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THE DIVING BEHAVIOR OF INTER-NESTING HAWKSBILL TURTLES, *ERETMOCHELYS IMBRICATA* (LINNAEUS 1766), ON MILMAN ISLAND REEF, QUEENSLAND, AUSTRALIA.

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***Abstract.*—This investigation addresses the behavior of Hawksbill Turtles, *Eretmochelys imbricata,* during their 14-day (average) in-water inter-nesting period. We deployed time-depth data loggers (TDs) 11 times on nine turtles during the 1997/98 and 1998/99 nesting seasons at Milman Island in north Queensland. Turtles that successfully laid a clutch of eggs had TDs attached to determine their normal inter-nesting behavior. We attached TDs to two unsuccessfully nesting turtles to observe the short 1 - 2 day period that they spent at sea before attempting to re-nest. The grand mean dive time, dive depth, and surface interval for the nine successfully nesting study turtles were: 31.2 min (Range: 0.2-74.0 min, SD = 13.0 min, N = 1,450); 5.7 m (Range: 0.9-20.6 m, SD = 3.5 m, N = 65,584); and 1.6 min (Range: 0.2-575.0 min, SD = 5.2 min, N = 1,450) respectively. The grand mean dive time, dive depth and surface interval for the two turtles that unsuccessfully nested were: 11.7 min (Range: 0.5-59.8 min, N = 261); 2.5 m (Range: -0.2-21.5 m, SD = 2.7 m, N = 6,087); and 12.5 min (Range: 0.5-603 min, SD = 40.8 min, N = 261), respectively. There was little difference between the day (0601-1800 hrs) and night (1801-0600 hrs) dive times of turtles that successfully oviposited. Day and night dive times for the two turtles that were unsuccessful in their initial nesting attempt were markedly different. Most turtles (8 of 9) attained deep dives, which were defined as those dives that were greater than two standard deviations from an individual's mean dive depth. The maximum depth of a deep dive was 21.5 m. Ascent and descent rates preceding and following other dives were highly variable. The turtles that unsuccessfully nested had distinctly uncharacteristic dive and surface behavior compared with turtles that successfully nested; however, they returned to a more typical dive pattern once they finished ovipositing.**

Key Words.— Diving; *Eretmochelys imbricata*; Hawksbill Turtle; Surfacing; Telemetry; Time-depth

INTRODUCTION

Eretmochelys imbricata (Hawksbill Turtle) is a cryptic species of marine turtle that spends most of its life in the ocean. They are occasionally seen when they break the surface to breathe or when females leave the sea to lay their eggs on tropical/subtropical beaches. Consequently, previous studies of *E. imbricata* focused on times when turtles are most obvious, i.e., on the beach while nesting.

Milman Island, an uninhabited vegetated sand cay (Loop et al. 1995) in the Far Northern Section of the Great Barrier Reef Marine Park is a high density nesting rookery of *E. imbricata* regionally (Dobbs et al. 1999). *Eretmochelys imbricata* arrive at Milman Island from feeding sites distributed over a vast geographical range (Miller et al. 1998) and may spend several months, nesting at two week intervals, in a localized area adjacent to the nesting beach (MacPherson 1998). Negative anthropogenic impacts on the nesting population, such as capture by prawn trawlers working close to the island, may seriously impact this species throughout the entire rookery drawing area (Eckert 1995a).

The general lack of data describing dive and surface behavior of turtles in a marine environment is not surprising given that the technology previously available was inadequate. Before the development of microprocessor technology (ca. 20 years ago) investigators tracked marine turtles with flipper tags (Caldwell 1962), balloons (Carr 1962), radio transmitters (Carr 1972) and tethered floats (Carr et al. 1974). These methods required researcher presence during tracking operations or relied on the return of tags to determine movements.

During the last 15 years improved technologies and equipment became available. In particular, reduced microprocessor and battery size, increased processing power, and greater data storage capabilities provided for the development of small, efficient, and robust telemetry equipment (Eckert 1999). These instruments now provide a relatively unobtrusive way of continuously collecting large sets of accurate dive pattern data over extended periods. Interpretation of these data now provides some insights into the

