

Leatherback Turtle, *Dermochelys coriacea*, Nesting and Nest Success at Tortuguero, Costa Rica, in 1990-1991

ALISON J. LESLIE¹, DAVID N. PENICK¹, JAMES R. SPOTILA^{1,3}, AND FRANK V. PALADINO²

¹Department of Bioscience and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104 USA;

²Department of Biology, Indiana-Purdue University, Fort Wayne, Indiana 46805 USA;

³Corresponding Author for Reprint Requests [Fax: 215-895-1273; E-mail: Spotila@coasmail.drexel.edu]

ABSTRACT. – Leatherback turtle nesting at Tortuguero, Costa Rica, in 1990 and 1991 took place from early March to early July and peaked in April for both years. We tagged 33 turtles in 1990 and 45 in 1991. Mean mass of 22 female turtles was 346.8 kg. Mean standard curved carapace length was 156.2 cm. Mean clutch size was 86 yolked and 53 yolckless eggs in 1990 and 80 yolcked and 33 yolckless eggs in 1991. Mean mass of 613 yolcked eggs was 84.3 g and mean diameter was 54.0 mm. In 1990, hatchlings emerged from 26 of 56 nests (46.4%). Poachers removed 14 clutches (25%), predators (dogs) destroyed 6 (10.7%), and tides and waves destroyed 10 (17.8%). Mean percent emergence for successful nests was 70.0%. In 1991, hatchlings emerged from 85 of 150 nests (56.7%). Poachers removed 17 clutches (11.3%), predators (dogs) destroyed 10 (6.7%), roots and debris destroyed 7 (4.7%), and tides and waves destroyed 31 (20.6%). Mean percent emergence for successful nests was 53.2%. Dogs destroyed an additional 40 (47.1%) of the 85 successful nests at emergence in 1991. Thus, 50 (33.3%) of the total number of nests studied in 1991 were destroyed by dogs. Poaching and predation were related to nest position on the beach, being highest in the mid- and upper beach zones. Soil temperature profiles predicted that both nesting seasons produced predominantly male hatchlings; 54% male in 1990 and 62% male in 1991. However, when we added the effect of metabolic heating, the sex ratio predictions went to 70.8% female in 1990 and 63% female in 1991. Rainfall had a profound cooling effect on incubation (sand) temperatures with mean sand temperature of 28.5°C in 1990 and 29.0°C in 1991. Water potential values of beach sand ranged from -1.5 to -8.5 kPa. An estimated 150-368 females nested at the Tortuguero beach.

KEY WORDS. – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; sea turtle; nesting; nests; hatchlings; predation; temperature; sex ratio; Costa Rica

The leatherback turtle, *Dermochelys coriacea*, is classified as an endangered species by the World Conservation Union (IUCN)(Groombridge, 1982). It spends the majority of its life in the ocean feeding on Cnidarians, such as *Cyanea capillata* (Musick, 1979), *Rhizoma octopus*, and *Cyanea* sp. (den Hartog and van Nierop, 1984), and on Ctenophores. Leatherbacks are unique sea turtles in that they inhabit ocean waters of extreme temperatures, including both tropical and sub-polar regions. They have a worldwide distribution, occurring as far south as the coast of New Zealand, Mar de Plata, Argentina, and the Cape of Good Hope, South Africa. In the northern hemisphere they occur off the coast of Labrador and Newfoundland in the Atlantic and off the coast of Alaska in the Pacific (Bleakney, 1975; Goff and Lien, 1988).

Leatherbacks primarily nest in the tropics with major nesting colonies in French Guiana, Suriname, Mexico, and Costa Rica. The area of Tortuguero (Fig. 1) on the Caribbean coast of Costa Rica is well known for its green turtle (*Chelonia mydas*) nesting population. In 1959, Carr and Ogren briefly observed the nesting behavior of leatherbacks in this region and concluded that these turtles were in need of further study (Carr, 1967). In 1985, Hirth and Ogren (1987) studied the nesting ecology of leatherback turtles at Laguna Jalova, which is located at the southern end of Tortuguero National Park. They stated that the Tortuguero-

Parismina area might be an important nesting area for the leatherback turtle. A survey conducted in 1989 by Paladino et al. (1990) indicated that a number of leatherback turtles nest in this area. Therefore, we undertook a study of the nesting ecology of *D. coriacea* at Tortuguero in 1990 and 1991.

Specifically, the goals of this study were: (1) to determine the number of leatherbacks nesting at Tortuguero and the number of nests they produced, (2) to determine percentage hatching success of *in situ* leatherback nests at Tortuguero, (3) to investigate extent and timing of predation and poaching and effect of beach erosion on nests, (4) to examine effects of other biotic and abiotic factors on hatching success, such as: rainfall, sand temperature, incubation time, clutch size, season, nest position on the beach, and moisture content of sand in relation to nest position, and (5) to obtain morphometric data on adults, eggs, and hatchlings. In order to ensure the survival of this species we need to understand its biology and ecology so that conservation efforts and management plans can be designed and implemented.

METHODS AND MATERIALS

Study Area. — We carried out this study at Tortuguero, Costa Rica (Fig. 1) during the 1990 and 1991 leatherback

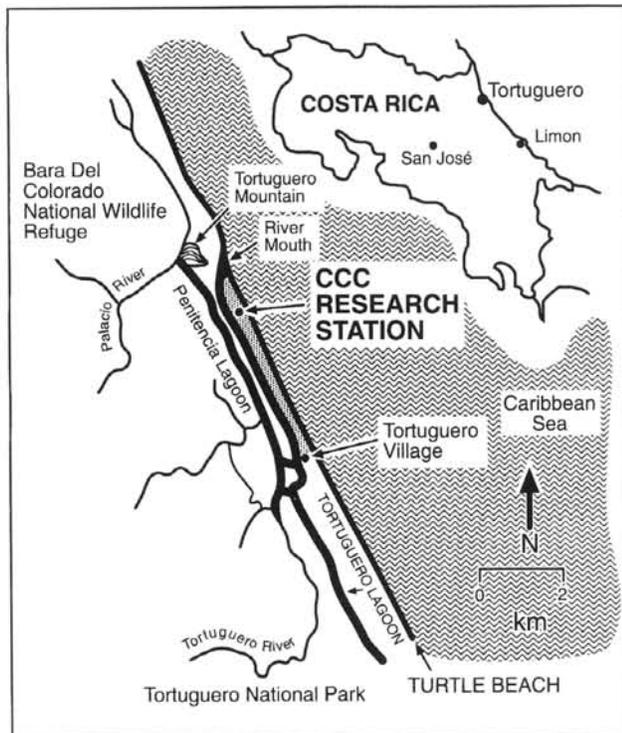


Figure 1. The nesting beach at Tortuguero, Costa Rica ($10^{\circ}30'N$, $83^{\circ}30'W$), extends from Río Tortuguero southwards beyond the boundaries of Tortuguero National Park to Parismina. Our study site was between the village of Tortuguero and the mouth of the Río Tortuguero (shaded area on map).

