Leatherback Sea Turtle Nesting at Gandoca Beach in Caribbean Costa Rica: Management Recommendations from Fifteen Years of Conservation

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Abstract. - Field research was conducted, from 1990 to 2004, at Gandoca Beach (9°59.972'N, 82°60.530'W), located within the Gandoca-Manzanillo National Wildlife Refuge at the southernmost extreme of the Caribbean coast of Costa Rica. Nightly patrols of the 8.85-km nesting beach were undertaken annually from the second week of February through the last week of July, and pertinent information regarding the nesting process was recorded. An estimated 90% of all nesting females were documented and uniquely tagged; these 2751 females deposited 8766 nests (believed to be a complete count). Averaged over the 15-year study period, 12.5% of all nests were left unaltered in situ; 12.9% were left in situ, with tracks camouflaged by beach patrollers; 33.9% were relocated to lower risk zones on the beach; and 25.4% were relocated to beach hatcheries. Poaching, which had once claimed nearly 100% of all eggs laid, averaged 15.5% annually during the study period, demonstrating a clearly declining trend, attributable to the presence of beach patrollers, policies associated with the wildlife refuge, and changing attitudes within proximal communities. A comparison of tag registries indicates an interchange of gravid females among nesting beaches both within Costa Rica and internationally with Panama and Colombia. The interchange reinforces the importance of joint efforts to address primary threats, including beach erosion, egg poaching, direct harvest of adults for meat (especially in Panama), and coastal development. The population is statistically stable but shows a steadily declining trend in the number of nests laid since 2000.

KEY WORDS. – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; marine turtle; population monitoring; conservation; management; protected area; nesting; tagging; hatcheries; Caribbean; Costa Rica

The leatherback sea turtle (Dermochelys coriacea) is protected by the national laws of Costa Rica (Ley de Conservación de Vida Silvestre No. 7317 in force since 1992) and is classified as critically endangered on the IUCN Red List of Threatened Species (Sarti 2000). Also relevant for Costa Rica is the fact that the species is listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which Costa Rica ratified in 1975, prohibiting international trade in parts or products; protected by the Convention on the Conservation of Migratory Species of Wild Animals (or the Bonn Convention), to which both Costa Rica (2007) and Panama (1989), a range state of the Gandoca population, are party; and considered by the Convention on Nature Protection and Wildlife Preservation in the Western hemisphere to be a species for whom protection, "as completely as possible", is of "special urgency and importance". In 2000, after more than 3 decades of precedent (as the Western Hemisphere Convention entered into force in Costa Rica in 1967), Costa Rica ratified the Inter-American Convention for the Protection and Conservation of Sea Turtles (IAC), with a stated objective "to promote the protection, conservation and recovery of sea turtle populations and of the habitats on which they depend . . . ". The national regulatory framework was significantly strengthened in November 2002 with passage by the national legislative assembly of law no. 8325 (Ley de Protección, Conservación y Recuperación de las Poblaciones de Tortugas Marinas), which implements the IAC, designates regulatory agencies, establishes penalties, and so on.

Notwithstanding the various levels of protection conferred on the species by national and international law, leatherbacks are believed to have lost more than 90% of their numbers in recent decades along the Pacific coasts of Central America and Mexico (Eckert and Sarti 1997; Spotila et al. 2000). Declines are attributed primarily to the poaching of eggs and gravid females, as well as the incidental capture of juveniles and adults in gill nets and longlines (Eckert and Sarti 1997; Spotila et al. 2000). Observed declines at some of the hemisphere's most important breeding colonies (e.g., Costa Rica, Mexico), as well as at smaller colonies in Guatemala, El Salvador, and Nicaragua, lent impetus and urgency to the IUCN designation of critically endangered. In contrast, some important nesting colonies outside the Pacific appear to be stable or increasing (Hughes 1996; Chacón 1999; Chevalier and Girondot 2000: Dutton et al. 2000).

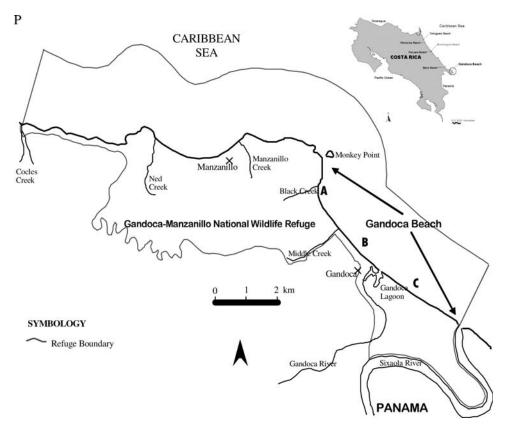


Figure 1. Gandoca Beach, located within the Gandoca-Manzanillo National Wildlife Refuge on the Caribbean coast of Costa Rica.

Nesting is distributed globally from 40°N to 35°S (Eckert 2001), including the Caribbean shores of Costa Rica, where the highest density nesting grounds are located at Gandoca Beach, Pacuare, and Tortuguero (Berry 1987; Troëng et al. 2004). The species also nests in significant numbers in adjacent northeastern Panama (Meylan et al. 1985; Troëng et al. 2004; Ordoñez et al. 2007).

Nesting at Gandoca Beach (Fig. 1), included in the Gandoca-Manzanillo National Wildlife Refuge (legally designated in 1985), has been systematically monitored since 1990. In Gandoca, the most significant threats to leatherbacks are the illegal collection of eggs for human use and the loss of nesting habitat, primarily because of natural cycles of erosion and the obstruction of nesting habitat by driftwood (Chacón 1999). Poaching along the Caribbean coastline has been documented for 2 decades (see Berry 1987), but, with the exception of efforts undertaken within protected areas, little has been done to reduce poaching pressure and to improve the conservation status of the species.

The objectives of the present study were to estimate the number of turtles nesting each year in Gandoca, evaluate the abundance and spatial distribution of nests laid, analyze temporal patterns in the reproductive effort, assess the results of nest conservation actions taken in the Gandoca-Manzanillo National Wildlife Refuge, and formulate policy recommendations for the management and long-term viability of Caribbean leatherback rookies.

