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Movements and diving behavior of interesting green turtles along Pacific Costa Rica

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Abstract

Using satellite transmitters, we determined the interesting movements, spatial ecology and diving behavior of East Pacific green turtles (*Chelonia mydas*) nesting on Nombre de Jesús and Zapotillal beaches along the Pacific coast of northwestern Costa Rica. Kernel density analysis indicated that turtles spent most of their time in a particularly small area in the vicinity of the nesting beaches (50% utilization distribution was an area of 3 km²). Minimum daily distance traveled during a 12 day interesting period was 4.6 ± 3.5 km. Dives were short and primarily occupied the upper 10 m of the water column. Turtles spent most of their time resting at the surface and conducting U-dives (ranging from 60 to 81% of the total tracking time involved in those activities). Turtles showed a strong diel pattern, U-dives mainly took place during the day and turtles spent a large amount of time resting at the surface at night. The lack of long-distance movements demonstrated that this area was heavily utilized by turtles during the nesting season and, therefore, was a crucial location for conservation of this highly endangered green turtle population. The unique behavior of these turtles in resting at the surface at night might make them particularly vulnerable to fishing activities near the nesting beaches.

Key words: *Chelonia mydas*, Costa Rica, East Pacific green turtle, interesting period, satellite telemetry

INTRODUCTION

Large marine animals are often wide-ranging and live in secretive and inhospitable environments; there-

fore, direct observation of their behavior is difficult. Satellite telemetry has been widely used to analyze the movements, behavior and physiology of marine mammals (Mate *et al.* 1999), fish (Block *et al.* 1998), sea birds (Jouventin *et al.* 1994) and sea turtles (Hays *et al.* 2000). Using this methodology, researchers are able to answer complex scientific questions about the movements of large fish (Block *et al.* 1998) and the extensive migration of whales (Mate *et al.* 1999).

In the case of sea turtles, satellite telemetry has greatly improved the understanding of movement patterns dur-

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ing migration (Shillinger *et al.* 2008) and during the internesting interval (Shillinger *et al.* 2010). Sea turtles are iteroparous and lay several clutches during a nesting season. The internesting period is the time between clutches when a female sea turtle develops the next clutch (Rostal *et al.* 1996), consuming stored energy (Hamann *et al.* 2002). Their behavior appears to be driven by energy optimization and is also related to the habitat type and condition of the nesting grounds (Hochscheid *et al.* 1999; Hays *et al.* 2002a,b). Lack of food availability in reproductive areas causes turtles to spend most of their time resting during the internesting period to minimize energy loss (Hays *et al.* 1999, 2002b). Sea turtles nesting in areas where food is available forage on occasion to augment energy reserves (Tucker & Read 2001). For example, green turtles fasting at Ascension Island dive to an average depth greater than 15 m to obtain neutral buoyancy to rest (Hays *et al.* 2000); green turtles in the Mediterranean rest and graze on the sea bed during internesting (Hochscheid *et al.* 1999; Hays *et al.* 2002b).

Use of satellite transmitters with data logging capabilities has demonstrated that sea turtles exhibit different dive patterns that can be described by their depths, durations and ascent–descent phases. These patterns represent the actual behavior of sea turtles underwater. These vary widely within species and in different environments. Several underwater behaviors have been recognized in sea turtles (Minamikawa *et al.* 1997; Hays *et al.* 1999; Hochscheid *et al.* 1999; Houghton *et al.* 2002). For example: resting behavior, commonly displayed by swimming to the sea floor, staying at a constant depth for a certain period of time, and returning to the surface to breath (Hays *et al.* 2000; Houghton *et al.* 2002); stationary foraging, where turtles display the same type of movements (Seminoff *et al.* 2006); and underwater exploratory surveys or turtle orientation, where turtles dive to a certain depth and swim back to the surface spending some time in the water column (Hochscheid *et al.* 1999). During the internesting interval, the predominant behavior is resting (Hays *et al.* 1999; Hochscheid *et al.* 1999; Houghton *et al.* 2002; Shillinger *et al.* 2010).

Several studies report movement patterns of green turtles (*Chelonia mydas* Linnaeus, 1758) during the internesting period (Godley *et al.* 2008), and they differ between populations. For example, green turtles in Thailand remain in a limited area within 6 km of nesting beaches (Kittiwattananawong *et al.* 2002), as do Hawaiian green turtles (Dizon & Balazs 1982). In contrast, green turtles at Ascension Island move to specific resting and

mating areas (Carr *et al.* 1974), and in the Caribbean they travel up to 130 km away from the nesting beach, remaining within 30 km of shore (Troëng *et al.* 2005).

The green turtle is listed as endangered by the International Union for Conservation of Nature (IUCN 2011) and the population in the eastern Pacific, along Pacific Mexico, is classified as endangered by the US Fish and Wildlife Service and considered highly vulnerable to extinction. The decline in green turtles in the eastern Pacific is due to harvest of eggs and adults, to habitat degradation at nesting beaches and feeding grounds and to by-catch from fisheries in the ocean (Seminoff 2004).

East Pacific green turtles are present from San Diego Bay to Peru (Green 1984; Quiñones *et al.* 2010). Little is known about green turtle breeding populations in the eastern Pacific. Three primary rookeries have been described: Michoacán, Mexico (Alvarado & Figueroa 1992), Isla Clarión in Archipelago Revillagigedo, Mexico (Holroyd & Trefry 2010) and the Galapagos Islands, Ecuador (Green 1984). Nombre de Jesús and Zapotillal, along the coast of Guanacaste on the Nicoya Peninsula, Costa Rica host an important secondary rookery for this species (Blanco *et al.* 2011). Even though a few studies describe the post-nesting migration of East Pacific green turtles (Green 1984; Seminoff *et al.* 2008), there are no studies about how these turtles behave during the breeding and nesting season.

The objective of the present study was to examine the movements and diving behavior of East Pacific green turtles during the internesting period and to measure their vertical habitat use along the Pacific coast of Costa Rica. We hypothesized that diving behavior during the internesting period would not differ from other green turtle populations and that turtles would mainly rest at sea floor at specific resting areas during internesting. We expected that the turtles would move to specific resting areas away from the nesting beaches.

To our knowledge, this is the first study on internesting movements and diving behavior of adult female East Pacific green turtles. We anticipate that the present study will help to elucidate differences in the behavior of green turtle populations from around the world, as well as to determine high use internesting areas in need of protection in northwestern Costa Rica.

MATERIALS AND METHODS

Study site

The study took place at 2 contiguous nesting beaches on the Nicoya Peninsula in northwestern Costa Rica (Fig.

1). We attached 12 ARGOS-linked satellite transmitters on green turtles nesting on Nombre de Jesús (10°23'3"N, 85°50'07"W), a 1 km beach, and on the neighboring Zapotillal beach (10°23'48"N, 85°49'48"W), a 700 m beach. The study took place from August 2007 to October 2007; 1 additional green turtle was telemetered in November 2009 (Table 1). These beaches hosted an im-

portant aggregation of nesting green turtles (approximately 15 turtles/night during peak season). Nombre de Jesús and Zapotillal were isolated and not developed, located approximately 10 km from the closest village. Although access to these beaches was difficult, numerous people went to the beach at night to collect turtle eggs. These beaches lacked any form of conservation protection.