nesting seasons. Leatherback nesting occurs there primarily from mid-March to late June. We studied the beach from mid-March to early July in 1990 and 1991, and received additional rainfall and ambient temperature data from Caribbean Conservation Corporation (CCC) for the period July to September 1991. The 35.2 km black sand beach stretches from Río Tortuguero south to Río Parismina. The portion south of the village of Tortuguero is within Tortuguero National Park, an 18,946 ha area of tropical wet forest. Along its entire length the beach is closely backed by a natural river and canal system. This is a high-energy beach with a medium-to-steep slope, constantly altered by both erosional forces and sand deposition. Because heavy tropical rains and stormy seas greatly accelerate these processes, configuration of the nesting beach platform varies constantly during nesting and hatching seasons.

The lower portion of the nesting beach, including the tidal area, consists mainly of open sand although portions can be heavily littered with logs and debris after storms. The middle portion of the beach is often heavily littered with a variety of debris including branches, logs, large rafts of water hyacinth (*Eichhornia crassipes*), sargassum (*Sargassum* sp.), coconut husks, tar balls, and a large variety and amount of plastic. Some debris originates from inland areas and is deposited on the beach after entering the Caribbean from the river mouths, some originates from the local village, and much is also deposited by long-shore currents. The upper beach is covered by various low, herbaceous, salt-

resistant plants including railroad vine (*Ipomoea pes-caprae*), sea purslane (*Sesuvium portulacastrum*), rush grass (*Sporobolus virginicus*), beach grass (*Uniola pittieri*), and a sedge (*Remirea maritima*). A border of cocoplum (*Chrysobalanus virginicus*) and seagrape (*Coccoloba uvifera*) separates the beach from coconut palm (*Cocos nucifera*) and tropical rain forest.

We studied the northernmost 4.8 km of beach from the village of Tortuguero (approximately 500 residents), to the mouth of Río Tortuguero. We divided the beach into 0.2 km sections marked by large, numbered wooden poles, starting in the north at Río Tortuguero, which is actually at position -0.4 km (the river mouth has shifted northwards by 0.4 km since 1955 when the beach was first divided and marked). Fowler (1979) described four beach zones and Spotila et al. (1987) used three of these zones. We subsequently modified Fowler's model to include seven beach zones (Fig. 2).

Nesting Adults. — Gravid leatherback turtles came ashore at night to nest. We patrolled the beach at night from 16 March until early July in 1990 and in 1991. Due to a shortage of staff we were unable to establish complete coverage of the beach at all times. We observed the nesting process and then tagged females on the left front and left rear flippers with monel flipper tags provided by Caribbean Conservation Corporation. The 1990 tags were a D-5500 and 5600 series, and the 1991 tags were a D-6700, 6800, and a 54,000 series with a University of Florida return address. We measured standard curved carapace length (SCCL) with a flexible measuring tape (± 0.1 cm) from the center of the nuchal notch to the posterior carapace tip (alongside the central dorsal ridge). We measured straight carapace length (SCL) as the straight line distance from the center of the nuchal notch to the distal tip of the carapace using a set of large wooden calipers and a measuring tape. We weighed a subset of the turtles after they completed nesting using a cargo net and a 500 kg winch and scale (± 5 kg) suspended from a tripod.

Natural Nests. — We recorded nest position on the beach according to its zone (Fig. 2), its location in relation to the nearest northernmost section marker, and date and time laid. Whenever possible we determined the clutch size during the actual laying process. We counted both yolked and yolckless eggs. Each morning until early July, we verified nest positions, numbered nests laid the previous night, and marked them by means of a 1 m long wooden stake. Care was taken not to mark the exact nest position for fear of attracting and encouraging both predators and poachers. Instead, we took measurements from the nest chamber to the stake in order to facilitate relocation of the nest site. However, nests were still often difficult to find later. By probing around the original nest site with a thin stick it was possible to locate the egg chamber from which hatchlings had emerged unnoticed.

We monitored each nest daily until emergence of the hatchlings or several days beyond the expected time of emergence. We checked nests for disturbance by water (tide or waves), predators and poachers, and placed each nest into one of either five (1-5 in 1990) or seven (1-7 in 1991)

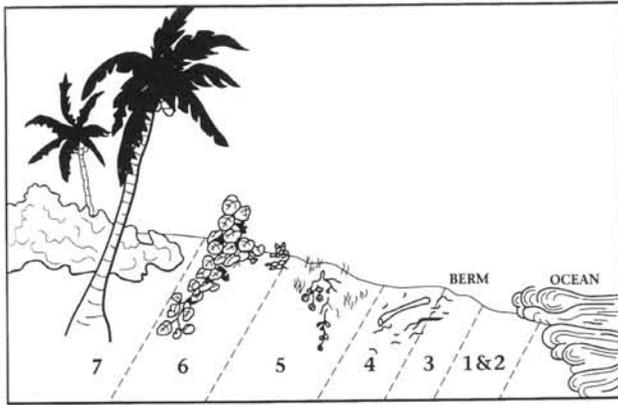


Figure 2. Diagrammatic representation of the 7 beach zones at Tortuguero. Zones 1 and 2 represent the tidal area. Zone 3 includes the area directly below the berm which is washed periodically by high tide. Zone 4, the low beach, is the area above the berm within 2 or 3 m of the berm edge. Zone 5 is the widest zone and represents the open, mid-beach area, which is usually devoid of vegetation. Zone 6, the vegetated mid-beach, is sparsely vegetated and borders the vegetation zone. Zone 7 is thickly vegetated with cocoplum and other vegetation.

categories: (1) hatched, (2) poached, (3) depredated, (4) tide-washed – inundated by tide, (5) wave-washed, (6) debris mats – these either prevented hatching by reducing gas exchange or prevented emergence of the clutch, and (7) root development – parasitism in which plant roots grew into the eggs. Hatchlings usually emerged at night. We determined hatching success approximately 12 hours after emergence by excavating the nest and counting the number of empty egg shells, unhatched eggs, and live and dead hatchlings remaining in the nest or nest chimney. We calculated percentage of hatchlings that emerged from each nest by subtracting the number of hatchlings (live and dead) remaining in the nest from the number of empty shells from yolked eggs and dividing this difference by total clutch size multiplied by 100 (Fowler, 1979). The sum of the number of unhatched eggs and empty shells removed from a nest provided a count of total clutch size, if a clutch count was not obtained at the time of laying. We observed, but did not include unyolked eggs in these counts.

