



Flexible inter-nesting behaviour of generalist olive ridley turtles in Australia

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ABSTRACT

While olive ridley turtles (*Lepidochelys olivacea*) occur throughout tropical oceans their physiological ecology has been poorly documented. In May 2005, satellite-relayed data loggers (SRDLs) were attached during oviposition to four adult female olive ridley turtles on the Wessel Islands, northern Australia. Subsequent nesting haul-outs were determined for two of these turtles using a combination of movement and diving data. Interesting intervals were relatively long (27 and 18 days, respectively) for hard-shelled turtles given the warm (27–28 °C) water temperatures, possibly due to a low metabolic rate for this species. Turtles travelled considerable distances during the interesting interval (200 and 125 km respectively), possibly associated with a search for food or alternative nesting sites. Changes in dive behaviour suggest that olive ridleys prepare for oviposition by searching for an appropriate beach over several days.

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1. Introduction

Recent technological developments have facilitated measurement of the at-sea behaviour of marine vertebrates (Hays, 2008; Hooker et al., 2007, and references therein), which greatly enhance our ability to quantify life history traits of often clandestine, exploited or threatened species. Air-breathing divers such as marine turtles are constrained by the need to return intermittently to the surface to breathe, so detailed quantification of their behaviour can provide important insights into their physiology, niches and habitat requirements (Georges et al., 2007; Hays et al., 2004). Indeed, the increased technical capacity of archival tags in recent years has provided excellent behavioural data useful for quantifying physiological limits (Hays et al., 2007); for example, energy conservation in green turtles during resting (Hays et al., 2000) or diving metabolic rates of leatherback turtles (Bradshaw et al., 2007).

The link between behaviour and physiology is particularly amenable to quantification in marine turtles, given their propensity to rest and forage across a wide range of depths and their ability to remain submerged for relatively long periods. Olive ridley turtles (*Lepidochelys olivacea*) are particularly interesting in this regard because of their unusually long and deep diving behaviour (McMahon et al., 2007) relative to other hard-shelled marine turtles (cf. Houghton et al., 2002) such as loggerheads *Caretta caretta* (Hochscheid et al., 1999), greens *Chelonia mydas* (van Dam and Diez, 1996), and hawksbills *Eretmochelys imbricata* (Lutz and Musick, 1997). Previous

work based on diving data has suggested that *L. olivacea* has potentially higher physiological thresholds to oxygen depletion (i.e., lower metabolic rates or higher oxygen storage capacity) than other hard-shelled turtles (McMahon et al., 2007). Without the capacity to measure metabolic rate *in situ* (e.g., Ponganis et al., 1993; Ponganis et al., 1997), further examination of detailed diving behaviour with respect to particular life history phases should provide more insight into the factors dictating foraging success and long-term survival.

For all animals, reproduction is strongly linked to an individual's physiological state. Olive ridley turtles usually nest each year on one to three separate occasions, so examining diving behaviour during and after nesting periods may provide important insight into their physiological state. Olive ridley turtles are generalist predators (Bjørndal, 1997) with a relatively high proportion of time spent at or near the bottom when foraging (McMahon et al., 2007). This observation, combined with the high variability in the duration of inter-nesting periods reported for this species (Kalb, 1999; Pritchard, 1969), leads to the hypothesis that lower relative metabolic rates decouple the negative relationship observed between water temperature and inter-nesting interval in other hard-shelled marine turtle species (Hays et al., 2002). This relationship is thought to arise from the dependence of egg development on ambient water temperature (Hays et al., 2002). To test that hypothesis, we compared temperature-divide duration data from olive ridley turtles monitored in northern Australia to the relationship provided in Hays et al. (2002) for green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles. Comparing detailed diving behaviour collected using satellite-relayed data loggers (SRDLs) between the inter-nesting and post-nesting periods