METHODS

Study Site. — Gandoca Beach (Playa Gandoca) is located within the Gandoca-Manzanillo National Wildlife Refuge. The beach extends for 8.85 km, from Punta Mona to the mouth of the Sixaola River on the border with Panama (Fig. 1). The northern boundary of the beach coincides with the southern boundary of coral reef formations in the vicinity of Punta Mona (Umaña and Chacón 1994). The high-energy coastline is associated with a narrow continental shelf, where strong prevailing currents flow in a north-south direction. Gandoca Beach is characterized by deep, unobstructed access, a combination of factors known to be favorable to leatherback nesting in many parts of the world (Eckert 1987). The beach erodes and accretes seasonally and is typically littered with natural debris and a wide variety of plastic discards and other urban and agricultural garbage carried by rivers to the ocean, only to be returned to the beach by ocean currents and tides.

Field Protocol. — Gandoca Beach features 7.7 km of nesting habitat; the remaining 1.15 km is characterized by estuaries unsuitable for nesting, because of ocean currents, river mouth erosion, and accumulated debris. Starting in 1990, field work commenced annually during the second week of February and continued through the last week of July. The 7.7 km of nesting habitat was divided into 3 sectors (A = 1950 m, B = 2850 m, C = 2900 m), from north to south, to facilitate data collection (Fig. 1). To

more precisely document the spatial distribution of nesting and, specifically, to identify priority conservation zones, the beach was further segmented by 50-m sequentially numbered location markers.

Each of the 3 beach sectors were covered nightly by two 4-hour patrols (2000–2400 hours, 2400–0400 hours), during which time trained research teams observed and registered nest-related behaviors and outcomes. To ensure that nesting events would not be missed, patrol schedules were established such that no point on the beach was left uncovered for more than 1 hour.

Turtles with no obvious evidence of prior tagging were recorded as neophytes; turtles with tags or obvious evidence of tag scarring were recorded as remigrants. Each female left the beach with 2 metal Monel-style tags fitted between the tail and a rear flipper, following the methodology of Balazs (2000). Starting in 1999, a sample of nesters were also marked with subcutaneous microchip (passive integrated transponder [PIT]) tags in the right shoulder (see Eckert and Beggs 2006).

Body measurements were obtained for each female encountered, following the methodology of Chacón (1999). For purposes of population-level analyses, the reported carapace length (and width) of each female was determined by averaging the measurements recorded during each of her nestings. Also recorded in each case were date and time, beach zone and marker number closest to the nesting attempt, tag number(s), ectobiota and skin injuries, clutch size (yolked and yolkless eggs), nest depth, and nest position relative to the ocean and the nearest marker.

Nests were classified as in situ, unaltered; in situ, with tracks and other field signs obscured by beach patrollers; relocated from high-risk zones to stable beach zones; or relocated to a beach hatchery. All nests laid in high-risk zones (including a radius of 100 m surrounding the mouths of Black Creek, Middle Creek, Don Nati Creek, Gandoca Lagoon, and other small and seasonal creeks) were relocated to hatcheries constructed in sectors A and B (Fig. 1).

Hatcheries. - Fenced hatcheries were constructed above the berm; sites were selected near location markers that exhibited the highest nest density in previous years, with the objective of reducing egg manipulation and transportation. On average, each hatchery was 55 m² in size. Eggs buried in hatcheries were carefully transplanted within 1 hour of their collection from the nest; each egg was counted, and yolkless eggs were placed last (atop the others), mimicking the natural order. Each nest was surrounded on the sand surface by a metal mesh cylinder to discourage predators (e.g., ghost crabs, Ocypode sp.; skunks, Spilogale putorius, Conepatus semistratus; raccoons, Procyon lotor; white-nosed coatis, Nasua narica) and a very fine cloth mesh (less than 1.0 mm) to avoid infestation by saprophagous flies. Artificial nests, whether constructed in the hatchery or on the beach, were dug to the same depth as natural nests (see Boulon 1999).

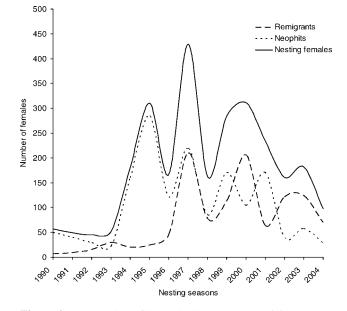


Figure 2. The number of leatherback sea turtles arriving to nest each year (1990–2004) at Gandoca Beach on the Caribbean coast of Costa Rica, showing the estimated ratio of remigrant (previously tagged) to neophyte (untagged) turtles. Nightly research patrols tagged 2751 individual females, representing an estimated 90% of turtles making landfall on the beach during the study period (during which time the beach was patrolled hourly and all crawls were documented).

Hatchery locations were changed every year to reduce the risk of localized sand contamination. Hatcheries were staffed and protected 24 hours a day during the incubation period.

Hatchlings. — Each nest was monitored 4 times daily (0600, 1200, 1800, 2400 hours) for temperature, as well as to collect any visible hatchlings. Temperature was monitored by using Type K thermocouples buried at various depths, depending on the research design. For both hatcheries and in situ nests, the incubation period and emergence success were determined, and a sample of hatchlings were measured and weighed.

RESULTS

Data gathered during 15 annual study periods (15 February to 31 July) between 1990 and 2004 indicated that an average of 181.47 females nested each year, composed of 76.8 remigrants (SD = 63.87, range = 7–210) and 105.7 neophytes (SD = 80.21, range = 22–285) (Fig. 2). Because of the degree of movement by individual females between nesting beaches, both within and among years (Table 1), no attempt was made to define internesting or remigration intervals; that is, the true interval between nesting within a reproductive season or the interval (in years) between reproductive seasons.

An average of 4 leatherbacks nested per night (SD = 4.38, range = 0-42) for the study period, depositing a total of 8766 nests on Gandoca Beach. An average of 583 nests were laid per year (SD = 303.3, range = 226-1135), with an average density of 75.7 nests/km. The number of

Country	Beach	Distance to Gandoca (km) ^a	Location (latitude/longitude)	Turtles observed		
Costa Rica	Tortuguero	117–153	N10°54.039′W83°50.167′	41		
	Parismina	105–119	N10°18.377'W83°21.216'	60		
	Pacuare	83-105	N10°28.081'W83°32.934'	70		
	Matina	74–91	N10°21.913' W83°27.653'	15		
	Black Beach	31–16	N9°69.530'W82°80.405'	46		
Panamá	San San	7.4-8.5	N9°52.912′W82°51.227′	59		
	Changuinola	7.6-23.6	N9°49.392'W82°47.390'	40		
	Soropta	16.6–36	N9°44.711′W82°41.850′	25		
	Bluff	38-50	N9°39.342′W82°23.950′	27		
	Larga	47–58	N9°35.049′ W82°19.526′	15		
	Chiriqui	113-140	N8°89.115′ W81°61.825′	3		
Colombia	Acandí	600-612	N8°50.038'W77°26.630'	5		
	Playona	608–620	N8°45.560′W77°22.270′	2		

Table 1. Documented intraseasonal movement between nesting beaches for leatherback sea turtles nesting at Gandoca Beach, Costa Rica, 1990–2004.