Turtle measurements

To find turtles, we patrolled the beaches at night. Each turtle found on the beach was scanned for a passive integrated transponder (PIT). Untagged turtles were marked with PIT tags in the right front flipper for later identification. We measured the curved carapace length (CCL; ± 0.5 cm) from the nuchal notch to the posterior-most edge of the marginal scutes, and curved carapace width on the widest point of the carapace using a flexible tape. All turtles were examined to document any external abnormalities, such as missing flippers or the presence of scars or lesions.

Interesting interval

From tagged individuals, we calculated the observed interesting period (OIP), which was the number of days observed between successful nesting events (Reina *et al.* 2002). The reported interesting interval for green turtles ranges from 10 to 17 days (Miller 1997); therefore, we assumed that observed intervals higher than 17

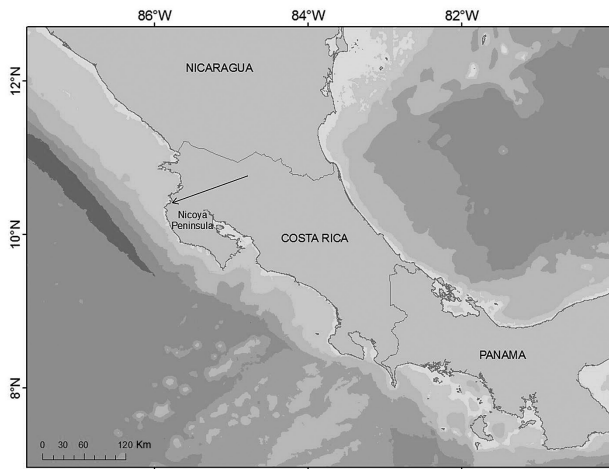


Figure 1 Location of study site. Satellite transmitters were deployed on turtles on 2 contiguous nesting beaches along the Nicoya Peninsula in Costa Rica: Nombre de Jesús (10°23'30"N, 85°50'07"W), a 1 km beach and Zapotillal beach (10°23'48" N, 85°49'48" W) approximately 700 m in length. Arrow points to nesting beaches.

Table 1 Attachment data for 12 East Pacific green turtles (*Chelonia mydas*) during the nesting season in northwestern Costa Rica. All individuals included in the study were in their interesting interval

Turtle ID	Attachment date	Beach	CCL (cm)	CCW (cm)	Days of transmission
1 [†]	26 Aug 2007	Zapotillal	87.5	79.0	10
2 [†]	2 Sept 2007	Zapotillal	82.0	80.0	8
3 [†]	9 Sept 2007	Nombre de Jesús	89.0	84.0	5
4 [†]	22 Oct 2007	Zapotillal	82.0	76.0	29
5	25 Aug 2007	Nombre de Jesús	89.5	85.9	11
6	22 Oct 2007	Zapotillal	86.1	83.0	39
7	22 Oct 2007	Zapotillal	82.2	81.8	25
8	27 Oct 2007	Zapotillal	86.5	71.5	16
9	27 Oct 2007	Zapotillal	85.0	83.5	39
10	27 Oct 2007	Zapotillal	----	----	11
11	27 Oct 2007	Zapotillal	84.5	78.3	22
12	6 Nov 2009	Nombre de Jesús	84.4	82.0	12

CCL, curved carapace length; CCW, curved carapace width. [†]Satellite transmitters recovered after premature release.

days indicated a missed nesting event and intervals lower than 10 days indicated a false nesting attempt.

Satellite transmitter attachment

We applied transmitters using a tethering technique first developed by Standora *et al.* (1982) and modified by Morreale *et al.* (1996) and Morreale (1999). In this technique, the transmitter trails behind the turtle without disturbing flow across the carapace. Any disturbance in the shape of the turtle will cause flow separation, increasing drag (Schlichting 1979), and, consequently, increasing energy expended by the turtle (Watson & Granger 1998). Therefore, transmitters attached to the shell of a turtle create more drag than those that trail behind the turtle. The tethering technique minimized energy expenditure while the turtle was swimming. The buoyant and hydrodynamic transmitter followed closely behind the turtle and floated with the antenna out of the water when the turtle rose to the surface. Another benefit to this technique was that the attachment could be performed in a short period of time with minimal disturbance of the turtle's natural behavior while it was on the beach. When we determined that a turtle was suitable for attachment, we cleaned the marginal posterior scute (i.e. overhanging edge) of the carapace with 70% alcohol, and made a 3 mm diameter hole with a sterile electric drill bit (battery-powered electric drill). Immediately after the procedure, we applied lidocaine and betadine antiseptic solution and inserted sterile surgical tubing into the small hole. We positioned plastic buttons with Y-shaped holes above and below the carapace to avoid friction and wearing damage to the carapace. The transmitter was connected to the buttons on the carapace by a flexible lanyard (monofilament fishing line, 400-lb test) that passed through the holes and was secured to itself with a corrosive metal crimp. The length of the lanyard was approximately 30 cm, depending on the CCL of the turtle. To avoid entanglement or long-term impediment of the turtles, we placed in line swivels and crimps that would break away with corrosion (Fig. 2). The attachment process took from 7 to 15 min for each turtle and was performed while the female was covering the nest after laying eggs, thus minimizing the impact on its nesting behavior.

Satellite transmitters

Satellite transmitters (Wildlife Computers Mk 10 PAT [Pop-up Archival Transmitting] tag) were configured to transmit opportunistic transmissions, so we could obtain real-time location data. We customized the satel-

lite transmitters with a buoyant case made out of syntactic foam. Satellite transmitters weighed approximately 115 g (approximately 0.2% of the turtle mass), had a hydrodynamic shape and were tethered behind the turtle, all resulting in minimized drag. The transmitter's positive buoyancy was 36 g, enough to bring the antenna of the transmitter out of the water each time the turtle surfaced but very minimal for adult green turtles. We programmed the tags with duty cycles of 10 h on and 14 h off to optimize battery life. The transmitter sampled and summarized dive depth, dive duration and time at depth data in categorized bins: dive depth, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 75, 100 and 200 m; and dive duration, 2, 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80 and 90 min. The location of the animals and the summarized satellite messages were transmitted via the Argos system.

Movement analysis

Locations of the turtles were classified by Argos system into location classes (LC) from 3 to Z based on accuracy of the location. For movement and home range analysis we only used LC 1, 2 and 3, for which accuracy was estimated to be better than 1500 m radius (Argos-CLS 2011).



Figure 2 Satellite transmitter attachment to an East Pacific green turtle (*Chelonia mydas*): (a) posterior marginal scute; (b) upper plastic button; (c) flexible lanyard (400 lb monofilament fishing line); (d) Corrosive link with metallic crimps and swivel; and (e) satellite transmitter (Mk 10 PAT tag, programmed for opportunistic transmissions).

To analyze the areas used by the turtles, we performed a Kernel density analysis (KDA) using ArcGIS 9.3 and Home Range Tools for ArcGIS (Rodgers *et al.* 2005). We performed a fixed KDA using the least-squares-cross-validation method to calculate the smoothing factor (Worton 1989). The core areas were determined by 25, 50, 75 and 95% utilization distribution (UD). We conducted 2 KDA. To distribute locations over time, we used 1 location a day for each individual (best location quality). The first analysis included the first interesting period of all turtles, from which we had a complete record of the first interesting interval (10 individuals, turtle ID 1, 4–12; see Table 1). The second analysis was conducted with turtles whose transmitters lasted more than 20 days, including 5 individuals (turtle ID 4, 6, 7, 9 and 11; see Table 1). This analysis only included the second interesting interval for each individual.