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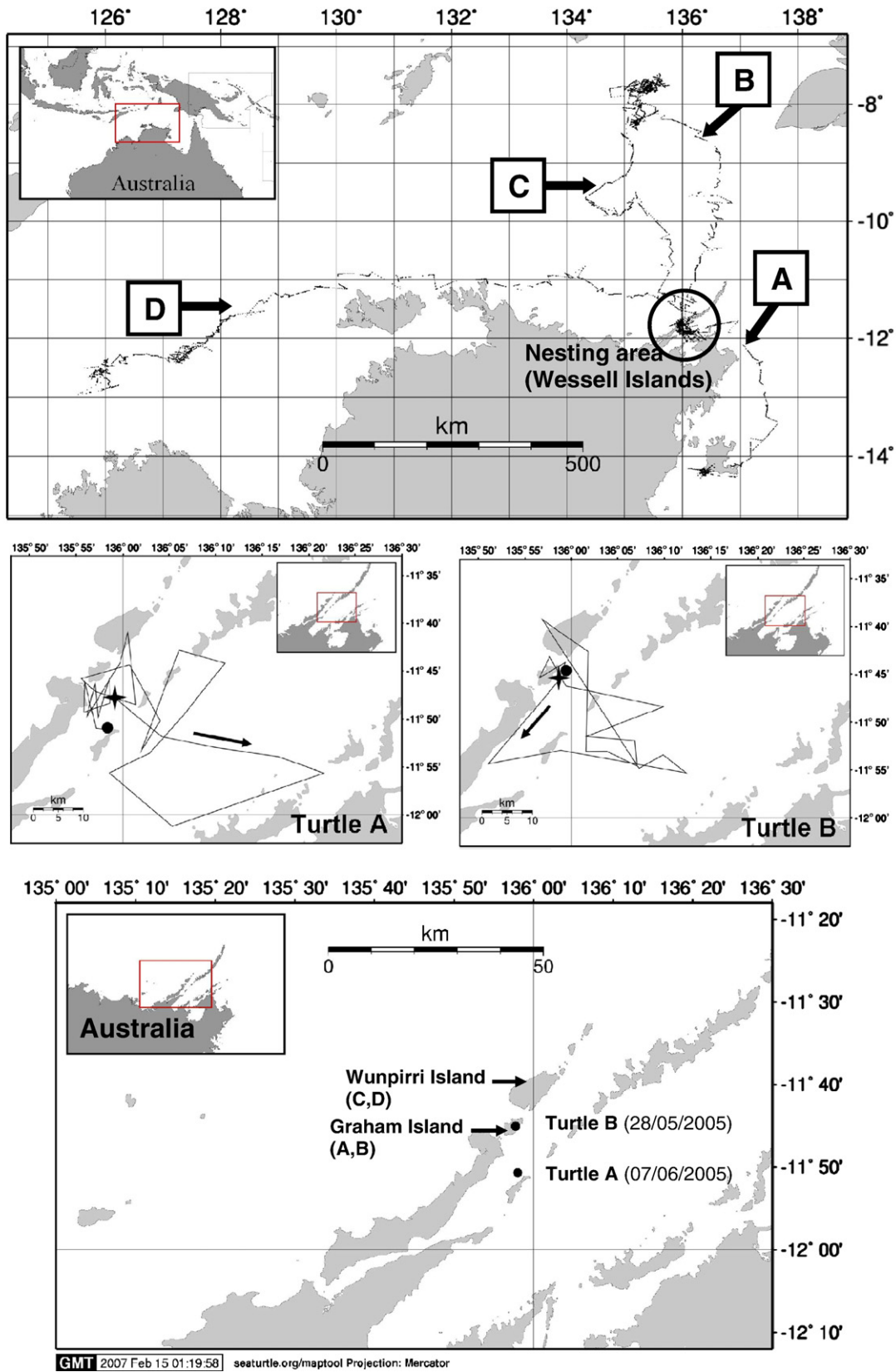


Fig. 1. Movement patterns of olive ridley turtles (*Lepidochelys olivacea*) during post-nesting migration and foraging for four adult females tracked using satellite-relayed data loggers (SRDL) from the Wessel Islands, Northern Territory, Australia. Top panel: the general distribution of individuals relative to the nesting areas. Middle panels: inter-nesting tracks for the two turtles which nested again after the SRDL attachment (Turtles A and B). The star indicates the position of the first recorded nesting event (at SRDL attachment) and the point indicates the last (inferred) nesting event. Directions of the tracks are represented by one arrow on each map. Bottom panel: location and dates of the attachment sites and the two recorded haul-outs. Turtle A nested in Alger Island and Turtle B in Graham Island again. Dates given as dd/mm/yyyy.

from two adult female olive ridley turtles (McMahon et al., 2007), we explore the ways that marine vertebrates can adapt their physiology and behaviour according to their life stage. By examining the change in dive durations, time allocation at depth, post-dive surface intervals, surface duration, maximum depth, and proportion of local bottom depth reached, we also infer whether turtles were active or not during the inter-nesting interval.

2. Material and methods

2.1. Data collection

In 2005, satellite-relayed data loggers (SRDLs) were attached to the carapace of 4 female olive ridley turtles nesting in the Wessel Islands of Arnhem Land in the Northern Territory of Australia (McMahon et al., 2007). Location and dive data were relayed via the Argos satellite network. SRDLs provided four measures of diving behaviour: (1) long-form dive profiles with information on dive shape, (2) short-form dives recording information for single dives, (3) 24-hour summary statistics of diving events based on all the data recorded, and (4) temperature-depth profiles of the deepest dive over a minimum time interval of 2 hours. Full details of SRDL function and deployment procedures can be found in McMahon et al. (2007).