^a Calculated as a range based on a straightline measurement originating from the nearest and farthest point of Gandoca Beach to same reference points at each foreign beach.

nests laid per month ranged from 0 to 408 and peaked during the period 70–90 days from the onset of the nesting season (Fig. 3). The peak corresponded to the months of April and May, which reported 35.2% and 36.1%, respectively, of all nests laid (Table 2). Nest density peaked between markers 15–20, 31–36, 64–76, and 111–116, which was consistent with earlier analyses (Chacón et al. 1996; Chacón 1999). Of the 8766 nests laid, an annual average of 31% (SD = 15.55%) of all nests were deposited on the berm, safely above the high-tide line. In contract, 32% (SD = 16.45%) were sited within the high-tide zone and 37% (SD = 12.10) were sited within the low-tide zone.

Over the course of the 15-year study period, 2751 gravid females, an estimated 90% of turtles making landfall at Gandoca Beach (during which time the beach was patrolled hourly and all crawls were documented), were uniquely tagged with external metal flipper tags; of

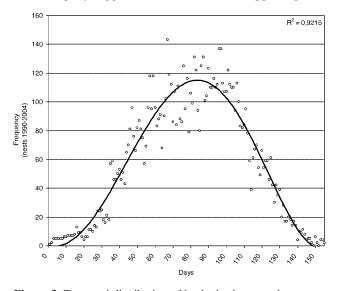


Figure 3. Temporal distribution of leatherback sea turtle nests at Gandoca Beach (1990–2004) on the Caribbean coast of Costa Rica. Day 1 corresponds to 15 February. Peak nesting (days 70–90) corresponds to the last week of April and the first 2 weeks of May.

these, 529 (19.2% of the tagged population) were also given PIT tags. Of the total, 408 females carried tags applied elsewhere in Central and South America (Table 1).

The average curved carapace length (CCL) was 153.2 cm (n = 2751, SD = 7.39 cm), ranged from 135 to 198 cm. The average curved carapace width (CCW) was 112.0 cm (n = 2751, SD = 5.53 cm). Clutch size averaged 113.3 (n = 5260 nests), composed of an average of 81.2 (SD = 17.88) yolked and 32.1 (SD = 14.24), or 28.4%, yolkless eggs. The average diameter of 3250 yolked eggs, randomly selected during reburial in the hatchery, was 53.2 mm (SD = 0.93 mm); the diameter of yolkless eggs ranged from 4 to 50 mm (mean = 31 mm, n = 2221).

A total of 2254 nests (including 184,828 yolked eggs) were placed in hatcheries, representing an average of 25.4% (SD = 10.60%, range = 0%–37%) of the total number of nests laid per annum. On average, 12.5% (SD = 7.8%, range = 0%–25%) of nests laid per annum were left in situ, unaltered; 12.9% (SD = 8.69%, range = 1%–28%) were left in situ, with field signs camouflaged by beach patrollers; 33.9% (SD = 15.61%, range = 5%–56%) were relocated to lower-risk beach zones, because of erosion, river currents, and/ or poaching (Fig. 4). Most nests were lost from high-risk zones near river mouths and also from beach segments most vulnerable to erosion (markers 6–11, 40–61, 67–73, and 80–95).

The average incubation period (defined as the number of days from oviposition to the first hatchling emergence at the surface of the sand) in the hatchery was 59.7 days (SD = 9.70 days, range = 47–74 days), with an average emergence success of 42.6% (SD = 35.14%, range = 0%–100%), producing 79,476 hatchlings. Upon emergence, a sample of 2621 hatchlings averaged 59.6-mm straight-line carapace length (SD = 4.46 mm, range = 54–61 mm) and 46.6 g (SD = 6.12 g, range = 39–52 g). Similarly, a sample of 818 nests left in situ, unaltered at the time of deposition and monitored weekly, had an average emergence success of 41.0% (SD = 25.78%, range = 0%–100%).

Preliminary results of temperature readings taken at regular intervals on a daily basis in the hatchery predicted,

Months	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	SUM	Average	SD	%
January	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0.0
February	1	0	0	2	7	8	7	5	5	7	18	14	7	0	0	81	5.79	5.33	0.8
March	24	4	21	26	68	63	26	164	34	73	169	77	65	52	35	901	61.86	48.46	09.5
April	83	149	114	86	160	408	124	403	168	197	396	150	214	209	99	2960	204.36	113.66	35.2
May	96	87	87	90	219	254	157	273	247	354	350	296	220	266	87	3083	214.00	97.69	36.1
June	82	4	4	43	65	161	69	235	125	147	87	178	105	143	33	1481	103.43	66.31	15.9
July	0	0	0	7	0	38	22	34	13	37	21	19	17	11	6	225	15.64	13.48	2.2
August	0	0	0	0	0	0	0	0	0	5	6	0	1	0	1	13	0.86	1.92	0.1
TOTAL	286	244	226	254	519	932	405	1135	592	820	1047	734	629	681	261	8744	582.93	303.33	

Table 2. Monthly number of nests laid at Gandoca Beach by leatherback sea turtles during the study period (1990–2004), with the average monthly contribution (%) to the annual reproductive effort.

based on a range of published values for western central Atlantic populations, a female bias in nests incubating in March and April, when the mean temperature in the center of the incubating egg mass was 30.4° C (SD = 1.43° C), and a male bias in nests incubating in June and July, when the mean temperature in the center of the incubating egg mass was 28.2° C (SD = 1.37° C). Temperature profile data and its interpretation will be prepared for later publication.