We opened unhatched eggs and examined them for signs of development and/or fly larvae infestation. We staged embryos according to a classification used by Alvarado and Figueroa (1990). Stage 1 included eggs that showed signs of blood vessel formation or eggs that contained a small, unpigmented embryo less than 10 mm long. Stage 2 embryos had pigmented eyes, a slightly pigmented body, and ranged in length from 10–20 mm, and stage 3 embryos were fully pigmented and greater than 20 mm long. Whenever possible we weighed and measured eggs immediately after deposition using a Pesola spring scale (± 0.05 g) and digital calipers (± 0.05 mm). We also measured length and mass of hatchlings immediately after hatching using the same instruments.

Temperature Monitoring. — We monitored sand temperature ($\pm 0.2^\circ\text{C}$) at two beach locations within the 4.8 km study area during both years by establishing thermal profiles

in each of three beach zones (4, 5, and 6; see Fig. 2). In 1990, each profile consisted of a meter stick with eight 24 gauge copper-constantan (Cu-Cn) thermocouples buried at depths of 0, 5, 10, 25, 30, 50, 75, and 100 cm. In 1991 each thermal profile consisted of three thermocouples buried at depths of 25, 50, and 75 cm. The mean nest depth for leatherbacks at this site was 75 cm. Therefore, we used temperatures from this depth to assess the effect of temperature on development and sex determination of leatherback eggs. We recorded sand temperatures every other day at approximately 1400 hrs with a portable, battery operated BAT-12 thermocouple meter (Physitemp Instruments). Several times during the course of both seasons we monitored sand temperatures every four hours over a 24-hour period to measure the effects of diurnal fluctuation.

Temperature Dependent Sex Determination. — The temperature of incubation during the middle third of development determines the sex of leatherback turtles (Mrosovsky et al., 1984). Since we were not able to measure the temperature of nests directly, we developed a method to estimate nest temperature based on our prior knowledge of the manner in which temperature varied in the different beach zones at Tortuguero (Spotila et al., 1987). Previous research demonstrated that the temperature in a given zone was similar throughout the zone. Therefore, in order to estimate the effect of sand temperature on sex determination we allocated each *in situ* nest to the nearest thermal profile station within the same zone as the nest. We assumed that the mean temperature at nest depth (75 cm) for the middle third of the incubation period, usually days 20–40, represented the incubation temperature for the nest (Spotila et al., 1987), and computed the sex ratios based on these temperatures. Then we added 0.5°C to the temperature of each nest to take into account the effect of metabolic heating and recomputed the sex ratios. Metabolic heating can raise the temperature of a nest during the middle third of development by about 0.5 to 1°C (Morreale et al., 1982).

Soil Moisture Tension. — We recorded soil moisture tension in 1991 using standard 1 m tensiometers (Model 2710 ARL, Soil Moisture Equipment Corp.) placed at a depth of 75 cm in each of three beach zones (4, 5, and 6) adjacent to thermal profile meter sticks. We recorded soil moisture tension directly from the vacuum dial gauge, in units of centibars of soil suction. We then converted these values to kPa. Several times during the course of the season, we monitored soil suction every four hours over a 24-hour period.

Weather. — We maintained a small weather station at the research station, Casa Verde, during both seasons. An all-weather plastic rain gauge measured precipitation daily. We recorded air temperatures (Weksler Max-Min thermometer) and weather conditions (cloud cover, rain) daily at noon.

RESULTS

Nesting Ecology. — We tagged 33 nesting female leatherbacks in 1990 and 45 in 1991. We reobserved 2 tagged turtles in 1990 and 1 in 1991 within the same season.

One turtle in 1990 was reported, via a tag return, to have nested at Bocas del Toro in Panama. There were no reobservations between seasons. Because we did not have complete coverage of the 4.8 km beach for the entire time during every night, we did not see many of the turtles that nested on this beach. Therefore, we could not determine nesting frequency and internesting interval. Mean mass of 22 females was 346.8 kg (SD = 55.4, range = 250–435 kg). Mean standard curved carapace length (SCCL) of 56 females was 156.2 cm (SD = 10.6, range = 124.0–180.3 cm). Straight carapace length (SCL) of 35 females was 151.1 cm (SD = 8.1, range = 137.1–170.0 cm). The regression equation for length vs. mass ($n = 22$) was $y = 5.032x - 417.7$ ($r^2 = 0.704$, $P < 0.0001$) where x = length in cm.

In 1990, leatherbacks laid 72 nests within the study area between March and early July. Nesting peaked in April when 38.9% of nests were laid, followed by May (27.8%), March (25.0%), and June (8.3%). Density was 15.0 nests per km. In 1991, leatherbacks laid 177 nests between March and early July. Nesting peaked during April when 62.1% of nests were laid, followed by May (20.9%), June (8.6%), March (8.0%), and July (0.6%). Density was 36.9 nests per km of beach.

Fate of Nests. — In 1990 mean clutch size of yolked eggs was 86 (range = 77–115) and of yolkless eggs 53 (range = 22–62). We were unable to determine the fate of 16 nests so they were excluded from further analysis. Hatchlings emerged from 26 (46.4%) of 56 nests. Hatching success of 23 nests was 70.0%, producing a total of 1274 hatchlings (Table 1).

Predation by feral and domestic dogs (*Canis familiaris*) accounted for the loss of 6 nests (10.7%) and tidal inundation destroyed another 5 (8.9%). Five nests (8.9%) were washed away by wave action and 14 (25.0%) were poached. South of Tortuguero, coatis (*Nasua narica*) and black and turkey vultures (*Coragyps atratus* and *Cathartes aura*) were also responsible for nest destruction in both 1990 and 1991, but we were unable to estimate the extent of that predation.