2.2. Determination of the haul-out and inter-nesting periods

Our first aim was to determine if a nesting event had occurred following initial SRDL deployment. Practically, a 'haul-out' begins when the SRDL has been continuously dry for a specified length of time (usually 10 minutes). It ends when continuously wet for another interval (usually 40 seconds). We assumed that a turtle had nested if a haul-out >45 min was recorded, and if this haul-out was recorded on or near land (i.e., within the error range of Argos Location Classes (details provided in Hays et al., 2001). This means that haul-out position alone cannot be relied on to define nesting events. Con-

sequently, we used a suite of data including location, haul-out duration and satellite location accuracy to determine putative nesting events. The inter-nesting period was defined as the period between the penultimate nesting event (recorded during the attachment) and the last nesting event (determined previously as a haul-out >45 min recorded on land). Both inter-nesting Turtles A and B left the nesting area after their second recorded nesting event, so the beginning of the post-nesting period (i.e., post-nesting migration) was defined as beginning after the last nesting event.

2.3. Diving behaviour

Dive data collected by the Argos transmitter (dive duration, surface duration and maximum depth reached during the recorded dives) were analysed and their distributions compared between the inter-nesting and post-nesting periods. All the analyses were done using the R Package V2.4 (R Development Core Team, 2004). To account for individual variation in diving behaviour, the dataset was separated into individuals (Turtle A and Turtle B). Our first hypothesis was that diving behaviour differs between periods, and this depends on the interval over which dive data are summarised. The data were organised as follows: one week before and after the last recorded nesting event (time step = 1 week), two weeks before and after the last recorded nesting event (time step = 2 weeks), approximately three weeks before and three weeks after, according to the length of the inter-nesting interval (time step = 3 weeks).

The proportion of time spent per day at the surface was plotted against the number of days between the first recorded nesting event and the last nesting event to examine whether turtles modify their diving behaviour in preparation for nesting. These results were compared to data collected for a similar period post-nesting. Long-form dive profiles were characterised for shape using the TAD index (Time Allocation at Depth) (Fedak et al., 2001; McMahon et al., 2007). The TAD can be used as an index of where the turtle centres its activity with respect to depth during a dive, and varies from 1 when

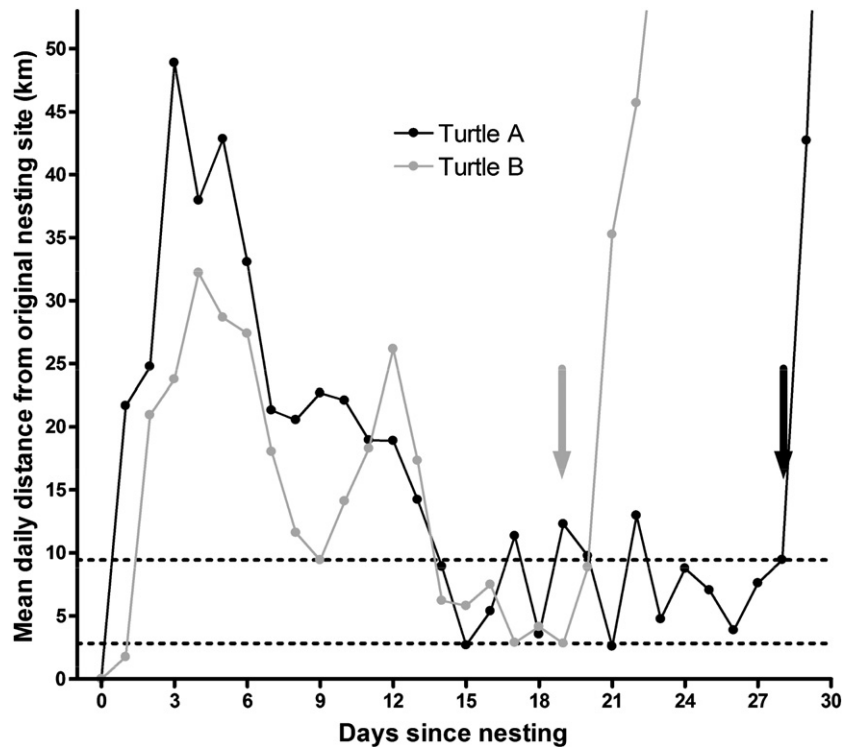


Fig. 2. Mean daily distance travelled from the first nesting site for Turtles A and B. Inferred subsequent nesting times are indicated by the black and grey arrows for Turtles A and B, respectively.