We analyzed the daily movement of turtles by calculating the distance between all points travelled in a given day. We then calculated the total movement in the first 10 days after a successful nesting event. We used 10 days because it was the shortest interesting time recorded in this study and provided a representation of the interesting period.

Dive analysis

Green turtles in the present study had an average CCL of 85 cm; therefore, we set dives to start and end at 1 m depth and to last more than 30 sec. Because the length of the lanyard was approximately 30 cm (less than half of CCL), once the transmitter crossed 1 m depth, the turtle would be clearly underwater. We considered that this did not influence the recorded behavior. Surface time was defined by the transmitter using the wet/dry sensor (Wildlife-Computers 2007).

Summarized dive information

We analyzed the diving behavior of turtles from the summarized dive information obtained from the Argos messages. The summarized dive information allowed us to calculate the percentage of dives accumulated in 4 h periods at different depths for all turtles and the average duration of dives, although these data did not allow us to determine the specific number or shape of dives that the turtles performed during the tracking period.

Retrieved transmitters

We retrieved 4 satellite transmitters, which archived complete detailed information on the animals' diving behavior, including every dive performed by turtles dur-

ing the tracking period (date, time, water temperature, dive depth, duration, bottom time and surface time). This allowed us to identify, analyze, count and classify individual dives. For these transmitters, we analyzed the relation between the total duration of dives and their depth. Even though we recognized different dive types (V-shaped dives, S-shaped dives and W-shaped dives) in the dive profiles of the 4 turtles, we specifically separated the U-dives from the total dives because this dive type was described as the predominant dive type performed by sea turtles during the interesting period (Hays *et al.* 1999; Hochscheid *et al.* 1999; Houghton *et al.* 2002), and was the predominant type of dive for this study. To identify U-dives, we calculated the relation between total duration of an individual dive and the time at the bottom of the dive. If the time at the deepest depth was 90% or more of the dive, we considered it to be a U-dive (Hays *et al.* 1999). We calculated the proportion of U-dives at depth and their duration for every turtle. We calculated the proportion of U-dives in relation to all other dives for individual turtles. We studied the behavior of turtles during the day and night. Based on the hours of light in the study area, night corresponded to 17.30 to 05.30 hours. We calculated and compared the surface time for each turtle during the day and night and also compared it to the percentage of U-dives performed by each turtle. In addition, we analyzed water temperature recorded by the transmitters. All statistical analyses were performed using SPSS.

RESULTS

The CCL of green turtles ranged from 82.0 to 89.5 cm ($\bar{X} \pm SD = 85.3 \pm 2.6$ cm, $n = 12$). Duration of satellite attachment for each turtle ranged from 5 to 39 days ($\bar{X} \pm SD = 19.4 \pm 11.8$ days, $n = 12$; Table 1). In general, premature release was due to the transmitter releasing itself through a failure in the pop-up emergency release mechanism or because of its removal from the turtle by people. Several transmitters were removed by egg collectors at night and moved to different localities in Costa Rica. Others were taken by fishermen in the ocean. On 2 separate occasions, transmitters were brought to land by artisanal fishing boats. Those transmitters were transported to a small fishing village, and it was not possible to recover them.

Observations on the beach

Poaching of eggs was common on Nombre de Jesús and Zapotillal as was the presence of artisanal fishing boats deploying gillnets and longlines. We estimated

that 90% of the eggs were collected at night or the following morning if researchers were not on the beach and relocated every clutch. Males were present in the waters off the nesting beach, and we observed mating on several occasions during daytime surveys of the beach. During the nesting season, seas were generally calm in the bays near the nesting beaches.

Interesting interval

Mean OIP was 12 ± 1.4 days ($\bar{x} \pm SD$, range 10–15, $n = 25$) during the months of July to November. Even though beach coverage was not complete during those months, we recorded information on enough consecu-

tive clutches to perform the analysis. The OIP was not correlated to turtle size (Pearson correlation, $n = 25$, $P = 0.910$).

Interesting areas

Turtles stayed within 15 km of the nesting beach to the north and south during interesting intervals (Fig. 3). Turtles spent most of the time in waters close to the nesting beaches during interesting, mainly limiting their movement to 1–4 km off the nesting beaches. The KDA for the first interesting interval showed that UD polygons of 50 and 95 included 2.6 and 11.0 km²,