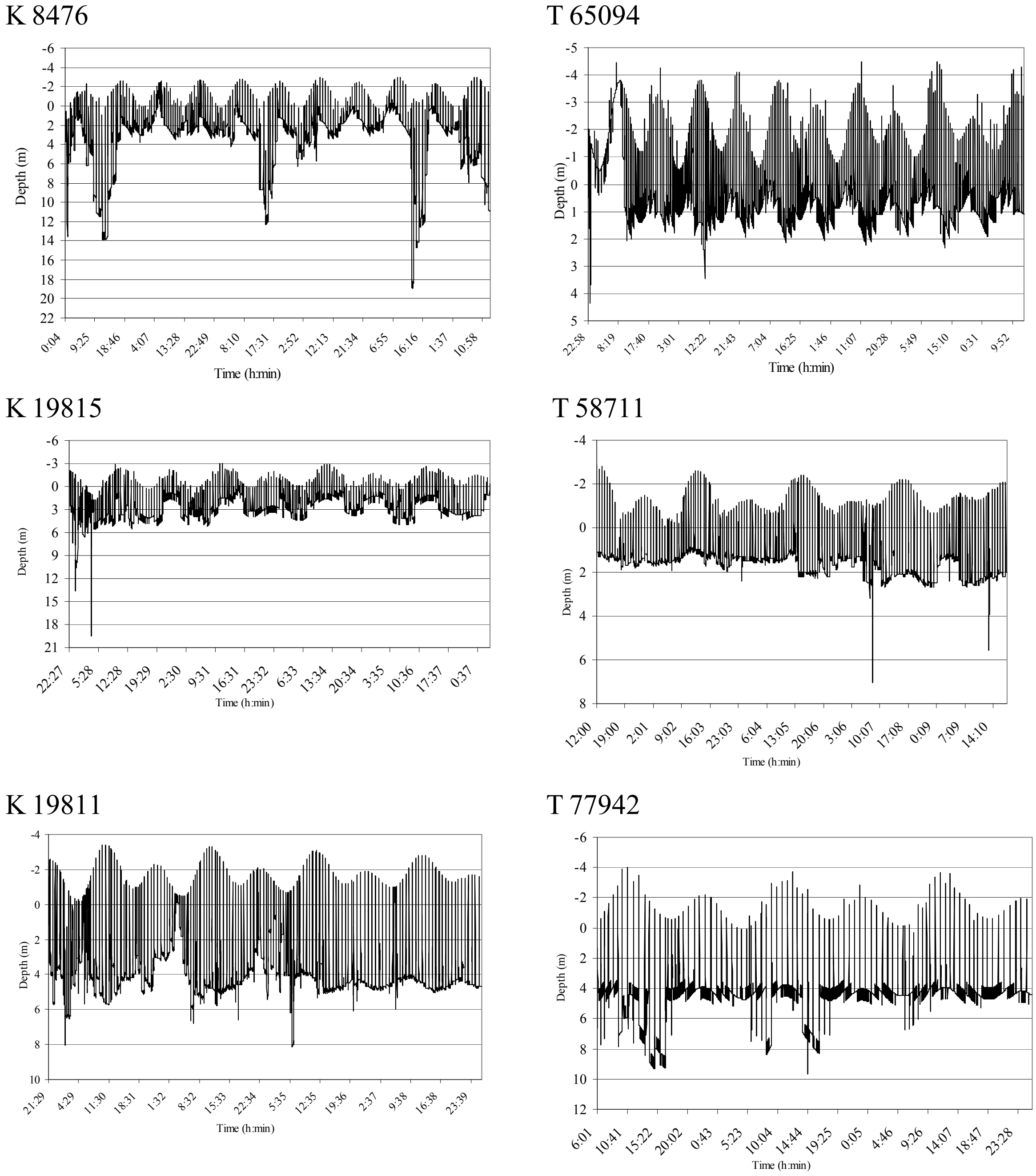


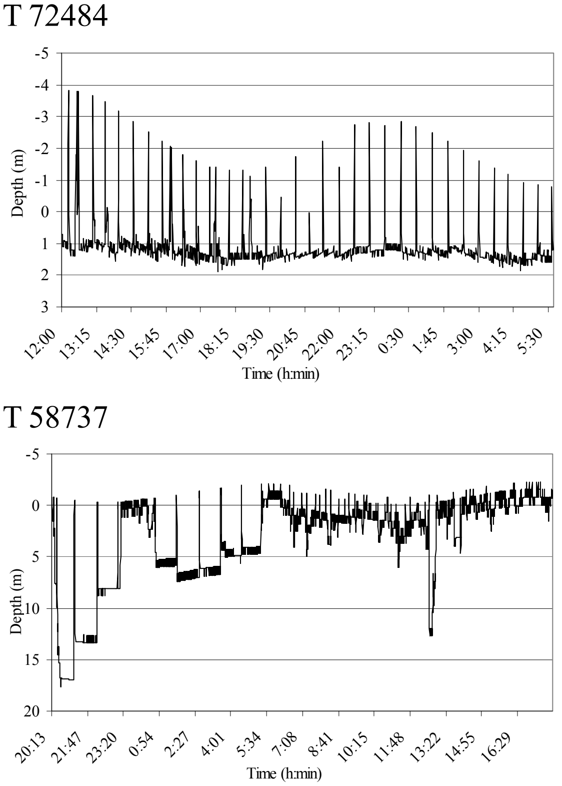
FIGURE 1. Dive profiles for successfully nesting Hawksbill Turtles, *Eretmochelys imbricata*, at Milman Island Reef, Queensland, Australia. Labels on charts refer to tag numbers on individual turtles referenced in the text. (*Continued on the next page*).

normally cryptic *E. imbricata* life history (Eckert 1995b; Tomkiewicz and Burger 1996; Andrews 1998).

From the perspective of turtle conservation and management, it is important to understand the range of behaviors these animals undertake, including how they spend their time while at a rookery (Bury 2006). There is, however, a lack of detailed information describing *E. imbricata* activities while at sea between laying their successive clutches of eggs.