Table 1
Lepidochelys olivacea

Turtle ID	Attachment (1st recorded nesting event)		Inter-nesting Interval	Haul-out >45 min recorded		
	Date	Location		Date	Duration	Location
A	11/05/2005	Graham Island	27 days	07/06/2005	00:57	Alger Island
B	10/05/2005	Graham Island	18 days	28/05/2005	01:39	Graham Island

Summary information from two satellite-relayed data logger (SRDL) deployments on inter-nesting olive ridley turtles (Turtles A and B – see also Fig. 1) from the Wessell Islands, Northern Territory, Australia. Dates given as dd/mm/yyyy; durations as hh:mm.

the dive area is maximally U-shaped, to 0.5 when the dive is V-shaped. The distributions of TAD were compared between periods as above.

To examine whether diel patterns in diving behaviour differ between the inter-nesting and the post-nesting periods, we calculated the local solar mid-time (LST) for each dive after (Bradshaw et al., 2002), and contrasted patterns in mean dive duration, maximum dive depth and the proportion of time spent diving per LST hourly bin between the two periods using the three time steps described above. We also examined movement patterns before and after nesting events by interpolating between Argos locations received. Horizontal movements were mapped using Maptool (www.seaturtle.org/maptool).

3. Results

3.1. Isolating nesting events from SRDL data

The four female turtles tracked went in three general directions after leaving the nesting sites. Turtles C and D left the nesting area

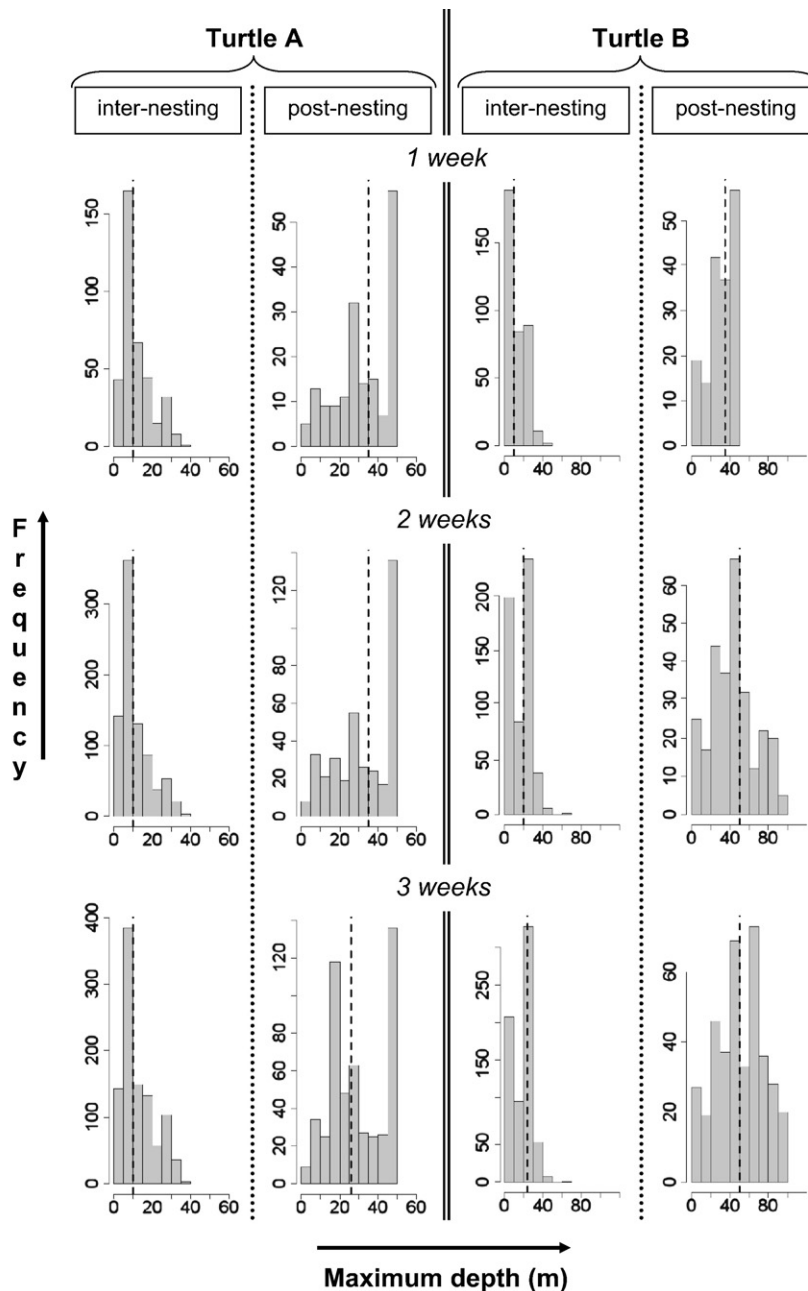


Fig. 3. Maximum dive depth for Turtles A and B during the inter-nesting and post-nesting periods. Histograms for different time steps: maximum depth distributions during 1, 2, 3 weeks before and 1, 2, 3 weeks after nesting. Median values = red dashed vertical lines.