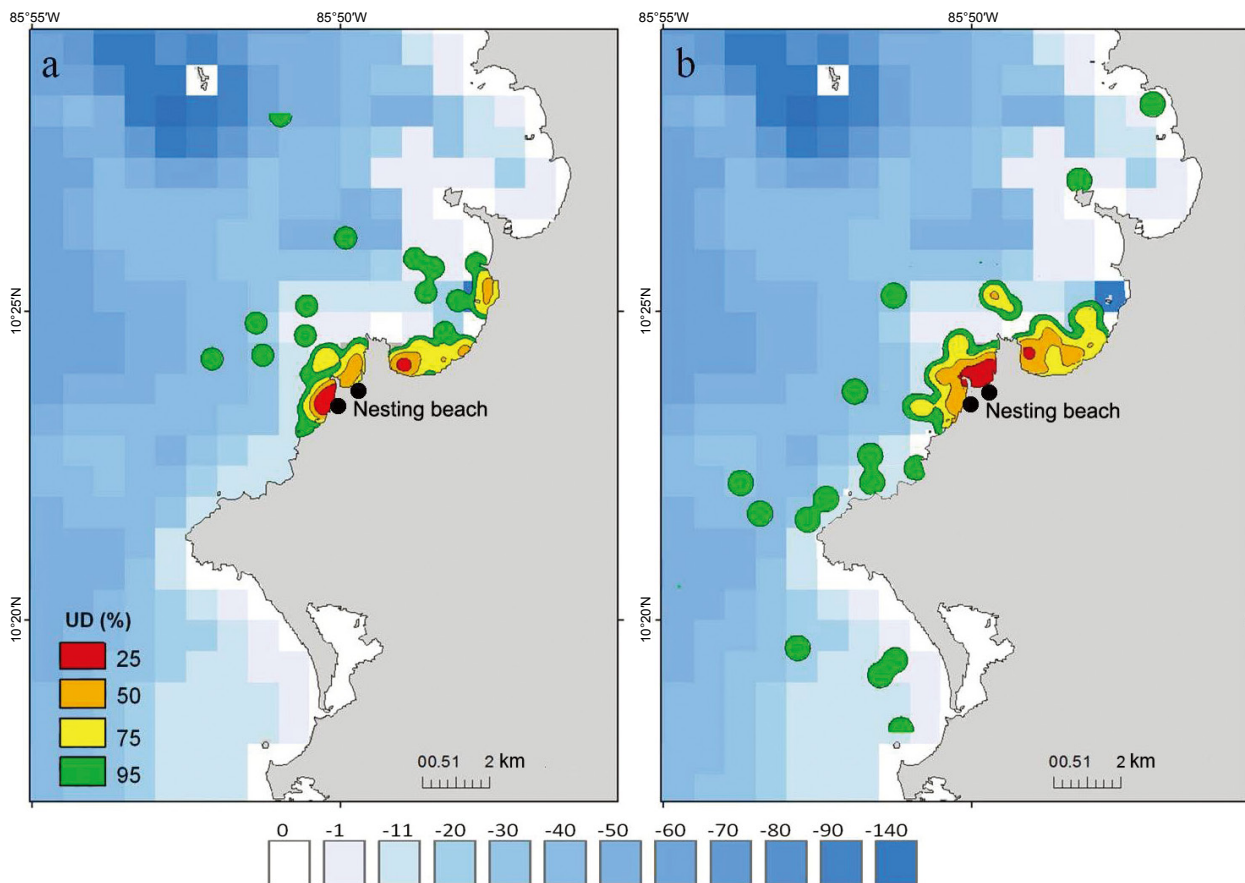


Figure 3 Fixed kernel density analysis (KDA) of interesting areas occupied by East Pacific green turtles (*Chelonia mydas*). Areas highly used were along nesting beaches (Nombre de Jesús and Zapotillal), and the neighboring bay. (a) KDA for the first interesting interval of all turtles from which we have a complete record of the first interesting interval (10 individuals). Utilization distribution (UD) 50% = 2.6 (orange) and 95% = 11.02 km² (dark green). (b) KDA for turtles whose transmitters lasted more than 20 days (5 individuals), including only the second interesting interval for each individual. UD 50% = 3 (orange) and 95% = 14.5 km² (dark green). Black dots indicate location of nesting beaches. Scale represents depth in meters.

respectively (Fig. 3a). Approximately 52% of the 50% UD was contained within the Bay of Nombre de Jesús and Zapotillal. Similarly, 50 and 95% UD polygons for the second interesting were 3.0 and 14.5 km² (Fig. 3b). Approximately 50% of the 50% UD polygon was contained within the bay of the nesting beach and the remaining 50% was in the bay of the neighboring beach. All the turtles tagged in the present study were between nesting emergences; we recorded the majority of these turtles nesting at least once more through satellite locations and direct beach observations.

During interesting, the minimum daily distance traveled was: 4.6 ± 3.5 km ($\bar{x} \pm SD$, $n = 12$, range 0.6–11 km). The daily movement was not correlated to turtle size (Pearson correlation, $n = 11$, $P = 0.119$). Mean distance covered in 10 days ranged from 7 to 211 km ($\bar{x} \pm SD = 52 \pm 60$ km, $n = 10$), also not correlated to CCL (Pearson correlation, $n = 11$, $P = 0.233$).

Diving behavior

Summarized dive information

Of all summarized dives for the 12 turtles during interesting, 69% took place in the first 5 m of the water column, with an additional 20% reaching depths between 5 and 10 m (Fig. 4a). Even though the majority of the dives were shallow, the depths ranged from 5 to 100 m.

The duration of all summarized dives performed by the turtles ranged between 2 and 90 min, and most dives were of short duration, with 71% between 2 and 10 min (Fig. 4b).

Retrieved transmitters

We retrieved 4 of the satellite transmitters, from which we obtained archival information on the detailed diving behavior of individuals. The total number of dives for each turtle was: Turtle 1 = 1375 (10 days); Turtle 2 = 833 (8 days); Turtle 3 = 725 (5 days); and Turtle 4 = 3692 (29 days). Mean water temperature recorded by the transmitters during interesting was 27.5 ± 1 °C ($\bar{x} \pm SD$), while water temperatures in the area ranged from 27.0 to 29.0 °C.

The 4 turtles spent most of their time resting at the surface (Turtle 1, 39.4%; Turtle 2, 35.7%; Turtle 3, 71.7%; and Turtle 4, 39.5%) and in U-dives (Turtle 1, 21%; Turtle 2, 31.6%; Turtle 3, 9.9%; and Turtle 4, 31.2%). These dives were characterized by shallow maximum depths, with $79.3 \pm 9.2\%$ of dives ranging between 3 and 5 m. Dives mainly took place in the first 10 m of the water column, independent of their duration. Turtle 4 performed the deepest dive (110 m) in 10 min

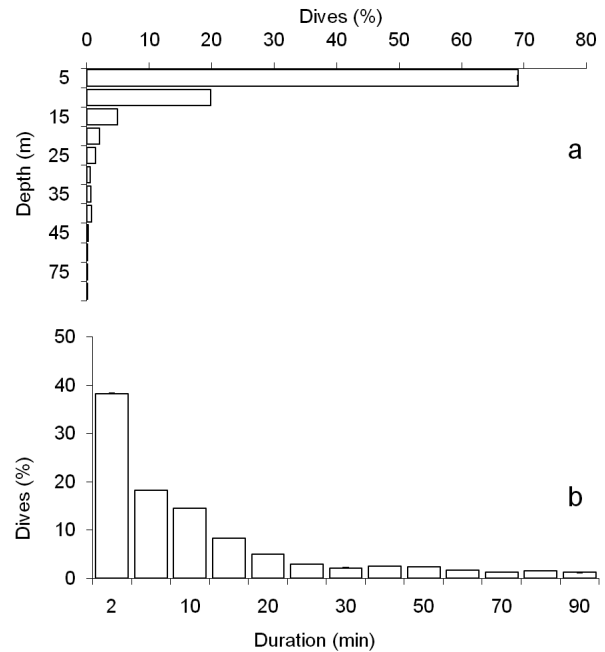


Figure 4 (a) Percentage of dives culminating at specific depth intervals during interesting for 12 East Pacific green turtles (*Chelonia mydas*) from satellite data obtained through the Argos system and summarized in bins. We calculated the average at depth in relation to the total dives for each turtle. (b) Percentage of duration intervals of dives during interesting for 12 East Pacific green turtles from satellite data obtained through Argos and summarized into bins. We calculated the average duration in relation to the total dives for each turtle

and the longest dive, 55 min, to a depth of 18 m. The modal durations of U-dives were 8, 11.5, 15 and 23 min for all 4 turtles, respectively.

During the interesting period, green turtles exhibited a strong diel pattern in their submergence behavior. Dive profiles indicated that Turtles 1 and 3 spent a large amount of time at the surface at night, as opposed to Turtles 2 and 4 (Fig. 5), which spent most of their time diving. Overall, there were significant differences between the surface time during day and night (ANOVA, $F_{1,18} = 48.775$, $P < 0.0001$; Fig. 6).

Turtles spent more time at the surface at night (Turtle 1, 56.5%; Turtle 2, 41.1%; Turtle 3, 95.7%; and Turtle 4, 46.23%) and more time performing U-dives during the day (Fig. 7a; see Fig. 5, 24-h dive profile). Total time of entire tracking duration spent involved in those activities together (U-dives and surface time) was $73\% \pm 4.73$.