Incidents of poaching declined logarithmically over the course of the study period, as illustrated by a standard curve fit to the data (Fig. 4). The most serious violations occurred proximal to points of public access to the beach.

DISCUSSION

The annual nesting season at Gandoca Beach extends from early February to late July, peaking in April and May (Rueda et al. 1992; Leslie et al. 1996; Chacón 1999; Suarez 2004). During the 15-year study period, 2751 individual females laid 8766 nests. Average clutch frequency could not be accurately estimated, because the annual reproductive effort is geographically dispersed (Table 1). The average nest density (75.7 nests/km) at Gandoca was higher than that reported by Leslie et al. (1996) for Tortuguero National Park (1990: 15 nests/km; 1991: 36.9 nests/km) on the northern Caribbean coast of Costa Rica, as well as higher than that reported by Suarez (2004) for La Playona, Urabá Gulf, Colombia (1998– 1999, 2002–2003: average 69.4 nests/km).

The spatial and temporal distribution of nesting coincides with earlier analyses done in Costa Rica (Gandoca: Chacón et al. 1996; Chacón 1999; Tortuguero: Leslie et al. 1996) and Colombia (Rueda et al. 1992; Suarez 2004). During the study period, nests were roughly equally distributed above (31%) and within (32%) the high-tide zone, and below the low-tide zone (37%). This is a consistent reality in Gandoca (in 1991, e.g., 64% of all nests were laid between the tide lines: Chacón et al. 1996). Eckert (1987) suggests that wide nest dispersal may enhance reproductive success in unpredictable environments; that is, whenever nest survival is not strongly correlated with available environmental information.

The average CCL and CCW (153.5 cm and 112.0 cm, respectively) of actively nesting females were not

dissimilar to results previously reported for Caribbean Costa Rica (e.g., Campbell et al. 1996; Chacón et al. 1996; Chacón 1999) and for other regional colonies (e.g., Hirth and Ogren 1987; Chu 1990; Hall 1990; McDonald et al. 1993; Hilterman and Goverse 2004; Suarez 2004) but are noticeably smaller than gravid leatherbacks nesting in the southern hemisphere (Espiritu Santo, Brazil: 159.8 cm, SD = 10.5 cm, range = 139–182 cm) (Thomé et al. 2007). Leatherbacks nesting on the Pacific coast of Costa Rica are smaller, on average, than those nesting on the Caribbean coast, including those nesting at Gandoca (Reina et al. 2002).

Neither clutch size nor the average diameter of yolked eggs differed appreciably from values reported elsewhere in Caribbean Costa Rica (Campbell et al. 1996; Leslie et al. 1996) or global sites summarized by Miller (1997). The average percentage of yolkless eggs per nest (28.4%) is lower than that reported earlier for the population (31.5%: Chacón et al. 1996) but higher than the 26.2% reported from Tortuguero (Campbell et al. 1996) and quite noticeably higher than the 19.6% reported from the southern hemisphere colonies nesting in Espiritu Santo, Brazil (Thomé et al. 2007). Neither hatchling size nor weight differed appreciably from literature values (e.g., Hirth and Ogren 1987; Miller 1997; Pritchard and Mortimer 1999).

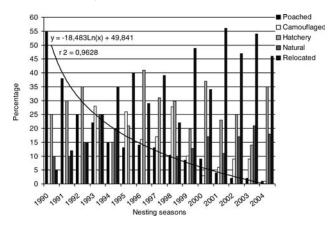


Figure 4. Distribution of nest treatment categories for leatherback sea turtles nesting at Gandoca Beach on the Caribbean coast of Costa Rica. The solid line illustrates a declining trend in the percentage of nests poached over the course of the study period (1990–2004).

Leatherbacks tend to nest in high-energy coastal environments often associated with steep, unobstructed offshore access and chronic cycles of erosion. Nests laid too near the sea are at risk from saltwater inundation, because of the disruption of chemical, gaseous, and thermal conditions optimal for successful embryo development (reviewed by Ackerman 1997). Eggs relocated to hatcheries would have been lost, under natural circumstances, because of the forces of coastal erosion, mainly near the mouths of rivers but also because of the deposition of some one third (37%) of all nests within the low-tide zone. Over the course of the study, 2254 nests (25.7%) were relocated to protected hatcheries after having been laid too near water. Maximizing hatchling production is a key element of the conservation effort at this site, and no effective alternative to the hatchery option has been identified to achieve this goal for otherwise doomed clutches.

The average rate of emergence success did not differ significantly between in situ nests (41.0%) and nests incubated in hatcheries (42.6%). In situ rates of emergence success were low compared with data presented by Hirth and Ogren (1987), Guadamuz (1990), Dutton et al. (1992), and Leslie et al. (1996), but fall within the range (19.8%-54.2%) reported by Bell et al. (2003) for Playa Grande, Costa Rica, between 1990 and 2000. Conversely, results were high compared with those reported by Hilterman and Goverse (2004), who registered a mean hatch rate of 28% in Suriname. Published studies document a wide range of average emergence successes at hatchery sites (for leatherback turtles) throughout the world, ranging, e.g., from 32% to 71.5% over a 19-year period in Malaysia (Siow and Moll 1982; Mortimer 1990). In the wider Caribbean region, hatchery results, including those reported here, generally fall within this range. Reynolds (2000) reported 54.2% emergence success for Playa Grande, on the Pacific coast of Costa Rica.

In the case of both in situ and hatchery incubated nests, 14%–15% of yolked eggs resulted in dead, full-term hatchlings. Reynolds (2000) attributed the premature death of embryos to unacceptably low levels of O₂ and high levels of CO₂ in the nest chamber, and noted that organic matter mixed with the sand could increase CO₂ concentrations and decrease O₂, potentially reducing survival. It is possible that excessive quantities of organic matter deposited by the Sixaola River contribute to a relatively low in situ hatch rate at Gandoca Beach. Erosion cycles and the subsequent loss of preterm nests also reduce overall emergence success.