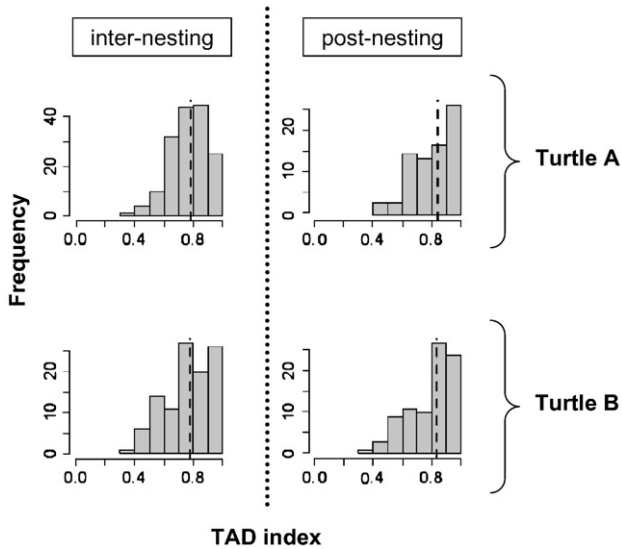


Fig. 4. Time-at-depth (TAD) dive index calculated for Turtles A and B during the three-week inter-nesting period and the three-week post-nesting period. Medians show a difference between the inter-nesting and the post-nesting periods.

immediately after the attachment, whereas Turtles A and B spent several days near the island where they were captured during nesting before leaving the region (Fig. 1; see also McMahon et al., 2007). No haul-outs exceeding 45 min were found for turtle C (haul-out maximum duration=36:41 min). For turtle D, 4 haul-outs were found over 45 min (2:44 h, 3:56 h, 1:35 h and 51 min), but they all occurred in major foraging areas (i.e., far from any land). It was assumed these two turtles did not re-nest after SRDL attachment. Turtles A and B each showed one haul-out exceeding 45 min (57 and 99 min, respectively). SRDLs assign an incrementing number to each

haul-out that occurs; both recorded haul-outs for Turtles A and B were consecutive, so we conclude that all haul-outs were recorded.

Haul-out locations were close to or on islands in the Wessel Islands group; Turtle A hauled out on Alger Island 28 days after initial nesting, and Turtle B near Graham Island 19 days after initial nesting (Figs. 1 and 2). To determine whether Turtle A had nested, location classes were analysed for each of the recorded haul-outs. Turtle A had Location Classes (LC) of 0 (precision follows a bivariate normal distribution with standard deviation [SD] in x and y coordinate error=4.29 and 15.02 km, respectively – Hays et al., 2001) and A (not enough messages to estimate precision), so we assumed that Turtle A hauled out nearby Alger Island <2000 m from the transmitted locations (Table 1). Turtle B was more precisely located at a haul-out: LC 2 (x and y coordinate error SD=0.28 and 0.62 km, respectively) and LC 3 (x and y coordinate error SD=0.12 and 0.32 km, respectively – Hays et al., 2001) at Graham Island (Fig. 1).

3.2. Horizontal inter-nesting movements

Both turtles spent their entire inter-nesting period in an area close (<50 km) to the deployment nesting sites in shallow waters (<70 m) around the Wessel Islands (Figs. 1 and 2). Distances travelled during the inter-nesting period were estimated from the mean daily positions. Turtle A travelled 200 km and Turtle B travelled 125 km based on locations with LC>0. Both turtles left their second nesting sites rapidly after laying eggs. Turtle A swam off in an easterly direction towards the English Company Islands and moved 48 km away from the departure point after 3 days of travel. Turtle B went southwest toward Echo Island and moved 32 km away from the departure point after 4 days) (Fig. 1).

3.3. Diving behaviour inter- and post-nesting

Both turtles were submerged more frequently during the inter-nesting period (46 and 38 recorded dives/day before the last nesting event, and 23 and 19 dives/per day after the last nesting event for

