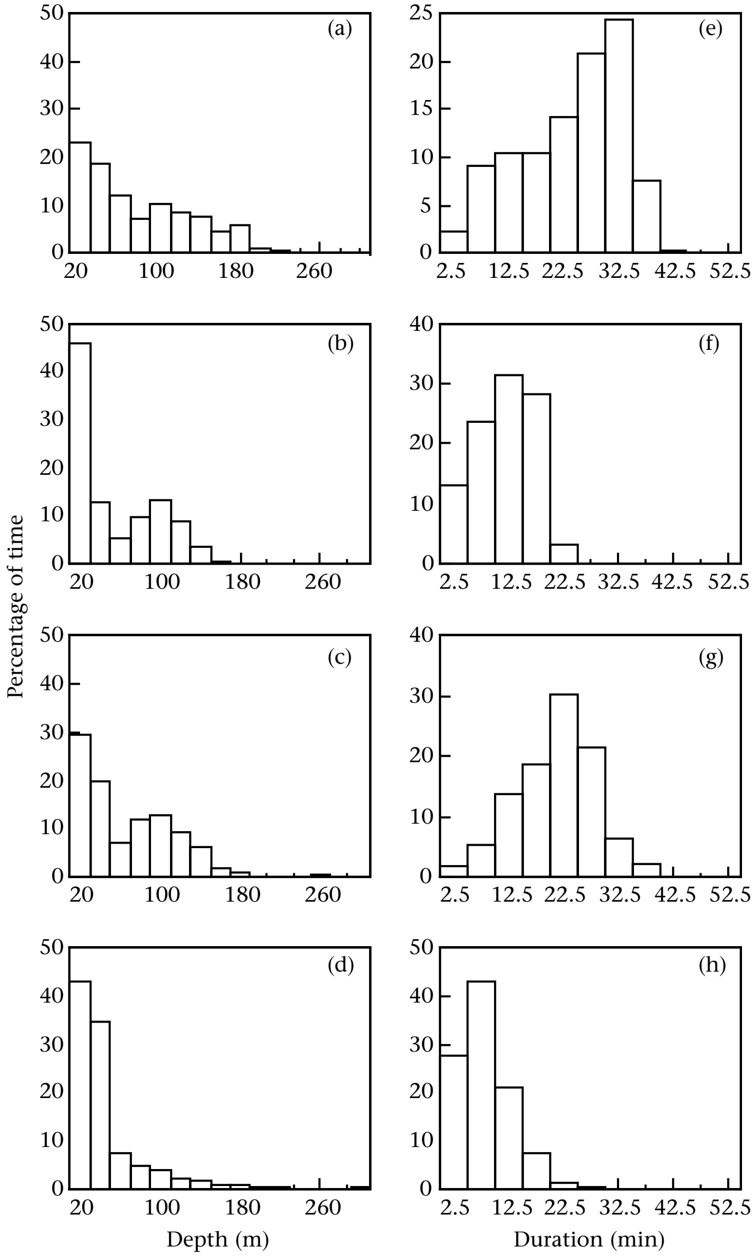

Figure 4. For four turtles, (a–d) the respective proportions of total time spent on dives with different maximum depths and (e–h) the respective durations of these dives. (a) and (e) = turtle 1, (b) and (f) = turtle 2, etc. To obtain each plot, individual dive profiles obtained with either a TDR (turtle 4) or an SRDL (turtles 1–3) were examined. Sample sizes for turtles 1–4 were 1091, 219, 782 and 1646 dives, respectively.

depth was generally shallower than 200 m. Occasionally there were 6-h periods where dives were much deeper, but these periods were never at night. This view from the summary statistics that deep diving was generally a daytime feature was confirmed by the exclusively diurnal nature of the individual deep dives.