The majority of nests were laid in zone 5 ($n = 30$), where 15 (50.0%) hatched, 1 (3.3%) was washed away, and 4

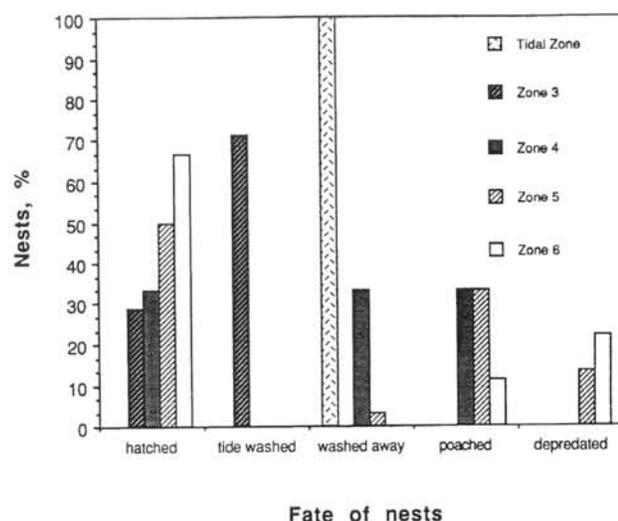


Figure 3. Fate of 56 leatherback nests laid at Tortuguero, Costa Rica, during the 1990 season. See Fig. 2 for a diagram of beach zones. There was 1 nest in the tidal zone, 7 nests in zone 3, 9 nests in zone 4, 30 nests in zone 5, 9 nests in zone 6, and 0 nests in zone 7.

(13.3%) were depredated (Fig. 3). The highest loss of nests ($n = 10$, 33.3%) in zone 5 was due to poaching. The highest percentage of nests hatched in zone 6 (66.6% of 9 nests). Nest loss in zone 6 was due to depredated and poaching. Tidal effects were greatest in zone 3, where 5 (71.4%) nests were inundated by the tide on numerous occasions and failed to hatch. Two (28.6%) nests in this zone survived to hatching. Three nests (33.3%) laid in zone 4 were washed away by tide, as was the single clutch of eggs laid in the tidal zone, which was entirely washed away within a few days of laying.

In 1991 mean clutch size was 80 yolked eggs (range = 58–114) and 33 yolkless eggs (range = 21–56). Changes in beach topography prevented us from determining the fate of 27 nests so we excluded them from further analysis. Hatchlings emerged from 85 (56.7%) of the 150 remaining nests. Mean hatching success of 81 nests was 53.2%, producing a total of 3513 hatchlings (Table 1). Dogs partially depredated 40 (47.1%) of 85 nests that hatched in 1991. We were still able to calculate the hatching success of these nests because dogs left egg shells and remaining unhatched eggs intact in the bottom of the nest chamber. An additional 10 clutches (6.7%) were completely destroyed by dogs shortly after laying, bringing the total number of nests depredated by dogs in the 1991 season to 50 (33.3%).

Tidal inundation destroyed more nests ($n = 20$, 13.3%) in 1991 than in 1990 ($n = 5$, 8.9%) (Table 1). Eleven (7.3%) were entirely washed away due to changes in beach topography. Poaching removed 17 (11.3%) clutches. Debris mats killed 6 (4.0%) clutches. These mats, up to 50 cm thick, consisted of large, dense masses of water hyacinth (*E. crassipes*), sargassum (*Sargassum* sp.), and piles of washed-up forest debris including logs, branches, and twigs. They either reduced gas exchange and killed the developing embryos or prevented hatchlings from crawling to the surface. Root development in 1991 destroyed a single nest

Table 1. Fate of leatherback nests laid at Tortuguero in 1990 and 1991. Values given are numbers (n) and percentages. We excluded nests whose fate we could not determine.

	1990		1991	
	n	%	n	%
Total Number of Nests Laid	72		177	
Number of Nests Excluded from Study	16		27	
Number of Studied Nests	56		150	
Nests Producing some Hatchlings	26	46.4	85	56.7
Hatching Success of Nests that Hatched	23	70.0	81	53.2
Nests Depredated by Dogs	6	10.7	50	33.3
Prior to Hatching	0	0.0	10	6.7
At Hatching	0	0.0	40	26.7
Tidal Inundation	5	8.9	20	13.3
Waves Washed Away	5	8.9	11	7.3
Poached	14	25.0	17	11.3
Obstructed by Debris	0	0.0	6	4.0
Root Growth	0	0.0	1	0.7

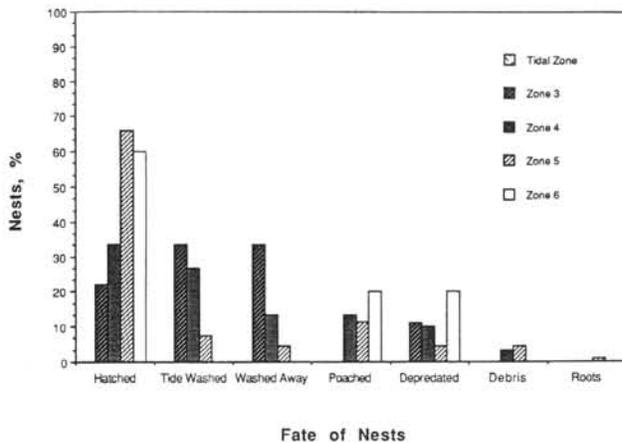


Figure 4. Fate of 150 leatherback nests laid at Tortuguero, Costa Rica, during the 1991 season. See Fig. 2 for diagram of beach zones. There were 0 nests in the tidal zone, 9 nests in zone 3, 29 nests in zone 4, 107 nests in zone 5, 5 nests in zone 6, and 0 nests in zone 7.

(0.7%). Plant roots appeared to utilize egg contents as nutrients. A network of roots totally surrounded eggs of this clutch, some even growing directly into the eggs. Roots came from low, herbaceous salt-resistant plants seen on the beach, including railroad vine (*I. pes caprae*) and beach grass (*U. pittieri*).

In 1991, as in 1990, the majority of nests were laid in zone 5 and 70 (65.0%) of these hatched (Fig. 4). Poaching removed 12 clutches (11.2%) and depredation destroyed 5 (4.7%). Surprisingly, tidal inundation killed 9 nests (8.4%) in this mid-beach area and 5 (4.7%) were washed away during storms. The second most successful beach zone was zone 4, where 10 nests (34.5%) hatched, 4 (13.8%) were poached, 3 (10.3%) were depredated, 8 (27.6%) were frequently inundated by the tide, and 3 (10.3%) were washed away. Within zone 3, inundation by tide and wave action accounted for the greatest loss of nests ($n = 6$). As in 1990, 2 nests (22.2%) within this low beach zone survived to hatching and 1 nest was depredated. No clutches were laid in the tidal zone in 1991. Three nests (60.0%) hatched in zone 6, with 1 nest poached and 1 depredated.