Nearly 15% (408 of 2751) of the females observed had been previously tagged while nesting outside of Gandoca. All had been tagged elsewhere in Central and South America; there were no observations of turtles tagged in the Eastern Caribbean. Most had been tagged elsewhere along the Caribbean coast of Costa Rica, with some arriving from as far away as Chiriqui Beach, Panama (130 km from Gandoca), and Acandi Beach and Playona, Colombia (600 km from Gandoca). These results support the observations of field workers throughout the region, as well as some quantitative studies (Eckert et al. 1989; Bräutigam and Eckert 2006), that site fidelity in leatherbacks is less focused than in other sea turtle species. Dutton et al. (1999) found virtually no evidence of stock separation, based on maternally inherited mitochondrial deoxyribonucleic acid haplotype frequencies, among the region's major nesting colonies (i.e., French Guiana, Suriname, Caribbean Costa Rica, and Atlantic Florida).

Intraseasonal movement among nesting beaches obscured a definitive assessment of the average internesting interval. Although the calculated modal interval of 8-12 days between nestings by tagged leatherbacks at Gandoca Beach agrees with data presented for other colonies in the region (e.g., National Research Council 1990; Dutton et al. 1992; Boulon et al. 1996; Steyermark et al. 1996; Miller 1997; Chacón 1999; Hilterman and Goverse 2004), it is also the case that 35% (1381 of 3945 documented intervals) exceeded 24 days, suggesting intervening nestings outside the study site. This hypothesis is borne out by records, e.g., in 2004, demonstrating that 25 females bearing tags from Gandoca Beach subsequently nested at Mondonguillo Beach approximately 100 km to the north. The predominance of internesting movement occurs (in both directions) between Gandoca Beach and other beaches, including Playa Negra in Costa Rica and San San, Changuinola, Soropta, Bluff, and Larga beaches in Panama, which are all within 78 km of one another.

Interseasonal remigration was also obscured by the relaxed site fidelity exhibited by the turtles in this population (Table 1). At some Panama beaches, 64% of all foreign-tagged turtles during the 2003 nesting season originated in Gandoca (C. Ordoñez, unpubl. data). And, although we have evidence of long-term tag retention in some individuals (e.g., in 2004, 8% of nesting females carried tags placed in 1994, 23% in 1995, and 11% in 1996), the habit of single tagging (or not tagging at all) by beach patrollers at some nesting beaches at Panama is known to compromise long-term tag retention and, thus, estimates of remigration cycles.

By using estimates published by Boulon et al. (1996) and Miller (1997), indicating an annual clutch frequency of 6.17 or 5.26, respectively, the annual average of 583 nests laid is some 52%–62% of what would be expected if females observed nesting at Gandoca actually laid their full complement of clutches there. Lower than predicted numbers of observed nests reflect localized renesting at neighboring beaches along the coast, both to the north and to the south. Similar complications arise in the evaluation of demographic parameters associated with other mainland nesting colonies in the region, such as in the Guianas (Girondot and Fretey 1996; Reichart et al. 2001; Hilterman and Goverse 2004).

The nesting pattern at Gandoca has high and low years, typical of most sea turtle populations, rendering problematic the determination of a clear trend in the size of the annual breeding cohort. Troëng et al. (2004) concluded that of the 3 "index beaches" on the Caribbean coast of Costa Rica, the most reliable data set for trend analysis is that of Gandoca. Nonparametric regression formulas (Fahrmeir and Lang 2001; Balazs and Chaloupka 2004) produced the most satisfactory results, indicating that the trend at Gandoca is stable (Troëng et al. 2004). Notwithstanding, the number of nests documented in 2004 was less than 25% of the number documented in 2000 and shows a persistent decline in recent years (Fig. 5). Whether this is an actual decline, a reflection of shifting patterns in the spatial distribution of the annual nesting effort, or a natural fluctuation in the breeding cycle of a stable metapopulation cannot be known without greater collaboration in data-sharing among range states and a long-term commitment to the monitoring of beaches known to be used by the "Gandoca population" (Table 1).

Based on 15 years of intensive study, it is clear that the most serious threats facing the nesting colony at Gandoca Beach are the continued (though much reduced) illegal taking of eggs, a problem widespread in Costa Rica (Campbell et al. 1996, Leslie et al. 1996, Troëng et al. 2004); shoreline erosion; garbage and mixed debris transported to the coast by river drainages; and egg loss to domestic and wild predators. Although the poaching of adult females is rare, the long-term threat posed to the population by a persistent loss of eggs to poachers, shoreline erosion, and predators should not be underestimated.

Although significantly reduced since 1990 (Fig. 4), poachers still claim an estimated 1%–3% of all clutches laid each year at Gandoca Beach; this is lower than that documented outside the protected area, indicating that an ongoing research presence, the support and involvement of proximal communities, and increased enforcement activity can result in significant conservation achievements, even in remote rural areas.

Seasonal erosion results from strong coastal drift currents that modify or eliminate beach sectors over the course of the annual nesting season, destroying in excess of 10% of all nests laid in some years. In addition, destruction or modification of the nesting beach as a result of upland deforestation, especially along river drainages, typically results in the deposition of a wide variety of debris and garbage on the beach during the rainy season, blocking access to gravid females and fatally trapping an unknown percentage of emergent hatchlings. Similarly, destruction or modification of the nesting beach because of deposition of logs, as well as plastic, metal, and other types of agricultural and domestic garbage, by the littoral current alters patterns of access, prevent gravid females from finding suitable nesting sites, especially near the mouth of the Sixaola River.

A variety of other anthropogenic factors threaten the population to a lesser extent, including beach-sand extraction for construction purposes, drainage of creeks and wetlands, agricultural runoff and discharge, artificial

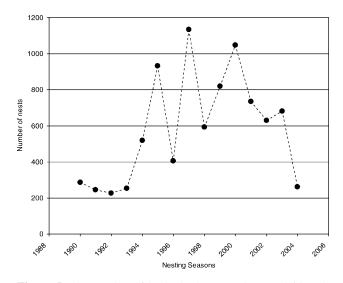


Figure 5. The number of leatherback sea turtle nests laid each year (1990–2004) at Gandoca Beach on the Caribbean coast of Costa Rica.

illumination from torches (flashlights) and bonfires, vehicles occasionally driving on the beach, and plastic products and pesticides originating in agricultural plantations and carried by rivers to the sea and later washed ashore. Beachfront illumination is increasing and may become problematic, not only for nesting and hatching sea turtles (see Witherington and Martin 2000) but also for the success of local tourism businesses that rely on the predictable presence of leatherback turtles near developed areas.