DISCUSSION

Marine nekton search for patchily distributed prey in a three-dimensional environment, and hence their swimming behaviour can have strong implications for their foraging success. For fish, there is no constraint on foraging imposed by the need to surface and breathe, so the decision on where to forage in the water column can be made simply on the basis of prey concentration (Sims & Quayle 1998; Sims 2000; Sims et al. 2003). For air-breathing vertebrates, however, the need to return continually to the surface to breathe imposes an additional factor influencing foraging success. If prey are not at the surface, then there is a commuting cost to get from the surface down to the prey, and the deeper the prey, the greater will be this commuting cost. Air-breathing vertebrates are generally thought to dive within their aerobic dive limit (e.g. Boyd 1997), so if prey are deeper, then the

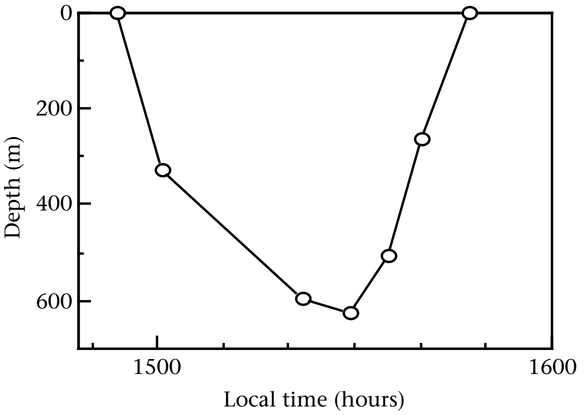

Figure 5. The profile of a dive to 626 m performed by turtle 1 on 26 August 2002. Symbols show the depth/time points relayed via the SRDL.

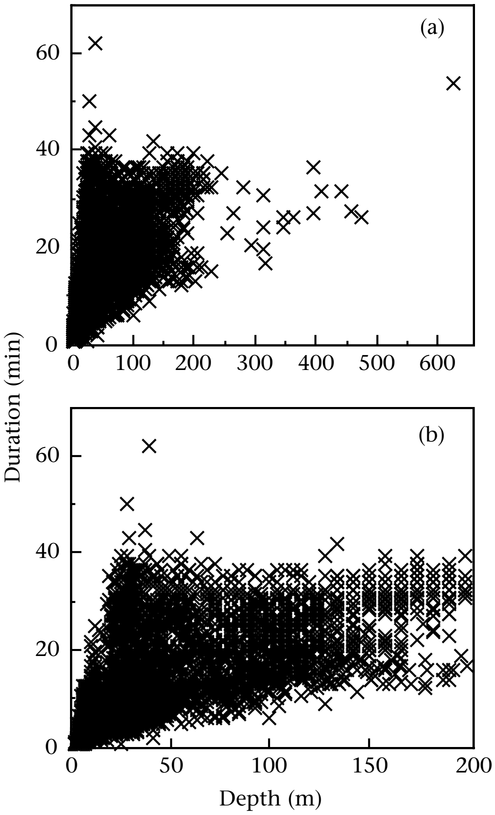

Figure 6. For all the dive profiles collected using either SRDLs or TDRs, the dive duration as a function of the maximum depth of each dive. (a) All dives ($N=3738$), (b) dives in the range 10–200 m ($N=3703$). Over the depth range 10–200 m, dive duration increased linearly as a function of maximum depth; least squares fit regression equation: duration (min) = 0.123 maximum depth (m) + 8.51 ($F_{1,3701} = 1731$; $r^2=0.32$, $P < 0.0001$).