Of 6120 yolkeggs examined from 77 of 177 nests laid during 1991 (Table 2), a total of 3238 eggs (52.9%) produced young that successfully pipped the eggshell. However, not all of these hatchlings emerged successfully from the nest. It was impossible to determine exactly how many hatchlings emerged because many were taken by dogs before reaching the sand surface. Another 1209 eggs (19.8% of total) showed no signs of development. We found dead embryos in 947 eggs (15.5%). We found a total of 304 stage 1 embryos (5.0%), 218 stage 2 embryos (3.6%) and 425 stage 3 embryos (6.9%). A further 726 eggs (11.9%) were rotten and contained larvae of the fly *Megaselia scalaris*. Adult flies traveled down ghost crab (*Ocypoda ceratophthalmus* and *O. kuhlii*) holes leading to the nest chamber and laid eggs within the egg chamber. It was impossible to determine whether or not these eggs had embryos. Mites of the genus *Caloglyphus* fed on dead

hatchlings in a number of nests, but we could not determine if they were the cause of death.

Leatherback Eggs. — Mean mass of 613 yolkeggs from 14 clutches was 84.3 g each (SD = 5.2, range = 59.4–97.0 g) and mean egg diameter was 54.0 mm (SD = 1.4, range = 47.5–58.0 mm). Mean egg mass per clutch was positively related to mean egg diameter: $y = 4.206x - 144.70$, where $x =$ egg diameter ($r^2 = 0.795$; $P < 0.0001$). Range of mean individual egg mass within clutch for these 14 clutches was 74.5–95.6 g and range of mean individual egg diameter within clutch was 51.4–56.8 mm.

Physical Factors and Sex Determination. — The 24-hour thermal profiles showed minimal temperature differences at all depths associated with leatherback turtle nests. Temperatures did not fluctuate more than 0.5°C at a depth of 75 cm (mid-nest depth) during a 24-hour period unless there was a heavy rain or prolonged sunny period. In 1990, mean sand temperature of zone 4 (just above berm) was $28.5 \pm 1.4^\circ\text{C}$ (S.D. over the season) at a depth of 75 cm (range = 25.8–32.6°C) (Fig. 5), temperature of zone 5 (open, mid-beach) was $28.6 \pm 1.4^\circ\text{C}$ (range = 25.9–33.5°C), and temperature of zone 6 (vegetated, high beach) was $29.7 \pm 1.6^\circ\text{C}$ (range = 26.1–33.0°C). Temperatures were highest in late April, mid-May and in early June. At the onset of the rainy season (toward the end of June) and in early July a gradual decrease in sand temperature occurred with the lowest temperatures recorded during July.

In 1991, mean sand temperature of zone 4 was $29.0 \pm 1.5^\circ\text{C}$ at a depth of 75 cm (range = 26.4–31.2°C) (Fig. 6), temperature of zone 5 was $29.5 \pm 1.6^\circ\text{C}$ (range = 26.4–31.9°C), and temperature of zone 6 was $29.9 \pm 1.6^\circ\text{C}$ (range = 26.6–32.2°C). Temperatures were highest at the end of April and at the beginning of May. There was a distinct decrease in sand temperatures during the first two weeks of May due to rain, and this was followed by a gradual increase in temperatures towards the end of the month. After a drop in early June, sand temperatures throughout the remainder of June and early July were relatively constant. A sharp decrease occurred once again in mid-July.

We estimated sex ratios of hatchlings from 24 *in situ* nests in 1990 and 81 *in situ* nests in 1991. Mrosovsky et al. (1984) and Rimblot-Baly et al. (1987) determined a pivotal temperature of 29.5°C for leatherbacks in Suriname, with

Table 2. Fate of yolkeggs from undisturbed leatherback nests at Tortuguero, Costa Rica, in 1991. Results from analysis of 6120 eggs from 77 of 177 natural nests.

	Mean	SD	Range	Total
Hatched shells/nest	42.1	19.0	5–77	3238
Stage 1 embryos/nest	4.0	6.2	0–47	304
Stage 2 embryos/nest	2.8	4.9	0–37	218
Stage 3 embryos/nest	5.5	4.9	0–50	425
Non-developed eggs/nest	15.7	13.1	1–80	1209
Rotten eggs/nest	9.4	8.7	0–34	726
Totals	79.5	13.8	47–114	6120

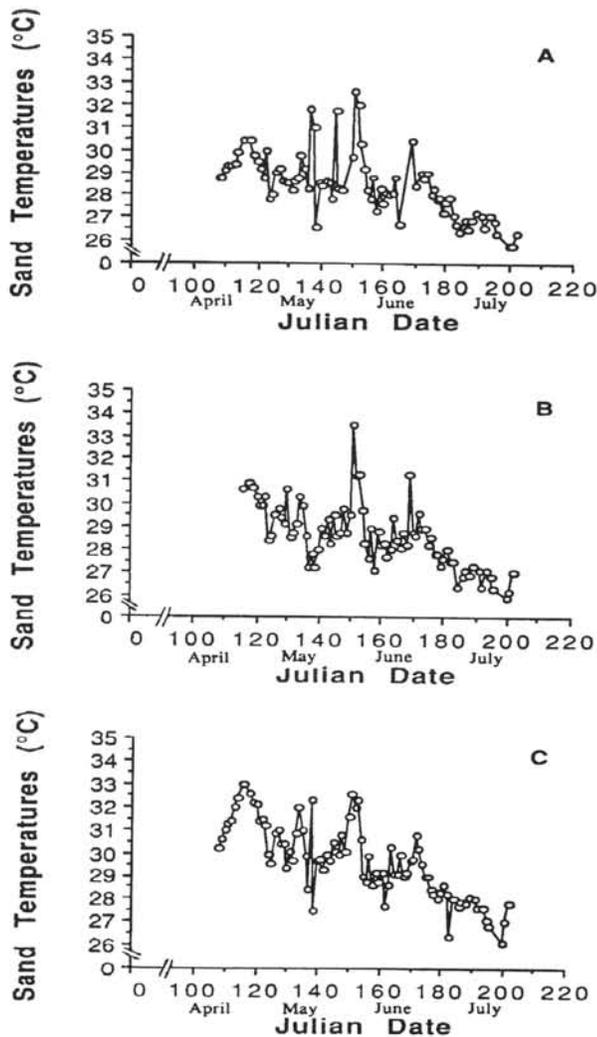


Figure 5. Sand temperatures at a depth of 75 cm recorded at Tortuguero, in three beach zones from 18 April to 21 July 1990. **A.** Temperature just above the berm (zone 4), **B.** Temperature of open, mid-beach (zone 5), and **C.** Temperature of vegetated, mid-beach (zone 6).