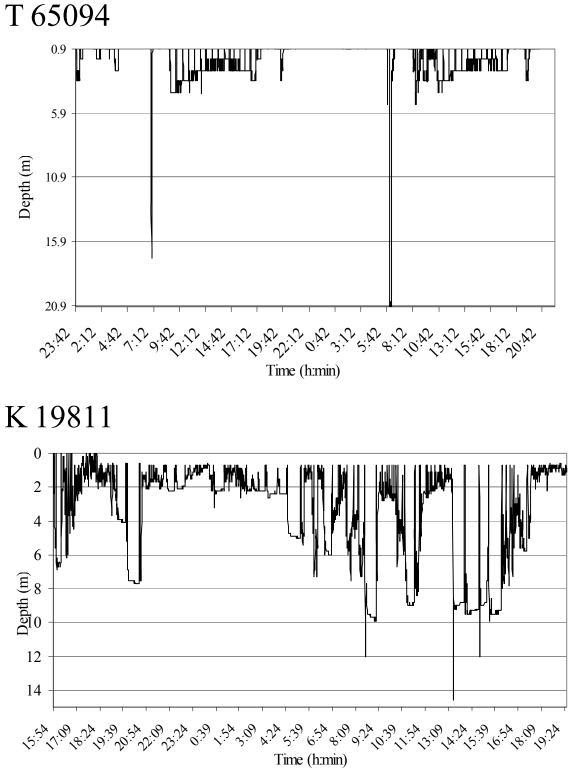
MATERIALS AND METHODS

We selected turtles from those that were in route to the sea following an actual or attempted nesting. We deployed 11 time-depth data loggers (TD) on nine turtles. We used the following selection criteria to maximize the likelihood of recovering TDs: strong nesting site philopatry; deposition of only one previous clutch of eggs at Milman Island in the current nesting season;


T 72484

T 58737

FIGURE 1 (*continued from the previous page*). Dive profiles for successfully nesting Hawksbill Turtles, *Eretmochelys imbricata*, at Milman Island Reef, Queensland, Australia. Labels on charts refer to tag numbers on individual turtles referenced in the text.


T 65094

K 19811

FIGURE 2. Dive profiles for unsuccessfully nesting Hawksbill Turtles, *Eretmochelys imbricata*, at Milman Island Reef, Queensland, Australia. Labels on charts refer to tag numbers on individual turtles referenced in the text.

and, tidal conditions facilitating turtle access to the nesting beach 14 days after TD attachment.

The majority of TD deployments followed a successful nesting. However, two turtles, T 65094 and K 19811, had TDs attached to them after they failed to lay a clutch of eggs. They had the same TDs reattached after they returned and successfully laid a clutch of eggs. We did this to investigate in-water behavior following successful and unsuccessful nesting emergences.

Description of telemetric equipment.—The TDs (8 Bit Minilog TD) (Vemco Pty Ltd., Nova Scotia, Canada) were designed specifically for investigating the underwater behavior of marine animals. TDs were able to measure pressure to 50 psi, which equated to depths from 0-34 m with ± 1.0 m accuracy and a 0.2 m resolution. Individual TDs recorded at 10, 30, 45, and 60 s intervals to gain both fine scale data during short term periods and at greater intervals to capture data for the duration of the interesting period. Three TDs recorded three, four, and five days after the turtle returned to the sea to capture the mid and last sections of an inter-nesting interval.

TD data logger attachment.—We secured TDs to the ventral surface of one (usually the left) supracaudal scute by a 6 x 50 mm stainless steel bolt and "nylock" self-locking nut. A 6 mm diameter hole was drilled using a rechargeable electric drill with a titanium twist bit. We drilled a second hole approximately 50 mm posterior to the attachment point, which was also fitted with a 6 x 50 mm stainless steel bolt and nut. Mann-Whitney U tests were used to compare diving behavior between turtles ($\alpha = 0.05$).

RESULTS

We recorded the dive profiles of nine turtles that successfully laid eggs and of two turtles that failed to complete oviposition (Fig. 1 and 2). One TD malfunctioned mid-way through a recording period, so we discarded the data recorded after this failure. The remaining TDs functioned effectively on 1,711 dives, with a total cumulative recording time of 884.9 hrs of diving and surfacing behavior. The pre-programmed recording intervals (10, 30, 45 or 60 s) captured data sets of 17 to 181 hr periods for individual turtles.

TDs indicated that all turtles returned to re-nest on Milman Island following their in-water inter-nesting

TABLE 1. Mean dive time, range (*R*), standard deviation (SD), and number of dives (N) for Hawksbill Turtles (*Eretmochelys imbricata*).

Turtle	Mean (min)	*R* (min)	SD (min)	N
K 8476	36.2	1.0 - 74.0	15.9	214
T 65094	26.3	1.0† - 47.0	12.6	266
K 19815	26.4	0.8† - 50.3	12.3	223
T 74256	47.5	1.0† - 61.0	13.1	147
K 58711[1]	33.8	1.5 - 57.8	11.2	176
K 19811	31.7	0.8† - 54.8	15.2	182
T 77942[2]	42.2	0.5† - 55.5	6.6	94
T 72484[3]	25.3	0.8† - 6.0	14.5	38
T 58737	11.8	0.2† - 58.8	16.0	110
Grand mean	**31.2**	**0.2 - 74.0**	**13.0**	**1,450**
T 65094*	16.0	1.0† - 38.0	13.8	70
K 19811*	7.4	0.5† - 59.8	1.6	191
Grand mean	**11.7**	**0.5 - 59.8**	**7.7**	**261**

*Unsuccessful nesting turtle.

† Minimum dive time is equal to the minimum recording interval of TD.

[1] 3 day delayed start.

[2] 4 day delayed start.

[3] 5 day delayed start.

period. Two turtles carrying TDs went unrecorded during nightly beach checks, and returned to the sea with TDs still attached. These turtles did not re-nest on Milman Island, so we lost the data on their TDs.