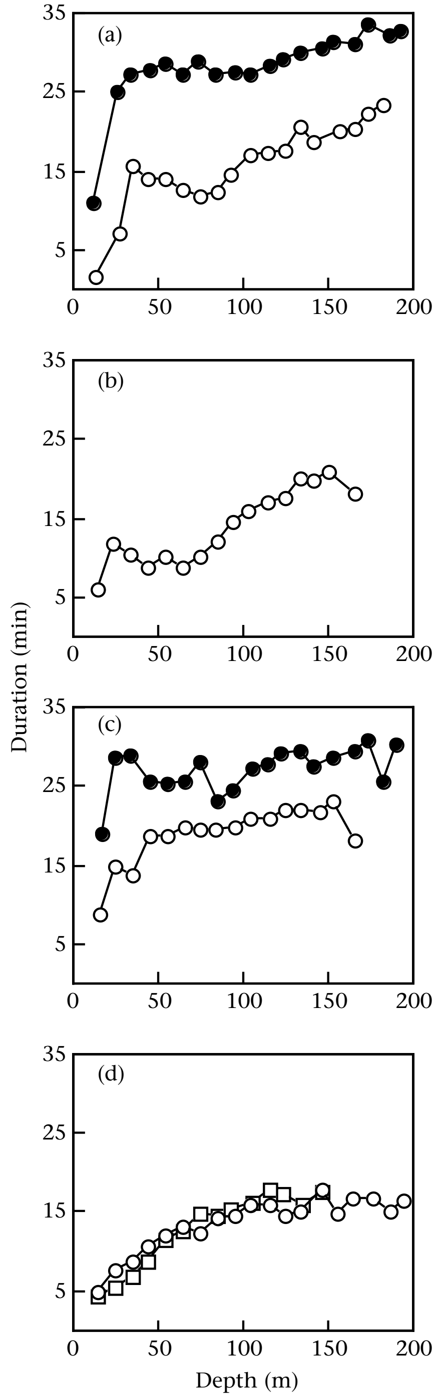

Figure 7. The mean duration of dives to depths separated into 10-m-depth bins. (a–d) Turtles 1–4, respectively. For (a) turtle 1 and (c) turtle 3, which moved out into the Atlantic, data were separated into the periods when the animals were within the Caribbean (○) and when they were in the Atlantic (●). Turtles 1 and 3 were defined as being in the Atlantic from 17 July 2002 onwards and 8 August onwards, respectively, because these were the dates of the first locations east of Martinique. (d) Different symbols show data from the two internesting intervals for turtle 4.

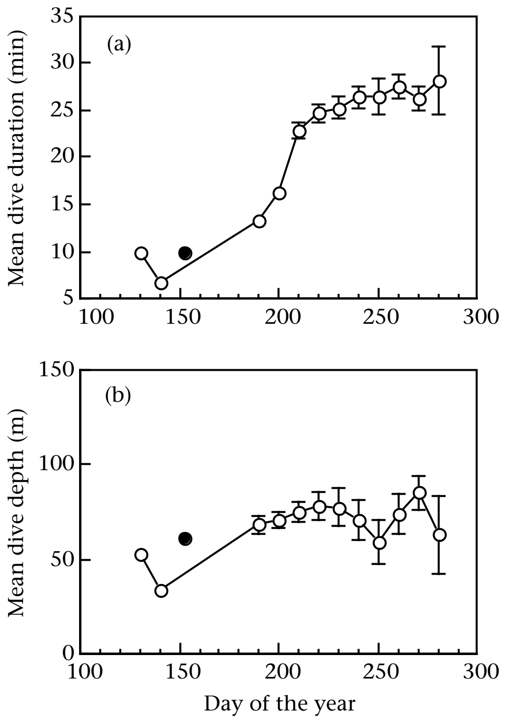

Figure 8. The mean (a) duration and (b) depth ± 2 SEs of individual dives recorded in 10-day intervals. Error bars smaller than the plot symbol are not shown. ○: This study; ●: mean values for a previous internesting study in the Caribbean, where 5096 dives were recorded from six individuals (Eckert et al. 1989). Turtles 1 and 3 entered the Atlantic on 17 July (day 199 of the year) and 8 August (day 220 of the year), respectively. Hence, from 8 August onwards, all dives were made in the Atlantic.