higher temperatures producing predominantly female hatchlings and lower ones producing predominantly males. Binckley (1996) found that the pivotal temperature for Pacific leatherbacks at Playa Grande, Costa Rica was 29.4°C. These temperatures represented no biological difference and this suggested that the pivotal temperature of leatherbacks did not vary between colonies. Therefore, we assumed that leatherbacks at Tortuguero had the same pivotal temperature (29.5°C) and assigned a nest as male or female depending upon our estimated incubation temperature. Therefore, in 1990, using sand temperatures, we estimated that 46% ($n = 11$) of nests would have produced predominantly female hatchlings and 54% ($n = 13$) of nests would have produced predominantly males. In 1991 only 38% ($n = 31$) of nests used in the sex determination estimate would have produced predominantly females and 62% ($n = 50$) of nests would have produced predominantly males. However, when we added in metabolic heating, the 1990 sex ratio was estimated as 70.8% female and 29.2% male and the 1991 sex

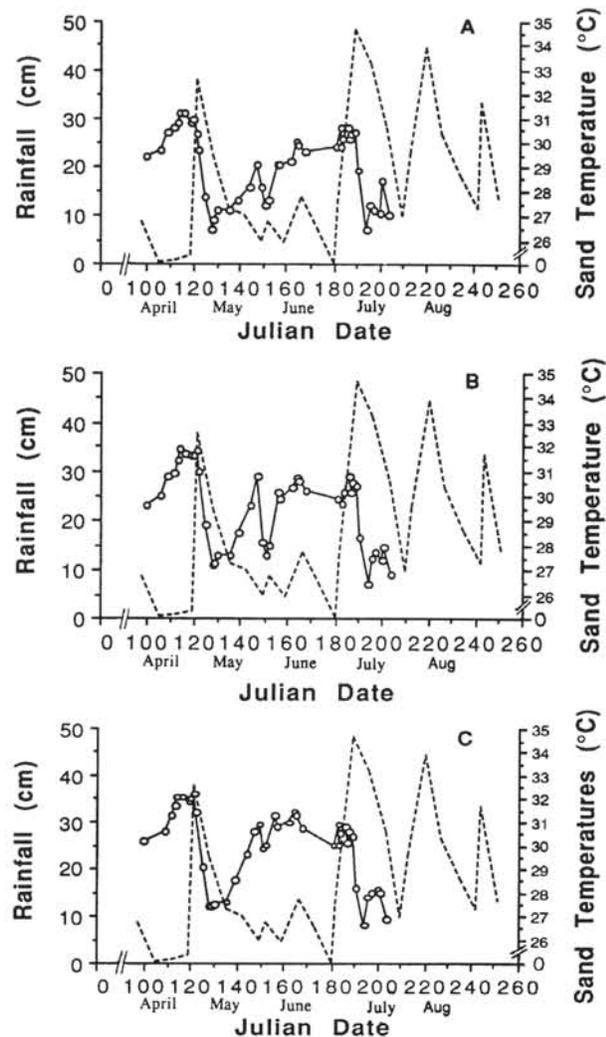


Figure 6. Rainfall (cm) (dashed line) recorded at Tortuguero, Costa Rica, from 6 April to 12 September 1991 and associated sand temperatures at a depth of 75 cm. **A.** Temperature just above the berm (zone 4), **B.** Temperature of open, mid-beach (zone 5), and **C.** Temperature of vegetated, mid-beach (zone 6).

ratio was 63% female and 37% male. Thus, metabolic heating probably created a strong female bias in the sex ratios of hatchlings that otherwise would have been male biased in both 1990 and 1991.

Rainfall and Soil Moisture. — In 1991, July was the wettest month (139.3 cm of rain)(Fig. 6). During May (normally dry), 86.7 cm of rain fell causing a drop in temperature in all beach zones. The two driest months were April and June (14.8 and 34.3 cm of rainfall). Soil moisture tension *in situ* was -1.5 to -8.5 kPa (Fig. 7). Soil moisture tension rose after heavy rains in the low beach and open mid-beach but remained more stable in the vegetated mid-beach area (zone 6).

DISCUSSION

Tortuguero is an important nesting beach for the leatherback turtle. We can estimate the nesting population size from our data and that of others. We measured a nesting

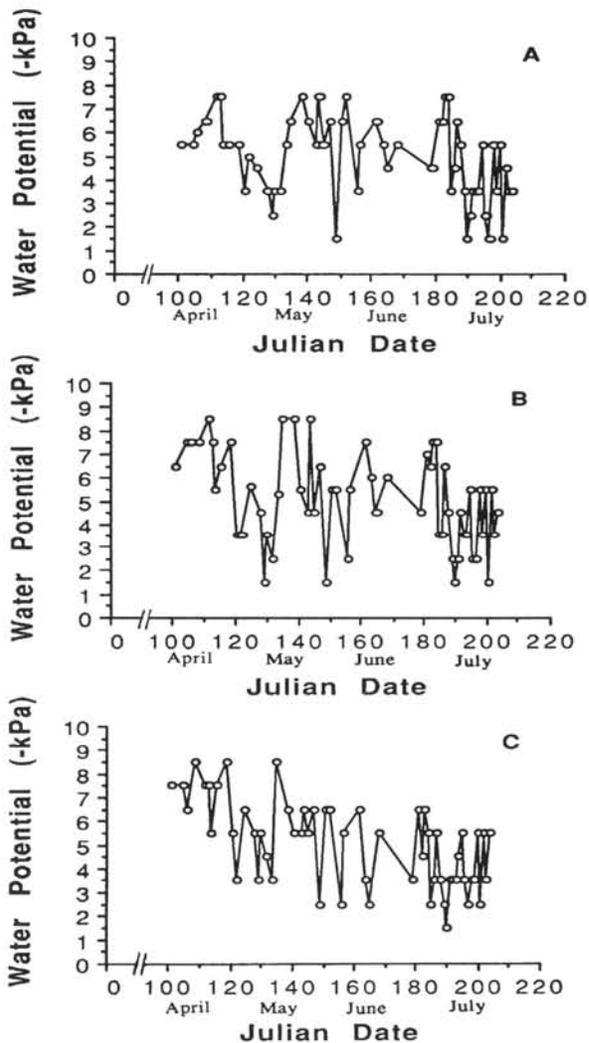


Figure 7. Water potential values (-kPa) recorded at a depth of 75 cm throughout the 1991 season. **A.** Water potential values just above the berm (zone 4), **B.** open, mid-beach (zone 5) and **C.** vegetated, mid-beach (zone 6).