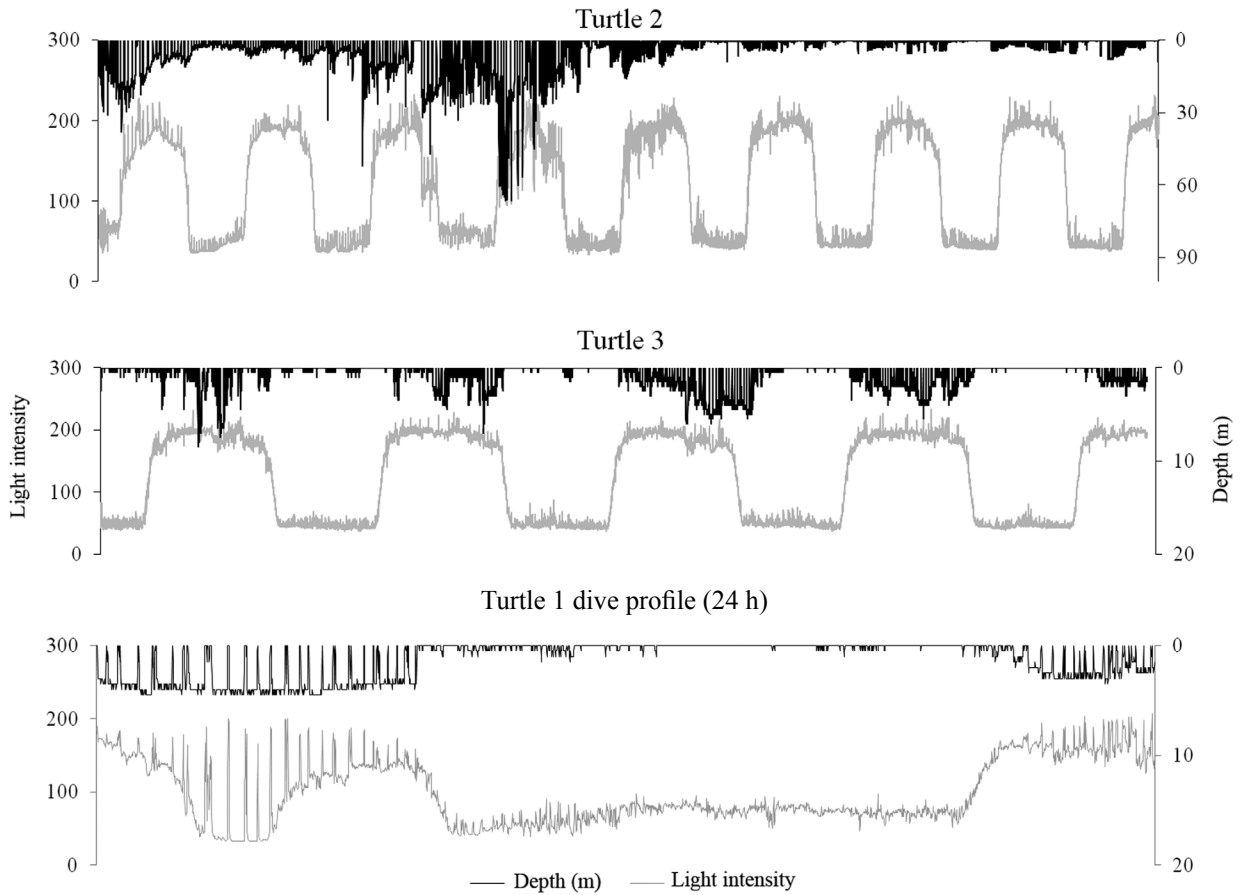


Figure 5 Dive profiles of 3 East Pacific green turtles (*Chelonia mydas*). Black lines represent depth and gray lines represent light levels. Elevated light levels represent daytime and low light levels represent nighttime. Turtle 2: dives performed during day and night. Turtle 3: dives mainly performed during the day, with prolonged time at surface during the night. Turtle 1 dive profile 24 h: detailed dive behavior showing U-shaped dives during the day and ‘surface resting’ during the night. Depth is in meters.

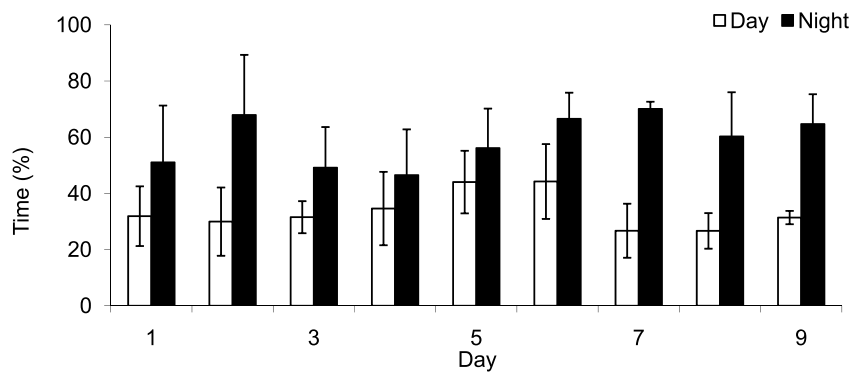


Figure 6 Percentage of time turtles spent at surface during day and night. Day represents the 12 h of light in the tropics. Days 1 to 4 included 4 individuals; days 5 to 9 included 3 individuals. Day 1: first day after successful nesting (transmitter attachment).

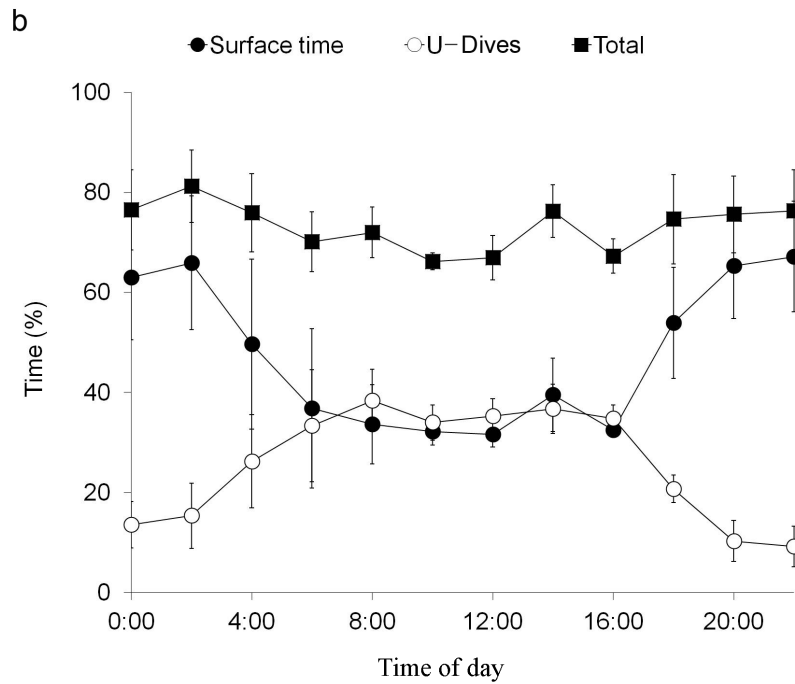
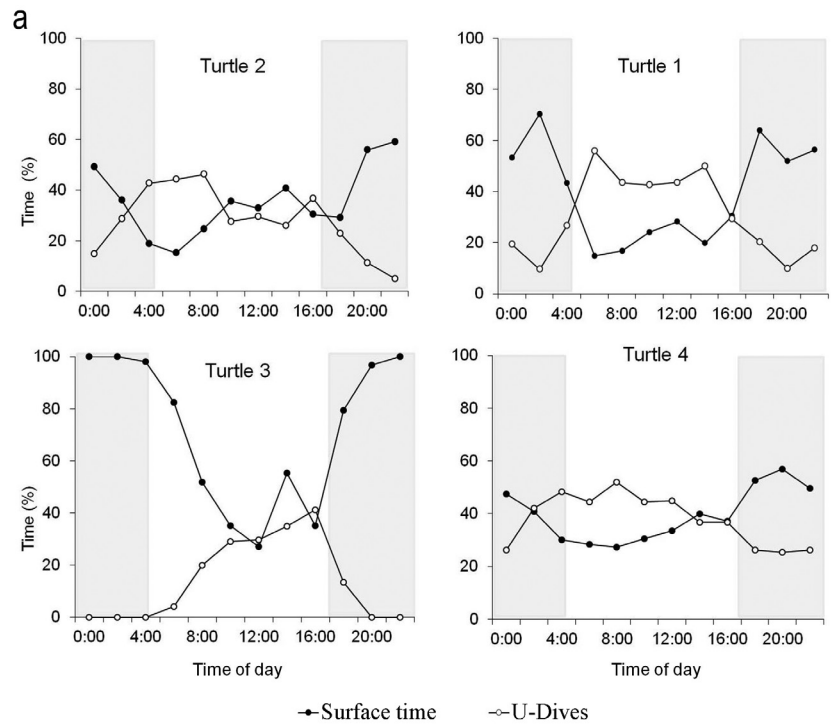