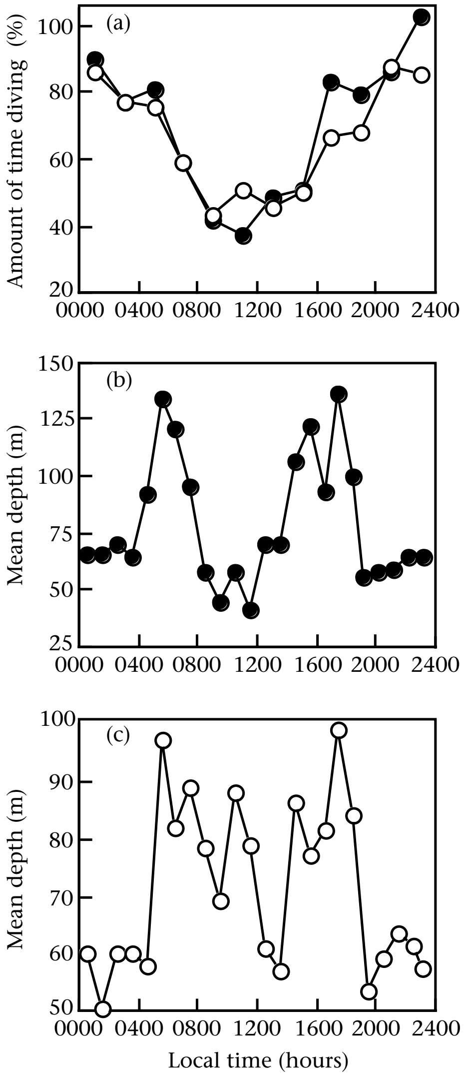

Figure 9. (a) The time spent diving to submergences deeper than 10 m throughout the day and night for turtle 1 (●) and turtle 3 (○). The mean dive depth in each hour of the day is shown for (b) turtle 1 and (c) turtle 3. In all parts, each point shows the mean value for each hour of the day.

time that can be spent at the prey depth becomes more limited (Thompson & Fedak 2001). Hence, the net energy intake for a dive will be determined by the prey depth and prey density: when diving on prey that are highly abundant at shallow depths, then, other things being equal, the dive will be more profitable compared to when the prey are deeper or less abundant. As prey move deeper and deeper, a situation must eventually arise where there is such a large negative energy balance from the dive that it is more profitable to remain at the surface.

Superimposed on these general considerations for the profitability of a dive is the ability of the diver to catch the prey. For visual hunters, feeding on fast motile prey, such as fish, the probability of prey escaping under different scenarios may influence the energetic profitability of a dive. For example, an approach from below, where it is dark, helps to conceal the attacker, so some pinnipeds adopt this strategy to minimize the chances of the prey escaping (Davies et al. 1999). For predators feeding on less motile prey, the consequences of prey avoidance may be less important, and instead prey perception by the predator may play a key role in dictating the foraging success on dives. Consequently, for some divers, the ambient light levels at prey depths may be important. For example, penguins often feed on euphausiids that exhibit diel vertical migration (DVM), occurring near the surface at night and deeper during the day (Wilson et al. 1993). Based on commuting costs alone, this would suggest that shallow nighttime diving would be more profitable. However, the ambient light levels at prey depths are often lower when the prey are near the surface at night than when they are deeper during the day, and because penguins are visual hunters, deep daytime diving is more profitable (Wilson et al. 1993).

Leatherback turtles are specialized predators of gelatinous zooplankton, feeding on groups such as scyphozoan jellyfish, pyrosomes and siphonophores (Davenport 1998). Sometimes these animals may be abundant near the surface, giving rise to accounts of leatherback turtles feeding near the surface during the day (James & Herman 2001). However, these gelatinous prey groups often exhibit DVM with deep daytime residence and shallow nighttime occurrence (Andersen et al. 1992, 1997). DVM is widely reported in both marine and freshwater zooplankton, with a normal pattern of a dusk ascent and