Dive profiles for successful nesting turtles.— Time-Depth dive profiles for nine turtles represent how deep turtles dove without the effect of tidal fluctuations on the depth recorded (Fig. 1). While turtles occasionally made deep dives, five of the nine turtles that nested successfully (T 74256, T 58711, T 77942, T 72484 and T 58737) maintained a constant depth upon returning to the sea. Two turtles, K 8476 and T 65094, maintained a close synchronicity with tidal change. K 19815 maintained a constant depth for 24 hrs and then generally followed the tidal cycle for the four remaining days. K 19811 followed the tidal fluctuations for the first 24 hrs and then maintained a relatively constant position for the remaining three days.

Dive profiles for unsuccessful nesting turtles.— Following an unsuccessful nesting attempt, T 65094 remained at the surface for most of the rest of the night, making shallow dives until daylight (Fig. 2). Early the next morning, this female made a single "deep" dive, then maintained a relatively shallow dive pattern throughout the rest of that day. The next 24 hrs mirrored the previous day, with the entire night spent at the surface, two deep dives early in the morning, and the rest of the day spent shallow diving. The TD data indicate that she probably unsuccessfully emerged to nest on the first night after her original failed nesting attempt. However, beach patrols did not record her on Milman Island. The dive profile displayed by K 19811 (Fig. 2), following an unsuccessful nesting attempt, was similar to those displayed by turtles that nested successfully. For example, K 19811 made repetitive dives that were shallower at night compared to during the day.

Dive Times.—The grand mean dive time, for the nine study turtles that successfully nested on Milman Island, was 31.2 min, (Range (*R*)= 0.2-74.0 min, SD = 13.0 min, N = 1450) (Table 1). Dive profiles for eight of the turtles were generally bi-modal, with peaks occurring at short dives (1-4 min), and also around the turtle's mean dive time. The exception to this was T 58737, who undertook the majority (24) of her dives for a short duration (0.2 min) and then conducted very few dives (1-4) that varied in length from 0.4-58.8 min.

The two turtles that unsuccessfully nested had mean dive lengths that were markedly different from each

Table 2. The mean diel dive times (X), range (R), standard deviation (SD), number (N), and difference between day and night dive times for study turtles.

Turtle	Day dive length (min)				Night dive length (min)				Mann-Whitney U
	$\bar{X}$	*R*	SD	N	$\bar{X}$	*R*	SD	N	*P*
K 8476	38.3	1.0† - 64.0	15.2	101	34.1	1.0† - 74.0	16.4	113	0.09
T 65094	27.0	1.0† - 43.0	10.7	136	25.6	1.0† - 47.0	14.4	130	0.57
K 19815	27.9	0.8† - 44.3	10.5	97	24.8	0.8† - 50.3	13.6	126	0.24
T 74256	45.9	1.0† - 61.0	8.8	71	49.1	1.0† - 60.0	16.0	76	< 0.05
K 58711[1]	31.6	1.5† - 57.8	12.1	98	36.0	3.0† - 52.5	9.5	78	< 0.05
K 19811	33.0	1.5† - 51.8	14.5	83	30.3	0.8† - 54.8	15.8	99	0.45
T 77942[2]	40.0	0.5† - 55.5	13.6	50	44.4	6.5 - 55.5	10.7	44	< 0.05
T 72484[3]	22.3	2.3 - 31.5	9.9	15	28.2	0.8† - 33.8	9.2	23	< 0.05
K 58737	15.3	0.2† - 54.5	12.7	45	8.3	0.3 - 58.8	17.5	65	< 0.05
Grand mean	**31.3**	**0.2 - 64.0**	**9.4**	**696**	**31.2**	**0.3 - 74.0**	**11.9**	**754**	
T 65094*	18.2	1.0† - 38.0	14.2	55	8.0	1.0† - 21.0	8.3	15	< 0.05
K 19811*	9.5	0.5† - 45.5	11.0	82	5.9	0.5† - 59.5	10.3	109	< 0.05
Grand mean	**13.8**	**0.5 - 45.5**	**12.6**	**137**	**6.9**	**0.5 - 59.5**	**9.3**	**124**	

* Unsuccessful nesting turtle.

† Minimum dive time is equal to the minimum recording interval of the TD.

[1] 3 d delay start.

[2] 4 d delay start.

[3] 5 d delay start.

TABLE 3. Diving characteristics of Hawksbill Turtles (*Eretmochelys imbricata*) at Milman Island Reef, Queensland, Australia. Below are the maximum dive time(s), the time of the dive's onset, the number of days after either the turtle returned to the sea or the TD began recording, and the total deployment time.

Turtle	Max Dive Time (min)	Onset of dive (hr)	Days after return to sea or beginning of TD recording	Recording period (days)
K 8476	74.0	0240 to 0354	4	5.6
T 65094	38.0	1411 to 1448	2	1.3
K 19815	50.3	0400 to 0450	2	4.2
T 74256	61.0	0813 to 0913	4	5.5
T 58711[1]	60.0	0753 to 0852	7	4.2
K 19811	54.8	0217 to 0316	2	4.2
T 77942[2]	55.5	2155 to 2250	1	2.8
T 77942[2]	55.5	1537 to 1632	2	
T 72484[3]	66.8	21 24 to 2230	1	0.7
T 58737	58.2	2113 to 2211	1	0.9
T 65094*	47.0	2320 to 0006	4 5	5.6
K 19811*	59.5	0217 to 0316	2	1.5

* Unsuccessful nesting turtle.

[1] 3 day delay start.

[2] 5 day delay start.

[3] 4 day delay start.

other. They were however, much shorter than most of the turtles that nested successfully (except K 58737). The grand mean dive time for the two turtles was 11.7 min (r^2 = 0.5-59.8 min, SD = 7.7, N = 261) (Table 1).