Figure 7 (a) Surface time and U-dives during the interesting for 4 East Pacific green turtles (*Chelonia mydas*). The shaded areas represent night (12 dark hours). Each data point represents an interval of 2 h. (b) Proportion of time spent at the surface and U-dives performed at different times of the day for 4 turtles. Total represents the sum of the proportion of time spent at the surface and the proportion of U-dives performed by the turtles. Each data point represents an interval of 2 h.

This indicated the great amount of time green turtles spent resting during internesting (Fig. 7b).

DISCUSSION

The data presented in this study were the first record of the movements and diving behavior of the East Pacific green turtles during the internesting period. These data helped us to understand the habitat use and spatial distribution of this ecologically important and previously unknown population.

Interesting interval

Even though East Pacific green turtles and Atlantic green turtles are the same species (Bowen *et al.* 1992), there are substantial differences in biology between East Pacific green turtles and other green turtles. For example, our data indicated that the internesting interval for green turtles nesting in Pacific Costa Rica was 12 days, as reported by Alvarado-Díaz *et al.* (2003) for green turtles in Michoacán, Mexico. It was shorter than the 14 days reported at Ascension Island by Carr *et al.* (1974) and at Tortuguero, Costa Rica (Bjorndal & Carr 1989). Development of clutches during internesting is directly affected by temperature (Sato *et al.* 1998), but similarities in water temperatures between Tortuguero, Atlantic Costa Rica (Standora *et al.* 1982), Ascension Island (Hays *et al.* 2002a) and the present study indicate that the shorter internesting interval of the green turtles in northwestern Costa Rica is not a result of higher temperatures. Therefore, the difference in the duration of the internesting interval might be related to differences in size of the turtles and number of eggs per clutch, as is shown for other sea turtles (Bjorndal & Carr 1989; Broderick *et al.* 2003; Wallace *et al.* 2006). For example, green turtles in Tortuguero, Costa Rica have an average CCL of 100 ± 5 cm, with a mean clutch size of 112 eggs, and the internesting interval is 14 days (Bjorndal & Carr 1989). Acquisition and allocation of energy determine the number of clutches in a given season (Hamann *et al.* 2002). Female green turtles in Pacific Costa Rica are smaller than their Atlantic conspecifics and produce smaller clutches, probably due to reduced food supplies related to El Niño cycles (Saba *et al.* 2007a,b,c). It apparently takes less time to complete production of yolk and albumin, and to shell a smaller clutch at the same temperature than it does a larger clutch.

Interesting movements

Satellite tracking indicated that the areas of importance during the internesting period of green turtles that nested on Nombre de Jesús and Zapotillal beaches were the waters off the nesting beaches and the neighboring bay (4 km north of the nesting beach). Contrary to our hypothesis, green turtles in Pacific Costa Rica remained in a particularly small area near the nesting beaches during the internesting period as occurred in some other populations (Kittiwattanawong *et al.* 2002). In contrast, green turtles nesting on Ascension Island gather in specific areas during interesting, where courtship and mating are commonly observed (Carr *et al.* 1974; Mortimer & Portier 1989), and in the Caribbean (Costa Rica) green turtles travel as far as 135 km from the nesting beach (Tröeng *et al.* 2005). The limited internesting movements of green turtles from Nombre de Jesús and Zapotillal indicated the unique behavior of this population and underscored the importance of coastal waters near the nesting beaches. The mean daily distance traveled by this population was 4 ± 3 km (speed of approximately $0.2 \text{ km}\cdot\text{h}^{-1}$), which was very low compared with turtles nesting at Tortuguero, which traveled out to 135 km at a speed of $0.9 \text{ km}\cdot\text{h}^{-1}$ (Tröeng *et al.* 2005) and at Ascension Island, where they moved to specific areas at a mean speed of 0.9 to $3.5 \text{ km}\cdot\text{h}^{-1}$ (Carr *et al.* 1974). Clearly, green turtles at Nombre de Jesús were not moving to distant areas as they did in other populations. They moved slowly and stayed within the same general area.

Diving behavior

The binned data obtained from satellite transmitters indicated that, during internesting, turtles performed short dives (2–10 min), mostly between depths of 2 and 10 m (90% of the dives). The depth of the majority of dives corresponded to the depth in the area where the turtles stayed during the internesting interval, indicating that the diving behavior of the turtles was mainly influenced by bathymetry of the internesting area. Along Nombre de Jesús, the depth ranged from 0 to 3 m in the first 300 m off the coast, and depth increased to 10 m, 900 m away from the coast. Conditions were similar in the neighboring bay, reaching 10 m depth at 1.3 km. Considering the internesting areas used by turtles, the depth of the area, depths of dives indicated by the binned data, and depth of U-dives indicated by the recovered transmitters, turtles spent most of their time while diving along the sea floor.

Duration of U-dives varied with individual turtles from 8 to 23 min. There was no relationship between dive depth and dive duration for U-dives as found in other populations (Houghton *et al.* 2002), although we found a weak relationship between depth and duration, including all dive types. In this study, the turtles spent a shorter proportion of their overall time carrying out U-dives as compared to other studies (Hochscheid *et al.* 1999). However, that was because they spent so much time resting at the surface. Green turtles did more U-dives during the day than at night. Turtles spent a large amount of time at the surface and the majority of the surface time occurred at night. The longest consecutive time at the surface was by a turtle that spent 12 h on the surface at night. A basking turtle can increase its body temperature almost 4 °C by exposing a substantial portion of the carapace to the sun (Spotila & Standora 1985). Because turtles were at the surface at night, they were not basking, but rather were probably 'surface resting'. U-dives, likely related to resting behavior, mainly took place during the day and there was a strong tendency for the turtles to go to the surface when the sun set. There was a negative correlation between the total surface time and the percentage of U-dives performed during the internesting. Combining the time turtles spent resting at the surface at night and in U-dives during the day, it appeared that green turtles invested 73% (± 4.73) of their total time during the internesting interval resting while their eggs were forming in the oviducts.

