

Nesting Ecology of the Hawksbill Turtle, *Eretmochelys imbricata*, in Guadeloupe, French West Indies from 2000–07

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ABSTRACT.—Hawksbills have been the focus of conservation efforts over several decades and their status in the Caribbean is continuously being evaluated. Surprisingly, it appears that the island of Guadeloupe hosts one of the largest Hawksbill populations in this region, highlighting the importance of making the most recent data available for the purposes of wildlife management. Numbers of nesting females and other biometric data collected over eight nesting seasons are presented as well as a number of biological observations unique to this population. A total of 452 females were tagged, 89 of which were thought to have been previously tagged, and 58 remigrants (turtles tagged in previous seasons) were observed. Four of the remigrants were seen in three different nesting seasons, and one was seen in four. Mean minimum curved carapace length was 87.9 cm, and mean clutch size varied significantly between two study years (2002: 137 ± 26 eggs; 2004: 159 ± 29 eggs). One turtle laid a clutch of 276 eggs, the largest ever recorded for a Hawksbill. The initial estimate of the nesting population in Guadeloupe is encouraging and perhaps is a sign of increasing numbers in the wider Caribbean region. This information is important when considering the status of this endangered species, and these data need to be easily accessible to the conservation community.

The Hawksbill Turtle (*Eretmochelys imbricata*) is a circumtropically distributed species, often seen in the waters of the Caribbean and tropical western Atlantic (Witzell, 1983). Historically, there has been a high demand for its richly patterned scutes used to make tortoiseshell products, resulting in large population declines through intensive harvesting (Groombridge and Luxmoore, 1989). In 1975, it was listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) thus prohibiting international trade. In 1996, the Hawksbill's status on the World Conservation Union's (IUCN) Red List of Threatened Animals was listed as Critically Endangered (Baillie and Groombridge, 1996). This listing was subsequently challenged but was upheld (Red List Standards and Petitions Subcommittee, 2001; Mrosovsky, 2004), and a justification of the Hawksbill's status was provided by Meylan and Donnelly (1999). This justification rested, in part, on data from a month-long study of Hawksbills, which was based on interviews with local fishers outside of the nesting season (December 1978) in Guadeloupe, French West Indies (Meylan, 1983). Although this study is the most often cited reference for the status of the Hawksbill in Guadeloupe, it provides no information about

the number of nests or the number of females returning to the area each year (Meylan, 1999). Overall, the listing of the Hawksbill relied too much on outdated or grey literature and personal communications, documentation of which was often unavailable or difficult to access (Mrosovsky, 1997). Although this is not meant as a criticism of Meylan (1999) per se, because the most current information available was used in the analysis, it highlights the need for researchers to make their data widely available in peer-reviewed journals. And although it is true that Guadeloupe represented only one of 35 geopolitical units analyzed in the Caribbean (Meylan 1999), the situation outlined above is likely occurring in many other areas.

Here we provide new and updated information on the Guadeloupe Hawksbill population, thus improving general knowledge about this nesting site. We present nesting numbers and other biometric data collected over eight nesting seasons (2000–07) for the most important Hawksbill rookery in Guadeloupe. Although monitoring has mainly been undertaken by local volunteers and students, there is a desire to establish a more permanent infrastructure in the area. In 1998, a local nongovernmental organization (AEVA) developed a marine turtle conservation program for Guadeloupe, subsequently handing these duties over to another organization called Kap'Natirel, who work in conjunction with the largely volunteer-based

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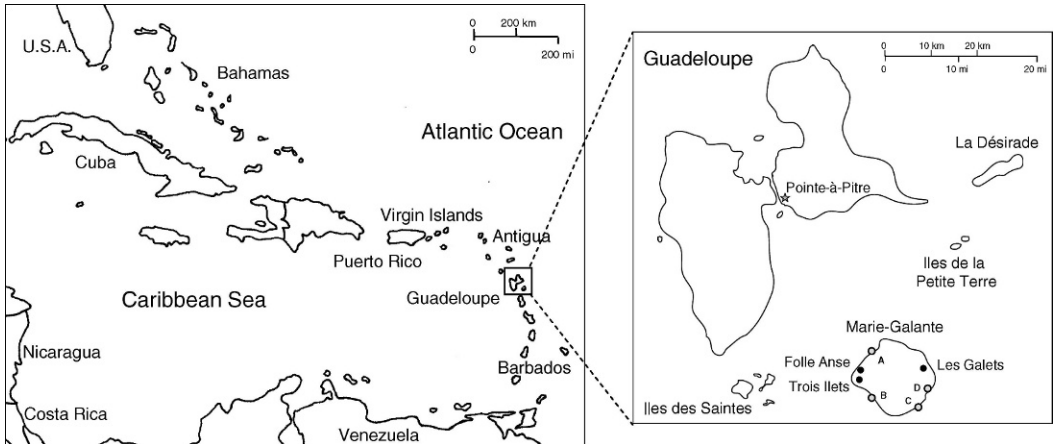


FIG. 1. Left panel: map of the Caribbean; some of the localities mentioned in the text are indicated. Right panel: map of Guadeloupe; Trois Ilets, Folle Anse and Les Galets beaches are highlighted. Other beaches indicated are A = Moustique, B = Anse Ballet, C = Petite Anse and D = Feuillère.