Diel Variation in Dive Times.—The grand mean dive period during the day was 31.3 min (*R* = 0.2 - 64.0 min, SD = 9.4 min, N = 696) while the mean nocturnal dive time was 31.2 min (*R* = 0.3 - 74.0, SD= 11.9 min, N = 754) for turtles that nested successfully. Despite this similarity, five of the nine turtles displayed significantly different day and night dive times, with four of the five turtles having longer duration dives at night (Table 2).

The grand mean day dive time for the two turtles that failed to lay a clutch of eggs was 13.8 min (*R* = 0.5-45.5 min; SD = 12.6 min, N = 137). The mean night dive duration was 6.9 min (*R* = 0.5-59.5 min, SD = 9.3 min, N = 124) (Table 2). There was a significant difference ($\alpha < 0.05$) in diel dive durations for these two turtles, with both demonstrating shortened nocturnal dives (in contrast to most of the turtles that nested successfully that exhibited differences between day and night dive times).

TABLE 4. The mean dive depths, range, standard deviation (SD) and number of depth records (N) for Hawksbill Turtles (*Eretmochelys imbricata*) at Milman Island Reef, Queensland, Australia.

Turtle	Mean depth (m)	Range (m)	SD (m)	N
K 8476	5.6	1.5 - 20.6	3.2	8004
T 65094	3.0	0.9 - 6.9	1.1	8070
K 19815	4.9	1.5 - 20.0	1.4	8087
T 74256	12.1	2.3 - 14.5	1.9	7950
K 58711[1]	3.7	0.9 - 8.8	0.8	8128
K 19811	6.3	1.1 - 9.7	1.5	8058
T 77942[3]	6.9	1.5 - 12.2	1.5	8126
T 72484[2]	3.4	1.1 - 5.2	0.7	1317
K 58737	5.5	1.5 - 19.1	4.0	7844
Grand mean	**5.7**	**0.9 - 20.6**	**1.8**	**65584**
K 65094*	1.2	0.0 - 21.5	1.9	2773
K 19811*	3.5	-0.2 - 14.6	2.8	3314
Grand mean	**2.5**	**-0.2 - 21.5**	**2.7**	**6087**

* Unsuccessful nesting turtle.

[1] 3 day delay start.

[2] 4 day delay start.

[3] 5 day delay start.

Number of dives/hour.—The grand mean dive frequency, for turtles that nested successfully was 0.5 dives/hr, being the reciprocal of their mean dive time of 31.2 min. T 74256 undertook dives most frequently (0.8 /hr), while T 58737 displayed the minimum rate (0.2 /hr). The mean dive frequency for the two turtles that failed to lay a clutch of eggs was 1.5 and 6.9 dives/hr.

Maximum dive times.—Twelve maximum dive times appeared in the 11 dive profiles collected (T 77942 undertook two dives of equal length). Eight of the 12 maximum dive times occurred at night (i.e., between 1800 and 0600 hrs) (Table 3). The other turtles' maxima occurred early in the morning (0752-0853 hrs and 0813-0913 hrs) and the mid to late afternoon (1411-1448 hrs and 1537-1632 hrs). No maximum dive times occurred in the middle of a day. The longest dive-time among all study turtles was by K 8476, lasting 74.0 min. This dive occurred between 0240 and 0354 hrs on the fourth night of her inter-nesting period.

Dive depths.—The grand mean dive depth for TD fitted turtles that nested successfully was 5.7 m (r^2 = 0.9-20.6 m, SD = 1.5 m, N = 65,584) (Table 4). Whereas most turtles shared a relatively uniform mean dive depth of around 5.7 m, T 74256 displayed a mean dive depth of 12.1 m or approximately twice the grand

Table 5. Surface interval times for Hawksbill Turtles (*Eretmochelys imbricata*) from Milman Island Reef, Queensland, Australia.

Turtle	Mean Surface Interval (Min)
K 8476	1.2 (*R* = 1.0† - 12.0, SD= 0.8, N= 214)
T 65094	4.1(*R* = 1.0† - 575, SD= 35.2, N= 266)
K 19815	1.0 (*R* = 0.8† - 3.0, SD= 0.6, N= 223)
T 74256	1.7 (*R* = 1.0† - 38.0, SD= 3.0, N= 147)
K 58711[1]	1.0 (*R* = 0.8† - 3.0, SD= 0.5, N= 176)
K 19811	1.6 (*R* = 0.8† - 48.0, SD= 3.6, N= 182)
T 77942[3]	1.1 (*R* = 0.5† - 2.0, SD= 0.7, N= 94)
T 72484[2]	0.8 (*R* = 0.8† - 1.5, SD= 0.2, N= 38)
T 58737	0.3 (*R* = 0.2† - 2.8, SD= 2.1, N= 110)
Grand mean	**1.6 (*R* = 0.2† - 575.0, SD= 5.2, N= 1450)**
T 65094*	23.6 (*R* = 1.0† - 603.0, SD= 79.6, N= 70)
K 19811*	1.3 (*R* = 0.5† - 21.5, SD= 2.1, N= 190)
Grand mean	**12.5 (*R* = 0.5† - 603.0, SD= 40.8, N= 260)**

* Unsuccessful nesting turtle.

† Minimum dive time is equal to the recording interval of TD.

[1] 3 day delayed start.

[2] 4 day delayed start.