During interesting, turtles need to save energy to yolk up, add albumin and shell eggs, crawl to the beach and lay eggs several times in the season. These behaviors increase energy expenditure during the nesting season, which could be a significant cost for reproduction (Wallace *et al.* 2005). During the reproductive season, sea turtles mainly rely on stored lipids to support metabolism and reproduction (Hamann *et al.* 2002), especially in areas where food is not plentiful. To maximize energy, green turtles at Ascension Island reach neutral buoyancy to rest by regulating the amount of oxygen in their lungs at a depth of 19 m (Hays *et al.* 2000); loggerhead turtles (*Caretta caretta* Linnaeus, 1758) do so at 14 m (Minamikawa *et al.* 1997). Because such depths were not available in most of the internesting areas for East Pacific green turtles in Costa Rica, the turtles rested at the surface as it was less costly in terms of energy than diving to the shallow sea floor to depths at which neutral buoyancy could not be achieved.

We cannot rule out the possibility that turtles were foraging while performing U-dives. Previous authors have widely interpreted U-dives to represent resting ac-

tivity, although on occasion some other activities, such as foraging or movement along the bottom, may occur (Minamikawa *et al.* 1997; Hays *et al.* 2000; Seminoff *et al.* 2006; Cheng 2009; Thomson *et al.* 2011). In general, sea turtles fast during the internesting period due to the lack of food availability in the breeding areas (Hays *et al.* 2000), but some populations do feed during the nesting season (Hochscheid *et al.* 1999; Tucker & Read 2001). Even though there was no seagrass and few algae were present on the bottom in the area near the nesting beach (Reina *et al.* 2005; Bernecker & Wehrmann 2009), our green turtles could have been consuming invertebrates (Amorocho & Reina 2007; Quiñones *et al.* 2010). As a result, and because we could not observe turtles in the water, we cannot rule out foraging behavior.

One of the reasons that sea turtles dive is to avoid predation (Lutcavage & Lutz 1997). However, by staying close to the beach, the Costa Rica green turtle population may be less exposed to predation than other populations, which would allow turtles to rest at the surface for long periods of time at night. Sea turtles also surface for long periods of time in response to anaerobic activities (Hochscheid *et al.* 2010), but this was not the case for turtles in the present study because they only dove for short periods of time. Thus, surface resting has been selected as a strategy for resting at night, when the danger of predation is minimized and the seas are relatively quiet. This resting behavior displayed by the green turtles nesting in northwestern Costa Rica is unique to this species.

Conservation implications

This research provides new information on the spatial ecology of this population and defines the geographical range used by East Pacific green turtles in Costa Rica during the internesting interval. The information from this project represents new insight into this part of their life cycle. Female green turtles spent the internesting period close to the nesting beaches in northwestern Costa Rica and used the complete water column. Males were present in the waters off the nesting beaches and we often observed mating in the area. Therefore, several parts of the lifecycle of this population occurred in this small portion of Costa Rica and this area was of great importance for the conservation of this population. At the same time, there was heavy fishing pressure in the area. On 2 occasions, transmitters were brought to land by artisanal fishing boats, indicating that turtles were being captured by fishermen during the internesting period. In addition, we observed turtles caught on longlines nearby. Gillnets were common in the area.

Because there is no previous information on the number of females nesting on these beaches, it is difficult to determine whether the impact of the egg poaching is already affecting these numbers. Nevertheless, it is essential that enhanced protection be provided both on the beaches and in the waters of northwestern Costa Rica, where there is a large breeding population of the highly endangered East Pacific green turtle. Their resting behavior at night may make them particularly susceptible to fishing activities near the nesting beaches.

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REFERENCES

- Alvarado J, Figueroa A (1992). Recapturas post-anidatorias de hembras de tortuga marina negra (*Chelonia agassizii*) marcadas en Michoacán, Mexico. *Biotropica* **24**, 560–66.
- Alvarado-Díaz J, Arias-Coyotil E, Trejo CD (2003). Clutch frequency of the Michoacán green sea turtle. *Journal of Herpetology* **37**, 183–5.
- Amorocho DF, Reina RD (2007). Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. *Endangered Species Research* **3**, 43–51.
- Argos-CLS (2011). *User's manual*. CLS, Argos. [Cited 27 Jan 2012.] Available from URL: <http://www.argos-system.org/manual/>
- Bernecker A, Wehrtmann I (2009). New records of benthic marine algae and cyanobacteria for Costa Rica, and a comparison with other Central American countries. *Helgoland Marine Research* **63**, 219–29.
- Bjorndal KA, Carr A (1989). Variation in clutch size and egg size in the green turtle nesting population at Tortuguero, Costa Rica. *Herpetologica* **45**, 181–9.
- Blanco GS, Morreale SJ, Vélez E *et al.* (2011). Reproductive output and ultrasonography of an endangered population of East Pacific green turtles. *The Journal of Wildlife Management* **76**, 841–6.
- Block BA, Dewar H, Farwell C, Prince ED (1998). A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 9384–9.
- Bowen BW, Meylan AB, Ross JP, Limpus CJ, Balazs GH, Avise JC (1992). Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution* **46**, 865–81.
- Broderick AC, Glen F, Godley BJ, Hays GC (2003). Variation in reproductive output of marine turtles. *Journal of Experimental Marine Biology and Ecology* **288**, 95–109.
- Carr A, Ross P, Carr S (1974). Internesting behavior of the green turtle, *Chelonia mydas*, at a mid-ocean island breeding ground. *Copeia* **1974**, 703–6.
- Cheng IJ (2009). Changes in diving behaviour during the internesting period by green turtles. *Journal of Experimental Marine Biology and Ecology* **381**, 18–24.
- Dizon AE, Balazs GH (1982). Radio telemetry of Hawaiian green turtles at their breeding colony. *Marine Fisheries Review* **44**, 13–20.
- Godley BJ, Blumenthal JM, Broderick AC *et al.* (2008). Satellite tracking of sea turtles: where have we been and where do we go next? *Endangered Species Research* **4**, 3–22.
- Green D (1984). Long-distance movements of Galapagos green turtles. *Journal of Herpetology* **18**, 121–30.
- Hamann M, Limpus CJ, Whittier JM (2002). Patterns of lipid storage and mobilisation in the female green sea turtle (*Chelonia mydas*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **172**, 485–93.
- Hays GC, Luschi P, Papi F, Seppia C, Marsh R (1999). Changes in behaviour during the inter-nesting peri-