“Guadeloupe Sea Turtle Network.” Despite a perennial lack of funds, the Ministry of the Environment (DIREN) hopes that this group will be more successful in its conservation endeavors. This paper is the result of a collaborative effort on the part of both experts and local residents in monitoring the nesting activities of this turtle population.

MATERIALS AND METHODS

Study Site.—The majority of the work was conducted on Trois Ilets and Folle Anse beaches, Guadeloupe, French West Indies (Fig. 1). The beaches are located between the towns of Grand-Bourg and Saint-Louis on the western coast of Marie-Galante, an island 40 km southeast of the main island of Guadeloupe (Fig. 1). Folle Anse is 1.3 km in length, and the beach ranges from 1–15 m in width. Trois Ilets, located approximately 200 m south of Folle Anse, is 2 km in length, and beach width varies between 1 and 9 m. Both beaches are backed by a coastal woodland forest, except for some open areas toward the southern end of Trois Ilets, where sheds have been installed for public use. The forest is composed largely of sea grape (*Coccoloba uvifera*), catalpa (*Catalpa* spp.), and manchineel (*Hippomane mancinella*). The area between the beaches contains a warehouse and is lit by a floodlight, but turtles rarely nest on the adjacent sand, probably because of the lack of trees and the presence of a rocky wall. The light itself does not deter females from exiting the water at this location (pers. obs.), but it is possible that it exerts some negative effect on nesting. Excluding the hurricane season, which extends from July to October, tidal

variations along the beach are negligible (< 0.3 m). Because of the proximity of the two beaches and to the fact that turtles frequently move between them, Trois Ilets and Folle Anse are simply considered one beach. They are bounded by the town of St-Louis to the north and by forest and a sugar refinery to the south. Since 2005, erosion has become more marked on the southern end and a 1-m high sand barrier now exists over a 250-m section of beach.

There are many other beaches on Marie-Galante where Hawksbills also nest (Fig. 1). No organized patrols have been set up, however, and the data that have been collected there are entirely the result of opportunistic observations.

Nesting Surveys.—The bulk of the nesting surveys have been done on Trois Ilets (and to a lesser extent Folle Anse) because it appears to host a regionally important nesting population and because a large percentage of the volunteers are local residents. Surveys were taken over the following time periods.

2000 (16 June to 5 September): A partial survey (i.e., not every night) of Trois Ilets was undertaken by a group of students and local volunteers.

2001 (7 July to 19 September): A more intensive survey was undertaken on Trois Ilets by the same group and one of the authors (ED).

2002 (22 May to 11 September): The most comprehensive nesting survey comprising the authors and at least three other people on the beach every night from 2000–0400 h was conducted. Folle Anse was patrolled from 25 June to 10 September from 2000–2400 h. Morning track counts were also done to identify nests that were laid after the patrolling had stopped.

2003 (7 May to 9 September): Occasional surveying was conducted, mainly by residents of Marie-Galante from 2000 h until 2300 h on Trois Ilets. The authors were present for three weeks in June and again for three weeks in August.

2004 (1 May to 10 September): Occasional surveying was conducted, mainly by residents of Marie-Galante from 2000 h until 2300 h on Trois Ilets. From 2 June to 10 September, one of the authors (SJK) patrolled the area with at least one other person from 2000 h until 0300 h. Folle Anse was surveyed more sporadically throughout the season. Hurricanes were particularly devastating in 2004 when Ivan (7 September) and Jeanne (14 September) made the beach inaccessible at night and effectively ended the patrols.

2005 (10 April to 25 August): A new tagging protocol was implemented where intensive surveying was done during two three-week periods around peak nesting. In this case, one of the authors (ED), local volunteers, and Kap'Natirel members patrolled Trois Ilets from 2000 h until 0600 h between 10 and 30 June and between 5 and 25 August. Morning track counts were done on Folle Anse during these periods. Outside of these dates, regular patrolling was conducted, mainly by residents of Marie-Galante from 2000 h until 2300 h on Trois Ilets.

2006 (7 April to 24 August): Intensive surveying was conducted between 10 and 28 June and 8 and 24 August. One of the authors (ED), local volunteers, and Kap'Natirel members patrolled Trois Ilets between 2000 h and 0600 h and did morning track counts on Folle Anse. Outside of these dates, regular patrolling was conducted, mainly by residents of Marie-Galante from 2000 h until 2300 h on Trois Ilets.

2007 (20 April to 14 October): Survey protocol was initially similar to the 2005 and 2006 nesting seasons; however substantial beach erosion prevented effective nightly patrols. One of the authors (ED), local volunteers, and Kap'Natirel members patrolled the beach when possible at night and did semiregular morning track counts on both Trois Ilets and Folle Anse.