[3] 5 day delayed start

mean for all turtles. T 65094 maintained the shallowest dive depth with a mean of 3.0 m. The grand mean dive depth for the two turtles that failed to nest was 2.5 m (*R* = -0.2-21.5 m, SD = 2.7 m, N = 6087) (Table 4).

Uncharacteristically "deep" dive depths.—"Deep" dives (submergences to a depth > mean + 2 SD for an individual turtle) occurred in 10 of the 11 profiles. The frequency that turtles exceeded a "deep" dive threshold varied among individuals. Three turtles (K 8476, K 19811, and T 74284) made only one "deep" foray each; whereas, K 19815 exceeded her "deep" threshold 12 times during one recording period.

Surface intervals.—The grand mean surface interval for turtles that nested successfully was 1.6 min (*R* = 0.2-575.0 min, SD = 5.2 min, N = 1450) (Table 5). The mean surface interval for the two turtles that failed to lay a clutch of eggs was 12.5 min (*R* = 0.5-603 min, SD = 40.8 min, N = 260) (Table 5). Minimum surface intervals of 0.5 and 1.0 min were related to the recording intervals pre-programmed into the TDs.

The surface interval times for all study turtles before and after uncharacteristically "deep" dives.—T 65094 was the only turtle to spend a markedly longer time at the surface prior to conducting a "deep" dive. Twenty hours after returning to the sea, having failed in her initial nesting attempt, T 65094 spent 603 min at the surface. The turtle then made a 2 min dive to 5.2 m followed by an 11 min surface interval. The turtle then dove directly to 21.5 m.

Surface intervals for all study turtles prior to, or following uncharacteristically "long" dives.—Three of the nine turtles conducted "long" dives. There were no distinct differences among the mean surface intervals before or after "normal" dives. All three of the turtles had the same mean surface intervals before and after a "long" dive.

Diel differences in surface behavior patterns in all study turtles.—Most nesting turtles displayed approximately equal or slightly longer surface intervals at night compared to day. T 58737 was the only study turtle that successfully nested to display significantly different (Mann-Whitney U Test; $\alpha < 0.05$) day and night surface-interval times. Conversely, both turtles that unsuccessfully nested (T 65094 and K 19811) displayed significantly different day/night surface intervals.

DISCUSSION

TDs were effective for describing the dive profiles of *E. imbricata* during their inter-nesting period.

Dive times.—While there were significant differences in dive times between turtles, many dive characteristics were similar both within and among turtles. Individuals occasionally took long dives; however, this is not typical diving behavior. These uncharacteristic events were particularly apparent for the two turtles that failed to lay a clutch of eggs and suggest a period of restlessness that continued until successful oviposition occurred.

The grand mean dive time of turtles that successfully oviposited (31.2 min) was similar to those times recorded for immature *E. imbricata* using TD equipment (day: 19-26 min, night: 35-47 min, grand mean: 31.5 min, SD = 26.2, N = 2,738)(van Dam and Diez 1997). They also reported diurnal foraging dives for immature *E. imbricata* ranging in duration from 0.1-49.7 min and resting nocturnal dives ranging from 0.7-73.9 min.

The two turtles that failed to lay a clutch of eggs at the first nesting attempt had erratic dive period patterns relative to and compared to other successfully nesting turtles. Previous reports of these types of uncharacteristic dive behaviors following unsuccessful nesting attempts exist in one other species of marine turtle. One *Chelonia mydas* that failed to lay a clutch of eggs at Ascension Island remained within the vicinity of the beach, traveling back and forth in near-shore waters until daylight, and then moved into deeper water (Mortimer and Portier 1989).

Physiological aspects of undertaking "long" dive times.—There were no strong positive relationships between mean dive times or depths with surface interval times. This supports results with other inter-nesting species (e.g., *Dermochelys coriacea*) (Eckert et al. 1986). ***Eretmochelys*** *imbricata* do not need extended surface "recovery times" to deal with longer dives. As with other species of turtle, *E. imbricata* conduct prolonged dives due to their high anaerobic tolerance and specialized physiological adaptations, such as resistance to large changes in blood gas and pH levels, and unique adaptations in brain energy metabolism (Kooyman 1989).

Dive depths.—The grand mean dive depth of 5.7 m is shallow compared to that other species of inter-nesting marine turtles. *Chelonia mydas* in Cyprus (Hays et al. 2002) maintained a mean depth of 2.7 m while foraging during their inter-nesting period; whereas, a fasting cohort of *C. mydas* at Ascension Island averaged 9.5 m. An extrapolation of previously reported *Caretta caretta* data (Sakamoto et al. 1993) indicated that the combined mean dive depth during an inter-nesting period for this group of turtles was 11.2 m. However, the mean dive depth for gravid *D. coriacea* was 61.6 m during inter-nesting periods (Eckert et al. 1989). Although 61.6 m may seem deep for an inter-nesting resting site, *D. coriacea* dive deeper than 1000 m to rest (Eckert et al. 1989).

The mean dive depths for some marine turtle species (e.g., *D. coriacea* in the Caribbean, Eckert et al. 1986; Eckert 2002) were considerably deeper than those reached by *E. imbricata* at Milman Island. This is may be an artifact of the shallow bathymetry of the sea floor adjacent to Milman Island.

Deep dives.—Telemetry data showed that although *E. imbricata* typically return to similar depths following surfacing, seven of the nine turtles made infrequent, albeit brief, forays to depths several times deeper than their mean dive depth. These were typically single dives with an immediate return to a typical dive pattern.