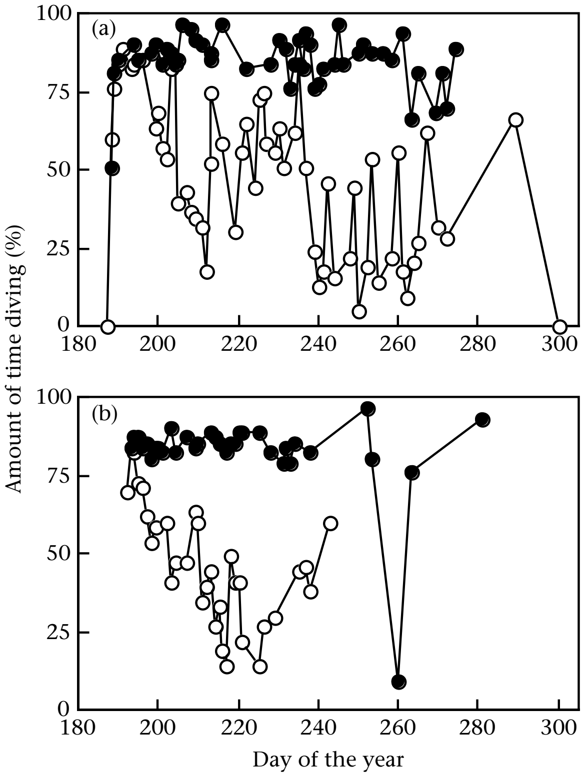

Figure 10. For individual 6-h periods that were exclusively within the night (●) or the day (○), the percentage of time spent diving (on submergences deeper than 10 m) for (a) turtle 1 and (b) turtle 3.

a dawn descent, and this is likely to be the cause of the diel patterns in leatherback diving that we observed. We recorded a consistent pattern for leatherbacks to spend much of the night diving, typically to modest depths, but then around dawn, dives became progressively deeper. This same leatherback turtle diel diving pattern has also been reported in the pioneering internesting studies in the Caribbean (Eckert et al. 1989). The most logical explanation for this pattern is that the turtles followed the descent of their prey around dawn. However, after dawn, the turtles spent less time diving, with this reduction in the time spent diving continuing until midday. This pattern of little diving around midday presumably reflects that the turtles' prey had descended to such a depth that the prey could no longer be profitably reached during dives. Migrating zooplankton move to daytime depths of many hundreds of metres (e.g. Andersen et al. 1992), that is, below the routine diving depth that we observed for leatherback turtles. Of course, although the leatherbacks dived less during the middle of the day, this does not preclude the possibility that they fed to some extent near the surface.

After midday, the time spent deeper than 10 m started to increase and mean dive depth gradually increased until it reached a maximal value 1–3 h before dusk. After dusk, the mean dive depth moved closer to the surface, a pattern that was maintained throughout the night. We interpret this pattern to reflect that the leatherback turtles started to dive deeper in the afternoon searching for their prey on the upward leg of its DVM. Once the prey was encountered shallower than 200 m, the leatherback turtles presumably increased their dive frequency because it was then profitable to dive, and as their prey continued to ascend, their ascent was tracked by the leatherbacks. This interaction between the vertical movements of prey animals and the diving behaviour of their predators occurs widely, with diel diving patterns associated with prey vertical migration seen not just in leatherback turtles (this study) but also in marine mammals (e.g. Le Boeuf et al. 2000) and marine birds (Wilson et al. 1993).