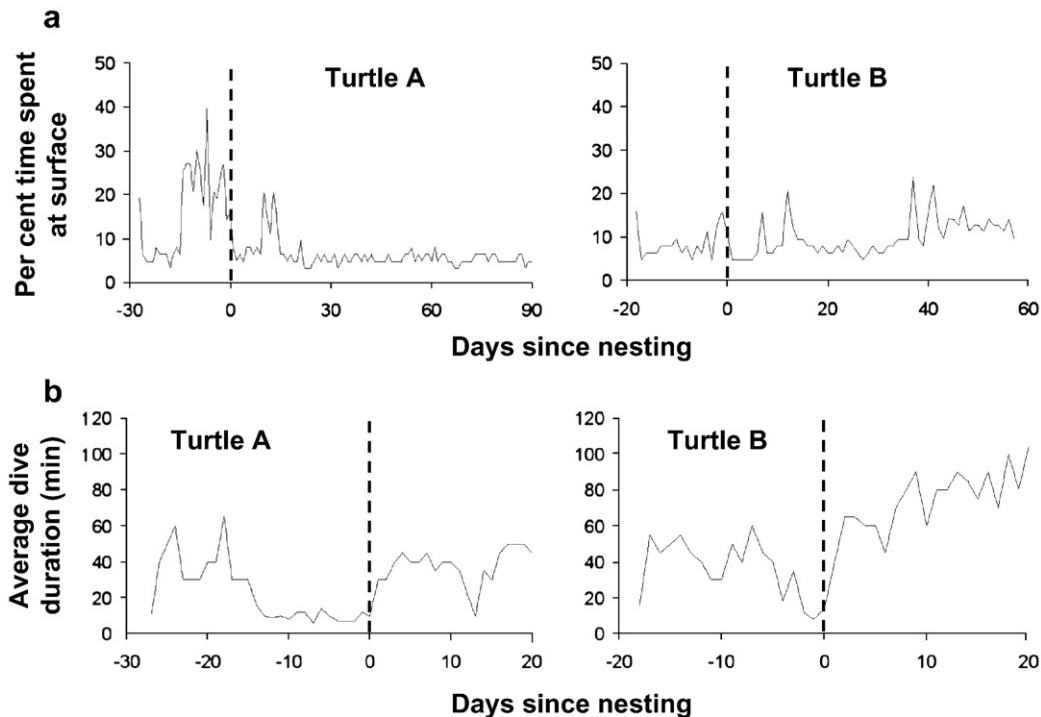


Fig. 5. (a) Proportion of time spent at surface for each day during the inter-nesting period (days<0), and since the last recorded nesting event (days>0) for the 4 female olive ridley turtles. Dashed lines represent the last nesting events. (b) Mean dive duration per day during the inter-nesting period and a part of the post-nesting migration. The dashed line represents the last nesting event.

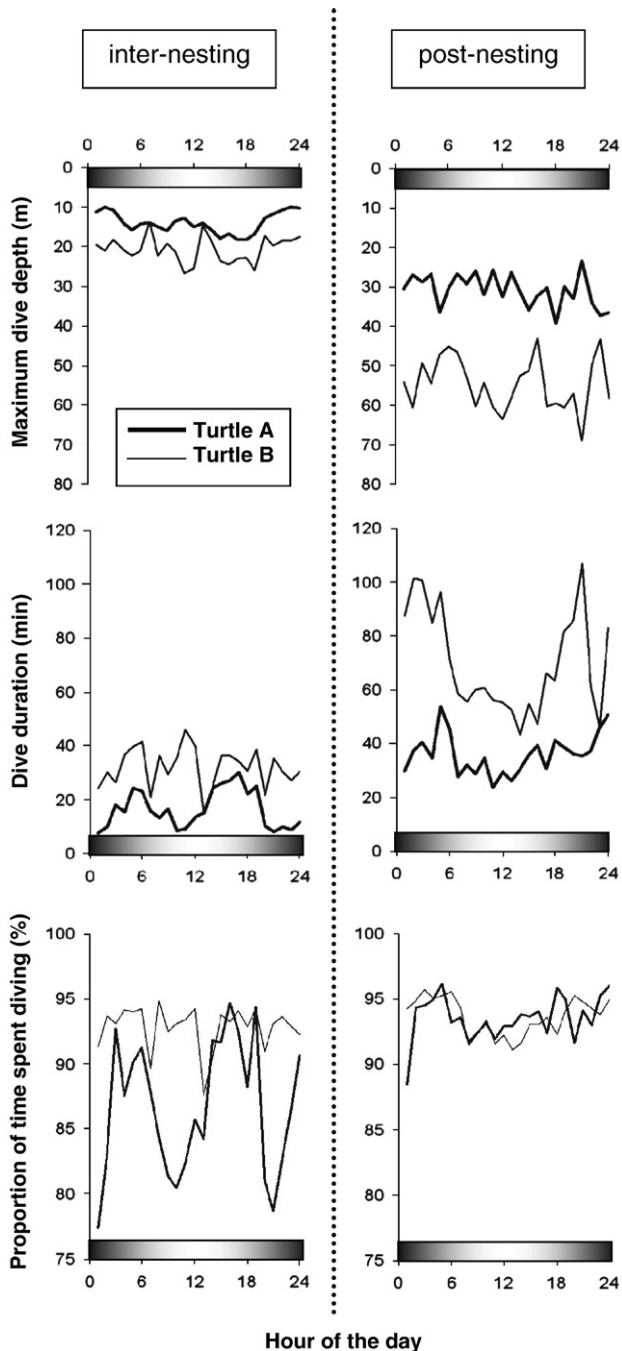


Fig. 6. Maximum dive depth, dive duration and proportion of time spent diving for each hour of the day for the two inter-nesting turtles. Data are separated into two periods: (1) 3-week inter-nesting and (2) 3-weeks post-nesting for comparison.