Four of the nine turtles made at least one dive to a depth greater than the 15 m sea floor available immediately adjacent to Milman Island. This suggests that offshore movements occur often. It seems unlikely that these occasional forays into deeper water were accidental given that turtles have a good sense of spatial orientation (Limpus and Reed 1985; Bonadonna et al. 1995; Papi 2001).

Dive profiles.—Individual dives separate into four generalized dive types (Minamikawa et al. 1997; Hochscheid et al. 1999; and Hays et al. 2000a). The most common type of dive consisted of a turtle remaining at a fixed depth for the majority of the submergence period, surfacing briefly, and then returning to the previous depth. Dives with a constant depth bottom phase following the initial descent and prior to the final ascent probably represented periods of inactivity within reefal structure or on the sea floor. While these "flat-bottomed" shaped dives were the most common, all nine turtles displayed a range of different dive types during this study. The three most common dive regiments were: (1) a slow step-wise descent to a depth where the majority of the submergence time was spent, followed by a rapid ascent to the surface; (2) the opposite pattern where a rapid descent was made to a depth for the majority of time, followed by a slow step-wise ascent back to the surface; and (3) a rapid almost vertical descent and ascent with very little time spent at the maximal depth. Some refer to the first two variants as "S" shaped dive patterns (Hochscheid et al. 1999; Storch et al. 1999), and were thought to be associated with feeding activities; the final one (3) is a "V" shaped profile.

Diving activity differences between successful and unsuccessful nesting turtles.—Following oviposition, *E. imbricata* generally displayed very rhythmic dive patterns with long times between surfacing events. Conversely, unsuccessfully nesting *E. imbricata* were active, particularly during the night, spending much of their time at the surface. Upon completion of successful nesting, turtles reverted to a more characteristic dive pattern.

Surface intervals.—The surfacing profiles of inter-nesting *E. imbricata* suggest that while turtles typically did not linger at the surface, some did spend extended time there, particularly if the nesting attempt was unsuccessful. *Eretmochelys imbricata* display the shortest mean surface intervals among several species of previously studied marine turtles. Inter-nesting *C.*

caretta demonstrated surface intervals of "less than 4 minutes" (Yano and Tanaka 1991). Two inter-nesting *C. mydas* at Ascension Island had surface intervals of 1.7 min and 2.2 min (Hays et al. 2000a), and inter-nesting *D. coriacea* had mean surface times of 4.9 min (Eckert et al. 1989).

Although inconclusive, it is unlikely that the 10 hours at the surface was preparatory for the "deep" dive by T 65094. Not only was the extended surface time not immediately prior to the "deep" dive, but no other turtle demonstrated a similar extended surface time prior to diving deep. In fact, the 11.0 min surface time of T 65094 immediately preceding her "deep" dive may reflect a transition from prolonged surfacing behavior to one of diving.

The two turtles that unsuccessfully nested during our study had the longest average surface intervals of all turtles previously studied. While a definitive explanation for these extended surface periods is unavailable, it could be associated with the turtle "getting its bearings" prior to re-emerging. As we captured no data at the very end of inter-nesting intervals, it is unknown if this is typical pre-nesting behavior. Once these two turtles had nested, their surfacing behavior reverted to more characteristic patterns.

Management implications.—During the northern Great Barrier Reef breeding season of *E. imbricata,* a percentage of the annual nesting cohort migrate from across a large range (Indonesia, Papua New Guinea, Solomon Islands, New Caledonia, Vanuatu and from throughout the Great Barrier Reef) to focus nesting activities on Milman and adjacent islands (Miller and Limpus 1991). Therefore, negative impacts on the nesting population have ramifications for the entire western Pacific range. By understanding *E. imbricata's* fine-scale spatial and temporal movements during nesting periods, conservationists can develop management guidelines to improve this species' protection.

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LITERATURE CITED

Andrews, R.D. 1998. Remotely releasable instruments for monitoring the foraging behavior of Pinnipeds. Marine Ecology Progress Series 175: 289-294.

Bonadonna, F., E.H. Chan, H.C. Liew, P. Luschi, and F. Papi. 1995. Data-logger and satellite tracking reveal goal oriented movements in the Green Turtle (*Chelonia mydas*). Pp. 446-448. *In* Alleva, E., A. Fasolo, H.P. Lipp, L. Nadel, L. Ricceri. (Eds.). Behavioral and Social Sciences. 82. Kluwer Academic Publishers, Dordrecht, Netherlands.

Bury, R.B. 2006. Natural history, field ecology, conservation biology and wildlife management: Time to connect the dots. Herpetological Conservation and Biology 1:56-61.

Caldwell, D.K. 1962. Comment on the nesting behavior of Atlantic Loggerhead Sea Turtles based primarily on tagging returns. Florida Academy of Science 25:288-302.

Carr, A. 1962. Orientation problems in high seas travel and terrestrial movements of marine turtles. American Scientist 50:359-374.

Carr, A. 1972. A case for long range chemo-receptive piloting in *Chelonia*. Pp. 469-483 *In* Galler, S.R., K. Schmidt-Leonig, G. Jacobs, and R. Belleville. (Eds.). Animal Orientation and Navigation. NASA 262.

Carr, A., P. Ross, and S. Carr. 1974. Internesting behavior of the Green Turtle, *Chelonia mydas,* at a mid-ocean island breeding ground. Copeia 1974: 703-706.