Conservation Recommendations

- Implement the 2006–11 strategic planning document (COMATO 2006), which resulted from stakeholder-led processes involving community organizations, science and conservation staff associated with the sea turtle field project, and Ministry of the Environment and Energy (MINAE) and Wildlife Refuge authorities, which aim to eliminate illegal sales of sea turtle products (mainly associated with species other than leatherbacks, and including meat, eggs, and shell) and ongoing trafficking in eggs to and from Panama, with some sales occurring openly along public bus routes and on main roads leading into major towns;
- Research and develop a comprehensive chapter for the management plan of the Gandoca-Manzanillo National Wildlife Refuge (PROAMBI, 1996) to address the longterm survival requirements of the area's sea turtles, and with special reference to coastal zone development issues;
- Create a working group of local stakeholders, including communities, nongovernmental organizations, and government, to advocate for (and update) the management plan (PROAMBI 1996), with special emphasis on addressing the root causes of illegal exploitation and mitigating threats (e.g., light pollution, sand mining,

waste disposal, uncontrolled public access) associated with development of the coastal zone;

- Strengthen the operational policies that govern physical access to Gandoca Beach and increase control activities during periods of peak tourist visitation (January–July); for example, require that visitors to the beach be accompanied by a licensed local guide between 1800– 0600 hours;
- Identify, manage, and safeguard the primary nesting regions along the beach; at the present time, there has been little attention given to differential management or site-focused intervention at particularly high-risk, highnest density, or high human use segments of the nesting beach;
- Develop educational materials, outreach workshops, and opportunities for direct participation for the people of Gandoca and the communities included in the wildlife refuge's buffer zone, with an aim to increase public awareness of development issues and increase community capacity to manage local sea turtle populations;
- Conduct a comprehensive socioeconomic study with the objective of identifying livelihood alternatives for communities that remain, at some level, dependent upon the consumptive use of the sea turtle resource;
- Assist in the implementation of livelihood alternatives through training, financing, market access, and other necessary actions;
- Maintain (and develop new) strategic alliances with national and international partners to conduct technological research, such as satellite tracking, to better understand extraterritorial movement patterns and identify range states;
- Conduct binational studies, facilitate joint project cooperation, and promote feedback among Central American range states; this should include joint training and personnel exchanges, data sharing (especially of tag returns and annual project reports), standardized field protocols and data forms, jointly developed educational and outreach materials, binational population trend analysis, and collaborative publications; and
- Strengthen Costa Rica's "Leatherback Sea Turtle Alliance" network, led by the national coordinator in Costa Rica for the Wider Caribbean Sea Turtle Conservation Network (WIDECAST), which embraces all projects working toward the conservation of this species in Caribbean Costa Rica; priorities should include a common database; standard field training; and integrated outreach programs, such as those involving recruiting volunteers and soliciting project support.

The importance of transnational cooperation in the conservation and management of migratory resources, such as sea turtles, cannot be overemphasized (for regional reviews, see Fleming 2001 and Bräutigam and Eckert 2006). Basic demographic data, important to management and including clutch frequency, fecundity, interseasonal

reproductive periodicity, and survival rates, cannot be determined with partial data sets. Neither management nor conservation goals can be achieved without the collaboration of range states, especially Panama (in this case), which share the nesting colony. Moreover, there is a need for collaboration among more distant range states, because gravid females visiting the shores of Central America ultimately return, after nesting, to the greater Atlantic metapopulation (Eckert 2006). Tag return data should be shared among wider Caribbean states, as well as with the United States and Canada, to assess the relative importance of foraging sites in the Gulf of Mexico and the northwestern Atlantic (James and Herman 2001; James 2004; Troëng et al. 2004, James et al. 2005a, 2005b), as well as the role of the North Atlantic Oscillation in foraging patterns and reproductive readiness. An inventory of conservation threats and solutions, together with the implementation of coordinated conservation action among range states, will provide the only genuine hope of survival for the leatherbacks of Caribbean Costa Rica.

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LITERATURE CITED

ACKERMAN, R.A. 1997. The nest environment and the embryonic development of sea turtles. In: Lutz, P. and Musick, J. (Eds.), The Biology of Sea Turtles. Boca Raton, FL: CRC Press, pp. 83–106.

- BALAZS, G. 2000. Factores a considerar en el marcado de Tortugas marinas, In: Eckert, K.L., Bjorndal, K.A., Abreu G., F.A., and Donnelly, M.A. (Eds.), Técnicas de Investigación y Manejo Para la Conservación de las Tortugas Marinas. Washington, D.C.: Grupo especialista en Tortugas Marinas UICN/CSE publicación No. 4, pp. 116–125.
- BALAZS, G. AND CHALOUPKA, M. 2004. Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. Biological Conservation 117:491–498.
- BELL, B., SPOTILA, J., PALADINO, F., AND REINA, R. 2003. Low reproductive success of leatherback turtles, *Dermochelys coriacea*, is due to high embryonic mortality. Biological Conservation 115(2003):131–138.
- BERRY, F. 1987. Aerial and ground surveys of *Dermochelys* coriacea nesting in Caribbean Costa Rica, 1987. In: Proceedings of the Second Western Atlantic Turtle Symposium. NOAA Tech. Memo. NMFS-SEFC-226. US Department of Commerce, pp. 305–310.
- BOULON, R., DUTTON, P., AND MCDONALD, D. 1996. Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Island: fifteen years of conservation. Chelonian Conservation and Biology 2:141–147.
- BOULON, R.H. 1999. Reducing threats to eggs and hatchlings: in situ protection. In: Eckert, K.L., Bjorndal, K.A., Abreu G., F.A., and Donnelly, M.A. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. Washington, D.C.: IUCN/SSC Marine Turtle Specialist Group Publication no. 4, pp. 169–174
- BRÄUTIGAM, A. AND ECKERT, K.L. 2006. Turning the Tide: Exploitation, Trade and Management of Marine Turtles in the Lesser Antilles, Central America, Colombia and Venezuela. Cambridge, UK: TRAFFIC International.
- CAMPBELL, C., LAGUEUX, C., AND MORTIMER, J. 1996. Leatherback turtle, *Dermochelys coriacea*, nesting at Tortuguero, Costa Rica, in 1995. Chelonian Conservation and Biology 2: 168–172.
- CHACÓN, D. 1999. Anidación de la tortuga *Dermochelys coriacea* (Testudines: Dermochelyidae) en playa Gandoca, Costa Rica (1990 a 1997). Revista de Biología Tropical 47(1–2):225–236.
- CHACÓN, D., MCLARNEY, W., AMPIE, C., AND VENEGAS, B. 1996. Reproduction and conservation of the leatherback sea turtle *Dermochelys coriacea* (Testudines: Dermochelyidae) on Gandoca, Costa Rica. Revista de Biología Tropical 44:853–860.
- CHEVALIER, J. AND GIRONDOT, M. 2000. Recent population trend for *Dermochelys coriacea* in French Guiana. In: Abreu Grobois, F.A., Briseño-Dueñas, R., Márquez, R., and Sarti, M., L. (Compilers). Proceedings of the 18th International Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-436. U.S. Department of Commerce, pp. 56–57.
- CHU, L. 1990. Observations on the nesting population of leatherback turtles *Dermochelys coriacea* in Trinidad. Caribbean Marine Studies 1:48–53.
- COMATO. 2006. Plan Estratégico para el Comité de Comanejo de las Tortugas Marinas en Playa Gandoca, Talamanca, Limón. Asociación ANAI. Documento elaborado por el Comité de Comanejo de las Tortugas Marinas de Playa Gandoca, con el apoyo financiero de Tropica Verde y Manfred hermsen Foundation. Mimeografiado, 55 pp.
- DUTTON, D.L., DUTTON, P.H., AND BOULON, R. 2000. Recruitment and mortality estimates for female leatherbacks nesting in St Croix, U.S. Virgin Islands. In: Abreu Grobois, F.A., Briseño-Dueñas, R., Márquez, R., and Sarti, M., L. (Compilers). Proceedings of the 18th International Sea Turtle Symposium. NOAA Technical Memorandum NMFS-SEFSC-436. U.S. Department of Commerce, pp. 268–269.