Turtles A and B, respectively). Both turtles were submerged for longer during the post-nesting period (1-week-median inter-nesting: Turtle A = 4.0 ± 1.4 min, Turtle B = 30.0 ± 3.2 min; post-nesting: Turtle A = 7.0 ± 2.5 min, Turtle B = 55.0 ± 4.4 min), and post-dive surface interval duration was greater during the post-nesting period (1-week median inter-nesting: Turtle A = 0.9 ± 0.2 min, Turtle B = 1.5 ± 0.1 min; post-nesting: Turtle A = 1.8 ± 0.3 min, Turtle B = 2.6 ± 0.1 min). Likewise, dives were shallower before nesting (Fig. 3). According to the proportion of local bottom depth reached per dive, both turtles nearly always dived to the bottom during the inter-nesting period (94.5% of the 1248 and 99.7% of the 696 inter-nesting dives by Turtles A and B, respectively). These differences appear to be due to bathymetric constraints during the inter-nesting period given that turtles stayed in relatively shallow

water throughout inter-nesting compared to deeper water during post-nesting dives.

The comparison of time-at-depth indices (TAD) reveals two distinct diving patterns emerging during the breeding period. Turtles spent more time at greatest depth (U-shaped dives) post-nesting (TAD near 1), whereas more V-shaped dives occurred during the inter-nesting period (TAD ~ 0.8) (Fig. 4). This suggests that turtles spent more time either resting and/or foraging after nesting, but exploring more during inter-nesting. However, the differences between the inter-nesting and the post-nesting patterns are small and higher resolution data are needed to provide insights about specific activities during the breeding season (Myers and Hays, 2006). Both turtles spent more time out of the water and dive duration decreased just before the last nesting event (Fig. 5).

3.4. Diel activity patterns

For both turtles, we used the individual dive profiles to calculate the mean of the maximum dive depth, dive duration and proportion of time spent diving for each hour of the 24-hour cycle. Dives were shorter in general during the day (maximum duration around 6:00 (sunrise) and 18:00 (sunset) and a minimum at 11:00) (Fig. 6). No differences were found between inter-nesting and post-nesting patterns. We identified no diel patterns for maximum dive depth, although there was greater variance during the post-nesting period. For the proportion of time spent diving, turtles spent more time diving at night after the final nesting event, but no diel patterns emerged during the inter-nesting period.

3.5. Temperature and nesting interval duration

Olive ridley inter-nesting intervals were unrelated to water temperature, which is in stark contrast to the negative relationship found for green and loggerhead turtles (Fig. 7). Olive ridley turtles had relatively longer inter-nesting intervals: 27 days for Turtle A and 18 days for Turtle B.

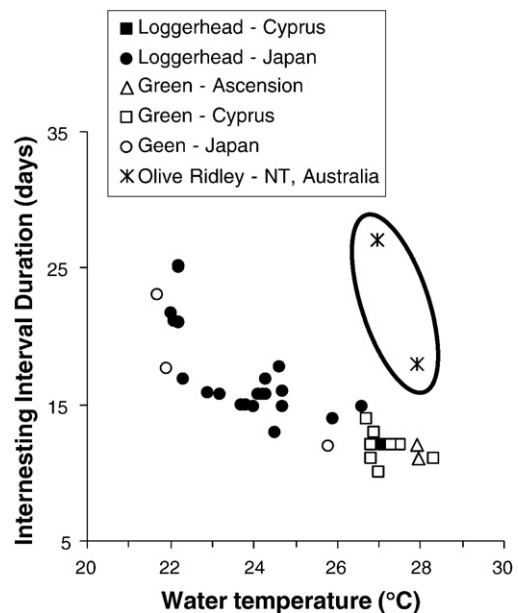


Fig. 7. Relationship between water temperature and inter-nesting interval durations for green turtles (*Chelonia mydas*) in Japan (○), Cyprus (□) and Ascension Island (△); for loggerhead turtles (*Caretta caretta*) in Japan (●) and Cyprus (■); and for olive ridley turtles (*Lepidochelys olivacea*) in northern Australia (*). Loggerhead and green turtles show a negative relationship between the duration of their inter-nesting intervals and water temperature turtles, with Australian olive ridleys deviating from the expected relationship.