It is well known that leatherback turtles move long distances outside the nesting season. For example, both conventional flipper tagging (Pritchard 1976) and satellite tracking (Duron-Dufrenne 1987; Eckert 1998) have shown that females that have nested in the wider Caribbean, then move long distances north and/or eastwards in the Atlantic. Similarly, leatherback turtles are routinely sighted at northern latitudes, such as around Nova Scotia in the western Atlantic (Bleakney 1965) and around the U.K. in the eastern Atlantic (Brongersma 1972) in the late summer. The minimum remigration interval (i.e. the interval between consecutive nesting seasons) is generally 2 years for leatherback turtles in the Caribbean (McDonald & Dutton 1996), and hence our tracked turtles are unlikely to return to Grenada until at least 2004. The pattern that we recorded of long-distance movements of satellite-tracked individuals into the Atlantic is consistent with these observations. It is axiomatic that these long-distance movements increased the foraging success of the leatherback turtles, that is, that food is more abundant in the Atlantic than in the Caribbean. If this were not the case, then we would expect leatherback turtles to remain year-round in the Caribbean, which they do not. The relation between dive depth and duration was not temporally and spatially invariant. Rather, when the turtles left their nesting beach and were still within the Caribbean, the duration of dives was much shorter than dives to those same depths once the turtles had moved out into the Atlantic. Our interpretation is that this pattern of increasing dive duration reflects improved foraging success on dives in the Atlantic than in the Caribbean. The pattern of increasing dive duration that we recorded as turtles moved into the Atlantic provides strong support for the theoretical predictions that divers will extend dives when in areas where the foraging success is higher (Thompson & Fedak 2001), and our results highlight the suitability of leatherback turtles for testing such models of dive performance.

There is always interest in the deepest and longest dives performed by animals, although by definition the longest and deepest dives are extreme events and are unlikely to reveal how an animal routinely behaves. Nevertheless, extreme dives may reveal something about the physiological limits of an animal's performance (Southwood et al. 1999). Studies on the depths and duration of leatherback dives have been constrained to the internesting period (Eckert et al. 1986, 1989; Southwood et al. 1999). These pioneering studies revealed that leatherbacks could, on occasion, dive very deeply, with a maximum recorded depth of 475 m (Eckert et al. 1986), and some dives might have been even deeper (Eckert et al. 1989).

Dive profiles relayed via satellite confirm that leatherbacks do occasionally dive deeper than 500 m, but such dives are rare. In contrast, some diving marine mammals, in particular northern and southern elephant seals, *Mirounga angustirostris* and *M. leonina*, respectively, routinely dive deeper than 500 m (e.g. Le Boeuf et al. 2000) with a maximum depth of over 1500 m (reviewed in Kooyman & Ponganis 1998). These differences in depth ranges between leatherback turtles and elephant seals might reflect differences in their physiological adaptations for deep diving, including their respective oxygen stores and metabolic rates. An alternative possibility is that this difference reflects the contrasting diets for these two groups: elephant seals feed on fish, which have a relatively high energy density, and leatherback turtles feed on gelatinous plankton, which have a low energy density. As a consequence of these different diets, the relative profitability of diving to different depths may vary between the two groups.

As with dive depth, consideration of the maximum dive duration may indicate something about an animal's physiological limits. For example, after a dive of 67.3 min for a leatherback turtle during the internesting period, Southwood et al. (1999) observed an unusually long surface interval of 31 min. Conversely, after a 33.8-min dive, the surface interval was only 3.7 min. This difference in surface interval led Southwood et al. (1999) to suggest that the aerobic dive limit for leatherback turtles might lie between 33 and 67 min. The dive durations of the thousands of dives from our study showed a noticeable ceiling at 40 min, beyond which we recorded few dives (Fig. 6). It is tempting to speculate that this ceiling is associated with the aerobic dive limit in this species.

In conclusion, we have used satellite-linked data loggers to obtain the first dive profiles of leatherback turtles during their open-ocean wanderings. We recorded the deepest-ever dive by a reptile (640 m) and found that this species habitually showed a diel pattern of pelagic diving, probably as a consequence of feeding on vertically migrating gelatinous prey. Leatherback turtles appear to be ocean nomads, rather than staying in a single restricted foraging site outside the nesting season. Although wide ranging, these oceanic wanderings appear adaptive, and leatherback turtles fundamentally change their diving behaviour as they move away from their breeding grounds.

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