- od and post-nesting migration for Ascension Island green turtles. *Marine Ecology Progress Series* **189**, 263–73.
- Hays GC, Adams CR, Broderick AC *et al.* (2000). The diving behaviour of green turtles at Ascension Island. *Animal Behaviour* **59**, 577–86.
- Hays GC, Broderick AC, Glen F, Godley BJ, Houghton JDR, Metcalfe JD (2002a). Water temperature and interesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. *Journal of Thermal Biology* **27**, 429–32.
- Hays GC, Glen F, Broderick A, Godley B, Metcalfe J (2002b). Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between 2 green turtle (*Chelonia mydas*) populations. *Marine Biology* **141**, 985–90.
- Hochscheid S, Godley BJ, Broderick AC, Wilson RP (1999). Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Marine Ecology Progress Series* **185**, 101–12.
- Hochscheid S, Bentivegna F, Hamza A, Hays GC (2010). When surfacers do not dive: multiple significance of extended surface times in marine turtles. *The Journal of Experimental Biology* **213**, 1328–37.
- Holroyd GL, Trefry HE (2010). The importance of Isla Clarión, Archipelago Revillagigedo, Mexico, for green turtle (*Chelonia mydas*) nesting. *Chelonian Conservation and Biology* **9**, 305–9.
- Houghton JDR, Broderick A, Godley BJ, Metcalfe JD, Hays GC (2002). Diving behavior during the interesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series* **227**, 63–70.
- IUCN (2011). *The IUCN Red List of Threatened Species*. Version 2011.2. [Cited 27 Jan 2012] Available from URL: <http://www.iucnredlist.org>
- Jouventin P, Capdeville D, Cuenot-Chaillet F, Boiteau C (1994). Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the king penguin throughout the breeding cycle. *Marine Ecology Progress Series* **106**, 11–9.
- Kittiwattananawong K, Chantrapornsy S, Mananansup M *et al.* (2002). Protective areas for interesting green turtle (*Chelonia mydas*) populations in Thailand. In: Nobuaki N, ed. Proceedings of the 3rd Workshop on SEASTAR2000; 16–19 Dec 2002, Bangkok, Thailand, pp. 45–8.
- Lutcavage ME, Lutz PL (1997). Diving physiology. In: Lutz PL, Musick JA, eds. *The Biology of Sea Turtles*. CRC Press, Boca Raton, FL, pp. 277–95.
- Mate BR, Lagerquist BA, Calambokidis J (1999). Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. *Marine Mammal Science* **15**, 1246–57.
- Miller J (1997). Reproduction in sea turtles. In: Lutz PL, Musick JA, eds. *The Biology of Sea Turtles*. CRC Press, Boca Raton, FL, pp. 51–81.
- Minamikawa S, Naito Y, Uchida I (1997). Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *Journal of Ethology* **15**, 109–18.
- Morreale SJ (1999). Oceanic migration of sea turtles (Dissertation). Cornell University, Ithaca, NY.
- Morreale SJ, Standora EA, Spotila JR, Paladino FV (1996). Migration corridor for sea turtles. *Nature* **384**, 319–20.
- Mortimer JA, Portier KM (1989). Reproductive homing and interesting behavior of the green turtle (*Chelonia mydas*) at Ascension Island, South Atlantic Ocean. *Copeia* **1989**, 962–77.
- Quiñones J, González CV, Zeballos J, Purca S, Mianzan H (2010). Effects of El Niño-driven environmental variability on black turtle migration to Peruvian foraging grounds. *Hydrobiologia* **645**, 69–79.
- Reina RD, Mayor PA, Spotila JR, Piedra R, Paladino FV (2002). Nesting ecology of the leatherback turtle, *Dermochelys coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica: 1988–1989 to 1999–2000. *Copeia* **2002**, 653–64.
- Reina RD, Abernathy KJ, Marshall GJ, Spotila JR (2005). Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology* **316**, 1–16.
- Rodgers AR, Carr AP, Smith L, Kie JG (2005). *Hrt: Home Range Tools for ARCGIS*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- Rostal DC, Paladino FV, Patterson RM, Spotila JR (1996). Reproductive physiology of nesting leatherback turtles (*Dermochelys coriacea*) at Las Baulas National Park, Costa Rica. *Chelonian Conservation and Biology* **2**, 230–36.

- Saba VS, Santidrian-Tomillo P, Reina RD *et al.* (2007a). The effect of El Niño Southern Oscillation on the reproductive frequency of eastern Pacific leatherback turtles. *Journal Applied Ecology* **44**, 395–404.
- Saba VS, Shillinger GL, Swithenbank AM *et al.* (2007b). An oceanographic context for the foraging ecology of eastern Pacific leatherback turtles: consequences of ENSO and coastal gillnet fisheries. *Deep Sea Research* **55**, 646–60.
- Saba VS, Spotila JR, Chavez FP, Musick JA *et al.* (2007c). Bottom-up and climatic forcing on the worldwide population of leatherback turtles. *Ecology* **89**, 1414–27.
- Sato K, Matsuzawa Y, Tanaka H *et al.* (1998). Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. *Canadian Journal of Zoology* **76**, 1651–62.
- Schlichting H (1979). *Boundary-Layer Theory*, 7th edn. McGraw-Hill, New York.
- Seminoff JA (2004). *Chelonia mydas*. In: *The IUCN Red List of Threatened Species*. Version 2011.2. [Cited 27 Jan 2012.] Available from URL: <http://www.iucnredlist.org>
- Seminoff JA, Jones TT, Marshall GJ (2006). Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? *Marine Ecology Progress Series* **322**, 269–80.
- Seminoff JA, Zárate P, Coyne M *et al.* (2008). Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endangered Species Research* **4**, 57–72.
- Shillinger GL, Palacios DM, Bailey H *et al.* (2008). Persistent leatherback turtle migrations present opportunities for conservation. *PLOS Biology* **6**, e171.
- Shillinger GL, Swithenbank AM, Bograd SJ *et al.* (2010). Identification of high-use internesting habitats for eastern Pacific leatherback turtles: role of the environment and implications for conservation. *Endangered Species Research* **10**, 215–32.
- Spotila JR, Standora EA (1985). Environmental constraints on the thermal energetics of sea turtles. *Copeia* **1985**, 694–702.
- Standora EA, Spotila JR, Foley RE (1982). Regional endothermy in the sea turtle, *Chelonia mydas*. *Journal of Thermal Biology* **7**, 159–65.
- Thomson JA, Heithaus MR, Dill LM (2011). Informing the interpretation of dive profiles using animal-borne video: a marine turtle case study. *Journal of Experimental Marine Biology and Ecology* **410**, 12–20.
- Troëng S, Evans DR, Harrison E, Lagueux CJ (2005). Migration of green turtles *Chelonia mydas* from Tortuguero, Costa Rica. *Marine Biology* **148**, 435–47.
- Tucker AD, Read MA (2001). Frequency of foraging by gravid green turtles (*Chelonia mydas*) at Raine Island, Great Barrier Reef. *Journal of Herpetology* **35**, 500–503.
- Wallace BP, Williams CL, Paladino FV, Morreale SJ, Lindstrom RT, Spotila JR (2005). Bioenergetics and diving activity of internesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino Las Baulas, Costa Rica. *The Journal of Experimental Biology* **208**, 3873–84.
- Wallace BP, Kilham SS, Paladino FV, Spotila JR (2006). Energy budget calculations indicate resource limitation in eastern Pacific leatherback turtles. *Marine Ecology Progress Series* **318**, 263–70.
- Watson KP, Granger RA (1998). Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). *Journal of Experimental Biology* **201**, 2497–505.
- Wildlife-Computers (2007). *Mk 10 User Guide*. [Cited 27 Jan 2012.] Available from URL: <http://www.wildlifecomputers.com>
- Worton BJ (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–8.