- DUTTON, P., MCDONALD, D., AND BOULON, R. 1992. Tagging and nesting research on leatherbacks sea turtles (*Dermochelys coriacea*) on Sandy Point, St. Croix, U.S. Virgin Island. Annual report to the US Fish and Wildlife Service. Division of Fish and Wildlife, Department of Planning and Natural Resources, U.S. Virgin Islands, 29 pp.
- DUTTON, P.H., BOWEN, B.W., OWENS, D.W., BARRAGÁN, A., AND DAVIS, S.K. 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). Journal of Zoology 248(3): 397–409.
- ECKERT, K.L. 1987. Environmental unpredictability and leatherback sea turtle (*Dermochelys coriacea*) nest loss. Herpetologica 43(3):315–323.
- ECKERT, K.L. 2001. Estado de conservación y distribución de Dermochelys coriacea. In: Eckert, K.L., Bjorndal, K.A., Abreu, G., F.A., and Donnelly, M.A. (Eds.), Conservación de Tortugas Marinas en la Región del Gran Caribe—Un Diálogo para el Manejo Regional Efectivo. Washington, D.C.: WIDECAST, IUCN/SSC Marine Turtle Specialist Group, WWF and UNEP-Caribbean Environment Programme, pp. 25– 33.
- ECKERT, K.L. AND BEGGS, J. 2006. Marine Turtle Tagging: A Manual of Recommended Practices. Wider Caribbean Sea Turtle Conservation Network (WIDECAST) Technical Report No. 2. Revised Edition. Beaufort, North Carolina, 40 pp.
- ECKERT, K.L., ECKERT, S.A., ADAMS, T.W., AND TUCKER, A.D. 1989. Inter-nesting migrations by leatherback sea turtles (*Dermochelys coriacea*) in the West Indies. Herpetologica 45(2):190–194.
- ECKERT, S.A. 2006. High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. Marine Biology. DOI: 10.1007/s00227-006-0262-z
- ECKERT, S.A. AND SARTI, M.L. 1997. Distant fisheries implicated in the loss of the world's largest leatherback nesting population. Marine Turtle Newsletter 78:2–7.
- FAHRMEIR, L. AND LANG, S. 2001. Bayesian inference for generalized additive mixed models based on Markov random field priors. Applied Statistics 50:201–220.
- FLEMING, E. 2001. Swimming Against the Tide: Recent Surveys of Exploitation, Trade, and Management of Marine Turtles in the Northern Caribbean. Washington, D.C.: TRAFFIC North America, 161 pp.
- GIRONDOT, M. AND FRETEY, J. 1996. Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978– 1995. Chelonian Conservation and Biology 2(2):204–208.
- GUADAMUZ, N. 1990. Registro de Anidamiento de *Dermochelys* coriacea (tortuga baula) en Playa Grande de Matapalo, Santa Cruz-Guanacaste. Heredia, Costa Rica: Escuela de Ciencias Biológicas, Universidad Nacional, 60 pp.
- HALL, K. 1990. Hatchling success of leatherback turtle (*Dermochelys coriacea*) clutches in relation to biotic and abiotic factors. In: Richardson, J.I., Richardson, T.H., and Donnelly, M.A. (Compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278. US Department of Commerce, pp. 197–200.
- HILTERMAN, M. AND GOVERSE, E. 2004. Annual Report on the 2003 Leatherback Turtle Research and Monitoring Project in Suriname. WWF-Guianas Forests and Environmental Conservation Project (GFECP). Technical Report of the Netherlands Committee for IUCN (NC-IUCN). Amsterdam, The Netherlands, 21 pp.
- HIRTH, H. AND OGREN, L. 1987. Some aspects of the ecology of the leatherback turtle *Dermochelys coriacea* at Laguna Jalova,

Costa Rica. NOAA-TR-NMFS 56. US Department of Commerce, 14 pp.