density of 15.0 nests per km in 1990 and 36.9 nests per km in 1991. Hirth and Ogren (1987) reported a nesting density of 27 nests per km at the southern end of Tortuguero National Park in 1985. Assuming an interesting interval of 10 days, and that each turtle lays an average of 6 clutches as Tucker and Frazer (1991) reported for Culebra, then the area from Tortuguero south to Parismina (35.2 km) may support an estimated 88–216 nesting leatherbacks annually. According to data from aerial surveys (Hirth and Ogren, 1987), the relative density of nests from Parismina south to Puerto Limon is 55% of that to the north. Therefore, using the same approach, this section (45 km) has an estimated nesting population of 62–152 nesting leatherbacks. Added together, the 80 km area of the Tortuguero nesting colony, extending from Río Tortuguero in the north to Puerto Limon in the south, provides the nesting ground for an estimated 150–368 nesting leatherbacks annually.

Nest Success. — Tortuguero leatherback nests that were not lost to predation, poaching, or physical factors had a

hatching success of 70.0% in 1990 and 53.2% in 1991. These values are similar to those of Hirth and Ogren (1987), who reported a hatching success of 70.2% for natural leatherback nests at Jalova, Costa Rica, 35 km south of Tortuguero. Eckert and Eckert (1990) reported hatching success for St. Croix leatherback nests of 53.2% in 1985, 55.5% in 1984, 48.9% in 1983, and 40.2% in 1982. Hughes (1974) reported a 76.2% hatching success for leatherbacks in Tongaland, South Africa. Benabib-Nisenbaum (1983) recorded hatching success of 51% for natural leatherback nests on the Pacific coast of Mexico. In Suriname, natural leatherback nests had emergence success of 40% (Schulz, 1975). Tucker (1989) noted a 72.2% hatching rate for leatherbacks at Culebra National Wildlife Refuge, Puerto Rico.

It is not clear what role, if any, the small yolkless eggs of leatherbacks play in determining this success. These eggs may provide a source of water in dry sand (Tucker, 1989), or may act as “spacers” that increase rates of gas exchange or reduce the rate of metabolic heating. Nests of other sea turtles have similar hatching success without the presence of yolkless eggs. Emergence success is 83.1% for natural green turtle (*C. mydas*) nests at Tortuguero (Fowler, 1979). Loggerheads (*Caretta caretta*) have a hatching success of 58.7–87.0% in Florida (Worth and Smith, 1976; Wyneken et al., 1988). Olive ridley (*Lepidochelys olivacea*) nests at Colola Beach in Mexico have an emergence success of 78.8% (Alvarado and Figueroa, 1990). Bacterial contamination can reduce mean hatching success to as low as 2% on olive ridley *arribada* beaches such as Nancite in Costa Rica (Cornelius, 1986). Thus, hatching success depends upon local conditions on the beach such as water content of the sand, grain size, and organic content, as well as biotic factors such as bacterial and fungal contamination, and even the mating success of the female, since 19.8% of the leatherback eggs at Tortuguero showed no development and may have been infertile.

Poaching and Predation. — Poaching and predation accounted for the highest loss of nests in both nesting seasons. A total of 25.0% of nests laid in 1990 were poached. In 1991, the percentage of nests poached was reduced to 11.3%, a decrease of 44.8%. By comparison, poaching at Parismina in 1989 and 1990 resulted in 100% loss of leatherback nests near the village (J. Spotila, *pers. obs.*). Hirth and Ogren (1987) stated that egg poaching was the greatest threat to the survival of the leatherback turtle on the Caribbean coast of Costa Rica. On the Caribbean coast of Panama not only eggs, but adult leatherbacks as well, are heavily poached (A. Meylan, *pers. comm.*). The decrease in poaching at Tortuguero was due to the continued presence of scientists and volunteers on the beach, involvement of the local community in the research program, and community education. Similar success in reducing poaching of green turtle eggs (Fowler, 1979) occurred because of village involvement in the long term research and conservation program started by the late Archie Carr (Carr and Giovannoli, 1957; Carr and Ogren, 1960; Carr, 1967; Carr et al., 1978; Spotila, 1988; Bjorndal and Carr, 1989).

Dogs destroyed nests throughout the nesting season at all stages of incubation (10.7% in 1990 and 33.3% in 1991). Nests were destroyed in all beach zones although nests laid in the higher zones succumbed more often to increased poaching and predation. The nearby seagrape (*C. uvifera*) and cocoplum (*C. virginicus*) plants provide protection and shelter for both predators and poachers. Fretey and Frenay (1980) noted that large numbers of leatherback hatchlings are lost to dogs in French Guiana, and Hughes (1974) reported 48.4% predation on leatherback nests in Tongaland, South Africa. High losses to predators also occur for green turtles (Hill and Green, 1971) and loggerheads (Hughes, 1974; Davis and Whiting, 1977; Margaritoulis, 1982). Fowler (1979) found that 50% of green turtle nests at Tortuguero were destroyed by dogs, coatis, black and turkey vultures, and ghost crabs. Our data indicated that dogs are a great threat to leatherback nests at Tortuguero.

Tides and Waves. — Nest loss due to tidal inundation and washing away by waves was highest in the lower beach zones and approximately 20% of the nests laid each season were destroyed. At Rantau Abang, Malaysia, nest loss to erosion was < 2.5% (Mrosovsky, 1983). However, Eckert (1987) reported that short-term erosion and accretion cycles would have resulted in the annual loss of 45–60% of the nests laid at Sandy Point, St. Croix, if they had not been translocated. Hughes (1974) reported the loss of “thousands of tons” of sand from nesting beaches in eastern Madagascar and southern Africa as a result of storms. On Matura Beach, Trinidad, available nesting habitat changed markedly from week to week (Bacon, 1970). Whole nests spilled into the sea from freshly eroding berms and cliffs. A similar situation occurred in the Guianas (Bacon, 1970; Pritchard, 1971; Mrosovsky, 1983). However, Fowler (1979) found that beach erosion was an unimportant factor for green turtle nests during the 1977 season at Tortuguero. Thus, her data and ours indicated that nest loss due to tidal effects was less common at Tortuguero than at many other leatherback nesting beaches.