4. Discussion

A dichotomy exists among marine turtle species with respect to the type of evolved life history strategy employed during the inter-nesting interval: some remain quiescent (e.g., green turtles at Ascension Island – Hays et al., 1999; loggerhead turtles in Cyprus – Hays et al., 2002; Houghton et al., 2002), while others forage (e.g., green turtles in Cyprus – Hays et al., 2002; leatherback turtles – Georges et al., 2007; Myers and Hays, 2006). Internal factors (body temperature, physiology) appear to control loggerhead and green turtle nesting intervals (Pritchard, 1969), which is illustrated by the clear relationship between water temperature and inter-nesting interval in other hard-shelled turtles (Hays et al., 2002; Sato et al., 1998).

We found reasonable evidence to suggest that nesting intervals of olive ridleys are apparently controlled more by direct external factors (tide and weather) than by internal factors (physiology). Egg retention capacity in olive ridley turtles appears to be an adaptation which enables delayed oviposition when environmental conditions are unsuitable (Plotkin et al., 1995), with most populations nesting *en masse* (in 'arribadas') at a few select beaches in the Atlantic, Pacific and Indian Oceans. When sea temperatures are high, metabolic rate is expected to increase proportionally, thus accelerating egg development. Arribada-nesting olive ridleys must have an innate capacity to lengthen or delay their nesting haul-outs to achieve simultaneous oviposition, and we hypothesise that solitary nesters like those of northern Australia can use this ability to delay nesting until optimal conditions prevail. As such, a slower metabolic rate may provide an advantage for delaying nesting in addition to permitting extended dive durations and depths to exploit a wide range of marine food sources (McMahon et al., 2007). This hypothesis could be tested by measurements of metabolic rate via respirometry for captive olive ridley turtles, as has been done for some other species (Hochscheid et al., 2005; Wallace and Jones, 2008).

Turtles artificially displaced 100 s of km from nesting beaches to distant sites can often show protracted searching behaviour, suggesting they might not have a detailed map sense that extends long distances from their nesting beaches in all directions (e.g., Lohmann et al., 2008; Luschi et al., 2001). However, the movement pattern appears different for undisturbed turtles in the breeding season. Our results for olive ridley turtles, and those shown previously for leatherbacks (Georges et al., 2007), demonstrate that turtles are able to return close to their original nesting site at the end of the inter-nesting interval. This implies they maintain a good sense of their position while making inter-nesting movements. It should also be noted that since female turtles store sperm after mating at the start of the nesting season (Lee, 2008), it is unlikely that the inter-nesting movements reflect a search for males.

Both sets of inter-nesting data examined appeared to support the conclusion that searching behaviour dominated prior to nesting when more time was spent at the surface and more erratic movements were observed. Additionally, dive durations decreased several days prior to nesting, thus suggesting a possible economy of reserves in preparation for egg laying. The implication is that turtles were more active in the days prior to nesting. This pattern of increasing activity as a nesting event approaches has been inferred several times before for sea turtles. Hays et al. (1991) used the pattern of uplinks from a satellite tag to infer that an inter-nesting loggerhead turtle in the Mediterranean spent longer at the surface as nesting events approached. Similarly, using limited data on dive duration relayed from satellite tags attached to green turtles at Ascension Island Hays et al. (1999) showed a decrease in dive duration as nesting events approached, consistent with a reduction in the occurrence of U-shaped dives, while Houghton et al. (2008) have shown the same pattern using time-depth recorders attached to inter-nesting hawksbill turtles. These results suggest that increasing activity towards the end of inter-nesting intervals may occur widely in hard-shelled marine turtles.

One possibility is that nesting beach selection may be a protracted affair. Certainly, the choice of nesting beach may be an important factor in the determination of egg survival (Lee and Hays, 2004), with some beaches having suboptimal conditions. Hence, one expects marine turtles would invest time to select suitable locations and times for nesting. Further insight into the activities dominating inter-nesting behaviour in this species will become increasingly possible due to advances in data-logging technologies (e.g., three-dimensional dive reconstruction and beak-movement patterns – Fossette et al., 2008).

Olive ridley turtles are perhaps one of the most abundant marine turtles in the world, even though many populations are classed as *Endangered* under the World Conservation (IUCN) Red List (IUCN, 2007) due to rapid declines in abundance resulting from egg poaching, beach development, fishing, and pollution. Whereas there is little evidence for similar declines in some of the solitary-nesting populations like those in Australia and French Guiana, this low metabolism-capable species may be equally at risk across its entire range with increases in global temperatures due to climate change. Indeed, current and predicted ocean temperature rises may seriously compromise ectothermic marine species such as marine turtles in the coming decades (McMahon and Hays, 2006).

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