Dobbs, K.A., J.D. Miller, C.J. Limpus, and A.M. Landry, Jr. 1999. Hawksbill Turtle, *Eretmochelys imbricata*, nesting at Milman Island, Northern Great Barrier Reef, Australia. Chelonian Conservation and Biology 3:344-361.

Eckert, K.L. 1995a. Anthropogenic threats to sea turtles. Pp 611-612 *In* Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles (Revised Edition). Smithsonian Institution Press. Washington. D.C., USA.

Eckert, S.A. 1995b. Telemetry and behavior of sea turtles. Pp 583-584 *In* Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles (Revised Edition). Smithsonian Institution Press, Washington. D.C., USA.

Eckert, S.A. 1999. Data acquisition systems for monitoring sea turtle behavior and physiology. Pp. 88-93 *In* Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A, and Donnelly, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group. Publication No. 4.

Eckert, S.A. 2002. Swim speed and movement patterns of gravid Leatherback Sea Turtles (*Dermochelys coriacea*) at St. Croix, US Virgin Islands. Journal of Experimental Biology 205: 3689-3697.

Eckert, S.A., K.A. Eckert, P. Pongranis, and G.L. Kooyman. 1989. Diving and foraging behavior of

Leatherback Sea Turtles (*Dermochelys coriacea*). Canadian Journal of Zoology 67:2834-2840.

Eckert, S.A., D.W. Nellis, K.L. Eckert, and G.L. Kooyman. 1986. Diving patterns of two Leatherback Sea Turtles (*Dermochelys coriacea*) during inter-nesting intervals at Sandy Point, St. Croix. U.S. Virgin Islands. Herpetologica 42:381-388.

Hays, G.C., F. Glen, A.C. Broderick,, B.J. Godley, and J.D. Metcalfe. 2002. Behavioral plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two Green Turtle (*Chelonia mydas*) populations. Marine Biology 141:985-990.

Hochscheid, S., B.J. Godley, A.C. Broderick, and R.P. Wilson. 1999. Reptilian diving: highly variable dive patterns in the Green Turtle *Chelonia mydas*. Marine Ecology Progress Series 185:101-112.

Kooyman, G.L. 1989. Diverse Divers, Physiology and Behavior. Springer-Verlag, New York, New York, USA.

Limpus, C.J., and P.C. Reed. 1985. The Loggerhead Turtle, *Caretta caretta*, in Queensland: Observations on internesting behavior. Australian Wildlife Research 12:535-540.

Loop, K.A., J.D. Miller,, and C.J. Limpus. 1995. Nesting by the Hawksbill Turtle (*Eretmochelys imbricata*) on Milman Island Reef, Australia. Wildlife Research 22:241-252.

MacPherson, S. 1998. Synopsis of U.S. nesting beach studies. Pp. 62-68 *In* Fair, P.A., and L.J. Hansen. (Eds.). Report of the Sea Turtle Health Assessment Workshop, Part I: Background and Information Needs. NOAA Technical Memorandum. NOS-NCCOS-CCEHBR-0003.

Miller, J.D., K.A. Dobbs, C.J. Limpus, N. Mattocks, and A.M. Landry. 1998. Long-distance migrations by the Hawksbill Turtle, *Eretmochelys imbricata*, from north-eastern Australia. Wildlife Research 25:89-95.

Miller, J.D., and C.J. Limpus. 1991. Torres Strait marine turtle resources. Pp. 213-226 *In* Lawrence, D., and T. Cansfield-Smith. (Eds.). Sustainable Development for Traditional Inhabitants of the Torres Strait Region. Great Barrier Reef Marine Park Authority. Workshop Series No.16. Proceedings of the Torres Strait Baseline Study Conference. Kewarra Beach, Cairns, Australia.

Minamikawa, S., Y. Naito, and I. Uchida. 1997. Buoyancy control in diving behavior of the Loggerhead Turtle, *Caretta caretta.* Journal of Ethology 15:109-118.

Mortimer, J.A., and K.M. Portier. 1989. Reproductive homing and internesting behavior of the Green Turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean. Copeia 1989:962-977.

Papi, F. 2001. Animal navigation at the end of the century: a retrospect and a look forward. Italian Journal of Zoology 68:171-180.

Sakamoto, W., K. Sata, H. Tanaka, and Y. Naito. 1993. Diving patterns and swimming environment of two Loggerhead Turtles during internesting. *Nippon Suisan Gakkaishi* (Bulletin of the Japanese Society of Scientific Fisheries) 59:1129-1137.

Storch, S., Z.M. Hillis-Starr, and P.R. Wilson. 1999. Turtles in the Reef: A closer look at the activities of Hawksbill Turtles in a Caribbean internesting habitat. Pp. 32-35 *In* Kalb, H.J., and T. Wibbels. (Eds.). Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Department of Commerce. NOAA Technical Memorandum. NMFS-SEFSC-443.

Tomkiewicz, S.M., and W.P. Burger. 1996. Advances in telemetry: implications for the study of sea turtles. Pp. 324-325 *In* Keinath, J.A., D.E. Barnard, J.A. Musick, and B.A. Bell. (Eds.). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum. NMFS-SEFSC- 387.

van Dam, R.P., and C.E. Diez. 1997. Diving behavior of immature Hawksbill Turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. Coral Reefs 16:33-138.

Yano, K., and S. Tanaka. 1991. Diurnal swimming patterns of Loggerhead Turtles during their breeding period as observed by ultrasonic telemetry. *Nippon Suisan Gakkaishi* (Bulletin of the Japanese Society of Scientific Fisheries) 57:1669-1678.

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