Physical Factors and Sex Determination. — Sand temperatures fluctuated during both the 1990 and 1991 nesting seasons due to changes in rainfall and cloud cover. The low beach zone just above the berm was the coolest due to the cooling effect of tides. Zone 6 was the warmest area of the beach. Amplitude of the temperature cycle decreased with increasing depth as seen in previous studies (Spotila and Standora, 1985; Spotila et al., 1987). Therefore, at mean nest depth (75 cm) there was little daily variation in temperature. Rainfall had a profound cooling effect on sand temperatures in all beach zones (Fig. 6). Cloud cover reduced solar insolation and heat was absorbed by infiltrating rain water (Packard et al., 1985).

Based on sand temperatures alone, 46% of leatherback nests in the 1990 season should have produced predominantly female hatchlings and the remaining 54% should have produced predominantly males. However, when we factored in metabolic heating, our prediction of sex ratio changed to 70.8% female and 29.2% male. In the 1991 season this predicted change was from 38% female and 62% male to 63% female and 37% male. The shift from male

biased to female biased sex ratios indicates the importance of metabolic heating to sex determination in leatherbacks. This should sound a note of caution for anyone who alters the natural composition of leatherback nests in beach or artificial hatcheries in an attempt to improve hatching success or to manipulate sex of hatchlings (Vogt, 1994; Mrosovsky and Godfrey, 1995). Dutton et al. (1992) estimated the 1992 sex ratio of hatchlings at Sandy Point, St. Croix, to be 75–100% male for nests laid February – April and 100% female for nests laid May – July. Based on these data they estimated an overall sex ratio of 60–70% female. Mrosovsky et al. (1984) determined that there are seasonal changes in the sex ratio of leatherback hatchlings in Suriname, with more males being produced in the wetter, cooler months of the nesting season and more females during the drier, warmer months. They estimated an overall sex ratio of 49% female. Thus, the sex ratio on leatherback beaches varies with location, season, and year. It may be that the presumed long life span of this species allows the sex ratio to balance out over many years (Mrosovsky, 1994). However, it is also possible that imbalances in hatchling sex ratios translate into skewed adult sex ratios and that this results in high rates of infertility and population decline like that observed in Malaysian leatherbacks (Chan, 1989, 1991).

Soil Moisture Tension. — Numerous chemical and physical characteristics of beach sand can affect the hatching success of clutches of eggs of all species of marine turtles. Substrates vary considerably (Stancyk and Ross, 1978; Mortimer, 1982) and yet few studies examine how substrate characteristics influence the biology of incubating eggs. Ackerman (1992) reported that soil type influences liquid water exchange while water vapor exchange is relatively independent of soil type. Data provided by Ackerman (1992) for 5 different sands from reptile nesting locations show that these soils all release their bulk liquid water at moisture potentials less negative (lower) than -10 to -15 kPa. There is little tendency for liquid water to move in sands drier than -50 to -100 kPa. This is because little movable bulk water remains and bound water is held more tightly as water potential decreases (Ackerman, 1992). In our study water potential values varied from -1.5 to -8.5 kPa indicating a very humid environment for incubating eggs (Fig. 7). Therefore, Tortuguero sand released its water readily and leatherback eggs were in positive water balance throughout development. They were more in danger of drowning in water than desiccating. We excavated a number of the nests that we classified as destroyed due to tidal inundation, and found the eggs to be totally submerged in water. Eckert (1987) reported that leatherback eggs failed to develop in nest cavities saturated with sea water. This also occurs in most, but not all, freshwater turtle species (Burger and Montevecchi, 1975; Plummer, 1976; Kennett, et al., 1993; Polisar, 1996).

The main reason for clutch failure during inundation appears to be that gas exchange is impeded when the eggs are in a moisture saturated environment (Ackerman and Prange, 1972; Kraemer and Bell, 1980; Packard et al., 1985). Oxygen diffusion between the atmosphere and the eggs in a

clutch may also affect the rate and success of embryonic development (Prange and Ackerman, 1974; Ackerman, 1980; Ackerman et al., 1985). Excessive rainfall can indirectly affect turtle nests by lowering the ambient sand temperature, thereby also increasing the incubation period, and affecting the sex of developing embryos. Rainfall may also harden the upper layers of sand, which can prevent hatchlings from emerging (Hendrickson, 1958).

Eggs. — Leatherback eggs from Tortuguero are similar in size (54.0 mm and 84.3 g) to those laid at other Western Atlantic beaches. The range of mean egg masses reported by Hirth and Ogren (1987) at Laguna Jalova, Costa Rica, was 72.6–103.5 g, and the range of mean egg diameters was 49.2–54.9 mm with a mean of 52.1 mm. Eckert and Eckert (1984) recorded a mean diameter of 54.1 mm for yolked eggs on Sandy Point, St. Croix. Mean egg diameters at other leatherback nesting beaches range between 50 and 55 mm, with those in the East Pacific being smaller than most others. For example, leatherback eggs at Playa Naranjo, Costa Rica (Pacific colony), have a mean diameter of 51 mm, whereas those from Atlantic nesting colonies such as Matina in Costa Rica, Suriname, and Trinidad have a mean diameter of 53 mm (Hirth, 1980).

There was a significant positive correlation between mean egg diameter (mm) and mean egg mass (g) ($r^2=0.795$; $P<0.0001$). Hirth and Ogren (1987) found a similar strong positive correlation between the log of the mean egg mass and the mean egg diameter ($r^2=0.83$, $P<0.0001$). Eckert and Eckert (1990) found no correlation between the size of the turtle and yolked egg diameter, clutch size, or number of clutches laid per season.

Conclusions. — The Caribbean coast of Costa Rica north of Limon supports a large nesting colony of leatherback turtles spread over 80 km. Hatching success is high and physical factors such as waves and tides have less impact on survival of Tortuguero nests as compared to other beaches. The greatest threat to survival of this colony is from poaching of eggs by humans and depredation by dogs. Conservation education can reduce the former and some form of dog control the latter. However, the increasing human population of this area and the lack of an organized educational effort throughout the region continue to threaten the survival of leatherbacks. Management and conservation of sea turtle populations such as this rests with the people who live in the particular area, although they may be assisted by outside efforts.

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