- HUGHES, G. 1996. Nesting of the leatherback turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963–1995. Chelonian Conservation and Biology 2:153–158.
- JAMES, M. 2004. Dermochelys coriacea (leatherback sea turtle). Migration and dispersal. Herpetological Review 35(3):264.
- JAMES, M. AND HERMAN, T. 2001. Feeding of *Dermochelys* coriacea on Medusae in the Northwest Atlantic. Chelonian Conservation and Biology 4(1):202–205.
- JAMES, M., OTTENSMEYER, C., AND MYERS, R. 2005a. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. Ecology Letters 8:192–201.
- JAMES, M., ECKERT, S., AND MYERS, R. 2005b. Migratory and reproductive movements of male leatherback turtles (*Der-mochelys coriacea*). Marine Biology 147:845–853.
- LESLIE, A., PENICK, D., SPOTILA, J., AND PALADINO, F. 1996. Leatherback turtle, *Dermochelys coriacea*, nesting and nest success at Tortuguero, Costa Rica, in 1990–1991. Chelonian Conservation and Biology 2:159–168.
- MCDONALD, D., DUTTON, P., AND BOULON, R. 1993. Tagging and nesting research on leatherback sea turtles (*Dermochelys coriacea*) on Sandy Point, St. Croix, U.S. Virgin Islands. US Fish and Wildlife Service, Department of Planning and Natural Resources, 26 pp.
- MEYLAN, A., MEYLAN, P., AND RUIZ, A. 1985. Nesting of *Dermochelys coriacea* in Caribbean Panama. Journal of Herpetology 19(2):293–297.
- MILLER, J. 1997. Reproduction in sea turtles. In: Lutz, P. and Musick, J. (Eds.), The Biology of Sea Turtles. Boca Ratón, FL: CRC Press, pp. 52–81.
- MORTIMER, J. 1990. Marine Turtle Conservation in Malaysia. In: Richardson, T.H., Richardson, J.I., and Donnelly, M. (Compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFC-278, US Department of Commerce, pp. 21–23.
- NATIONAL RESEARCH COUNCIL. 1990. Decline of the Sea Turtles: Causes and Prevention. Washington, D.C.: National Academy of Sciences, 259 pp.
- ORDOÑEZ, C., TROËNG, S., MEYLAN, A., MEYLAN, P., AND RUIZ, A. 2007. Chiriqui Beach, Panama, the most important leatherback nesting beach in Central America. Chelonian Conservation and Biology 6(1):122–126.
- PRITCHARD, P.C.H. AND MORTIMER, J.A. 1999. Taxonomy, External Morphology, and Species Identification,. In: Eckert, K.L., Bjorndal, K.A., Abreu G., F.A., and Donnelly, M.A. (Eds.), Research and Management Techniques for the Conservation of Sea Turtles. Washington, D.C.: IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 21–38
- PROAMBI. 1996. Plan de manejo del Refugio Nacional de Vida Silvestre Gandoca/Manzanillo. Área de Conservación La Amistad Caribe, Sistema Nacional de Áreas de Conservación-MINAE. Fundación para la Investigación (FUNDEVI), Universidad de Costa Rica. San José, Costa Rica, 150 pp.
- REICHART, H., KELLE, L., LAURENT, L., VAN DE LANDE, H.L., ARCHER, R., CHARLES, R., AND LIEVELD, R. 2001. Regional sea turtle conservation program and action plan for the Guianas

(Eckert, K.L. and Fontaine, M. Eds.). World Wildlife Fund— Guianas Forests and Environmental Conservation Project, Paramaribo. WWF Tech. Report GFECP No. 10.

- REINA, R.D., MAYOR, P.A., SPOTILA, J.R., PIEDRA, R., AND PALADINO, F. 2002. Nesting ecology of the leatherback turtle, *Dermochelys coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica: 1988–1989 to 1999–2000. Copeia 2002(3): 653–664.
- REYNOLDS, D. 2000. Emergent success and nest environment of natural and hatchery nests of the leatherback turtle (*Der-mochelys coriacea*) at Playa Gandoca, Costa Rica, 1998–1999. Master's Thesis, Drexel University, Philadelphia, Pennsylvania, 50 pp.
- RUEDA, J.V., ULLOA, G.A., AND MEDRANO, S.A. 1992. Estudio sobre la Biología reproductiva, la ecología y el manejo de la tortuga canal (*Dermochelys coriacea*) en el Golfo de Urabá. In: Instituto Nacional de los Recursos Naturales Renovables y del Ambiente (INDERENA), Bogotá, Colombia, pp. 62–65.
- SARTI M., L. 2000. Dermochelys coriacea. In: IUCN 2003. Cambridge, U.K.: 2003 IUCN Red List of Threatened Species.
- SIOW, K. T. AND MOLL, E.O. 1982. Status and conservation of estuarine and sea turtles in West Malaysian waters. In: Bjorndal, K.A. (Ed.), Biology and Conservation of Sea Turtles. Washington, D.C.: Smithsonian Institute, pp. 339–347.
- SPOTILA, J.R., REINA, R.D., STEYERMARK, A.C., PLOTKIN, P.T., AND PALADINO, F. 2000. Pacific leatherback turtles face extinction. Nature 405:529–530.
- STEYERMARK, A., WILLIAMS, K., SPOTILA, J., PALADINO, F., ROSTAL, D., MORREALE, S., KOBERG, M., AND ARAUZ, R. 1996. Nesting leatherback turtles at Las Baulas National Park, Costa Rica. Chelonian Conservation and Biology 2:173–183.
- SUAREZ, A. 2004. Patrones reproductivos de la anidación de Dermochelys coriacea en la Playona-Acandí, Colombia, en las temporadas 1998–2003. Tesis de grado. Universidad de Antioquia, Facultad de Ciencias Exactas y Naturales, Instituto de Biología, Medellín, 48 pp.
- THOMÉ, J.C.A., BAPTISTOTTE, C., MOREIRA, L.M. DE P., SCALFONI, J.T., ALMEIDA, A.P., RIETH, D.B., AND BARATA, P.C.R. 2007. Nesting biology and conservation of the leatherback sea turtle (*Dermochelys coriacea*) in the State of Espiritu Santo, Brazil, 1988-1999 to 2003-2004. Chelonian Conservation and Biology 6(1):15–27.
- TROËNG, S., CHACÓN, D., AND DICK, B. 2004. Possible decline in leatherback turtle *Dermochelys coriacea* nesting along Caribbean Central America. Oryx 38(4):1–9.
- UMAÑA, R. AND CHACÓN, D. 1994. Asentamiento en estadios postlarvales de la langosta Panulirus argus (Decapoda: Palinuridae), en Limón, Costa Rica. Revista de Biología Tropical 42(3):585–594.
- WITHERINGTON, B.E. AND MARTIN, R.E. 2000. Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches (Revised Edition). Florida Fish and Wildlife Conservation Commission, FMRI. Technical Report TR-2. Tallahassee, Florida, 73 pp.

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