During the nesting seasons, individual turtles were tagged with monel 1005-681 (National Band and Tag Co., Newport, KY, NBTC) through the first, most proximal scale on the trailing edge of each front flipper. Because of tag shortages in 2002, some females were tagged with smaller monel 1005-4 NBTC, placed between the two proximal scales of each front flipper. Tagging and data collection were done after laying had begun, because disturbances prior to this will often cause a female to abort nesting.

Because of the high incidence of tag loss (see Results), inconel 1005-681C NTBC tags replaced the monel brand in 2005. They were placed at the same location on the front flippers.

Data Collected.—For each female, the following data were collected: (1) position along the beach: in 2002 and 2004–07, numbered markers were placed parallel to the shoreline at 20-m intervals along the patrolled area; (2) zone of the beach: in 2002 and 2004–07 each nest was categorized as being in the forest (completely surrounded by trees), forest border (near the forest but not completely surrounded), low-lying vegetation (presence of grass or beach creepers), or open sand; (3) size of turtle: minimum over-the-curve carapace length (CCLmin) was measured along the midline from the anterior point of the nuchal scute to the posterior notch between the supracaudals; (4) date and time of nesting; and (5) tag numbers and evidence of previous tagging (e.g., holes, scars).

Nesting was considered to have taken place if oviposition was seen and was inferred if the interval between two nesting events was greater than 20 days. The interesting interval for Hawksbills is usually between 10 and 19 days (Bjorndal et al., 1985; Pilcher, 1999). The observed interesting interval (OII) was calculated as the number of days between observed nesting events. Intervals greater than 20 days were either excluded or divided by two or more depending upon the length of the interval, with the assumption that the female nested unobserved during that time.

Observed clutch frequency (OCF) was calculated as the number of observed clutches for an individual female throughout the season. This measure is dependent upon survey intensity and, therefore, represents a minimum estimate of actual nesting activity. A more realistic assessment of nesting, the estimated clutch frequency (ECF) was calculated as $ECF = 1 + (\text{number of days between the first and last nests of a female} / \text{median interesting interval})$ (Reina et al., 2002).

Mean remigration interval, the time between successive nesting seasons for an individual turtle after she has been tagged, was calculated as the number of years between nesting seasons / number of remigrant turtles (Miller, 1997). If a turtle was observed nesting in more than two seasons, a mean individual remigration interval was calculated first and then used in the population estimate.

Clutch sizes were calculated in 2002 and 2004 by excavating the nests after emergence and counting the number of hatched (only the eggshell remained) and unhatched (including pipped) eggs. Hatching success was defined as

TABLE 1. Number of tagged turtles, remigrants, confirmed and unconfirmed clutches, and minimum curved carapace length (CCLmin) of nesting Hawksbills on Trois Ilets and Folle Anse, Guadeloupe from 2000–07.

	New turtles (tagged without scars)	Retagged turtles (already had scars)	Remigrants*	TOTAL All turtles seen in a season	Confirmed clutches	Unconfirmed clutches	CCLmin (N of measured turtles ⁶)
2000	16	—	—	16	27	—	86.3 ± 3.8 (15)
2001	35	—	—	35	61	—	88.6 ± 4.0 (32)
2002	73	4	2	79	214	90	88.3 ± 4.4 (69)
2003	34	—	6	41	87	—	88.9 ± 3.9 (28)
2004	43	20	17	81	208	—	87.3 ± 4.3 (40)
2005	49	35	10	94	155	105	88.3 ± 4.2 (45)
2006	59	21	11	91	162	106	87.1 ± 3.9 (54)
2007	30	9	18	57	108	151	87.5 ± 5.1 (27)

* Includes turtles seen in multiple nesting seasons.

⁶ Remigrants and turtles with scars are excluded.

the number of hatched eggs divided by the total number of eggs (Miller, 1999). Emergence success was defined as the number of hatched eggs minus the number of hatchlings remaining in the nest divided by the total number of eggs.

Statistical Analyses.—To test for differences in variables among years, data were analyzed using a one-factor ANOVA (Sokal and Rohlf, 1981). Regression analysis was used to test for relationships between size of turtle and clutch size. A two-tailed unpaired t-test was used to test for differences in clutch size between 2002 and 2004. Analyses were done using GraphPad Prism version 3.00 (GraphPad Software, 1999). Values are expressed as means ± SD.

RESULTS

Nesting Activity and Number of Nesting Females.—In general, the number of females observed on Trois Ilets and Folle Anse increased from 2000 to 2007, but this varied predictably with respect to survey intensity (see Materials and Methods). Sixteen turtles were tagged in 2000; 35 turtles were tagged in 2001; 77 turtles were tagged and two remigrants observed in 2002; 35 turtles were tagged and six remigrants observed in 2003; 63 turtles were tagged and 17 remigrants observed in 2004; 84 turtles were tagged and 10 remigrants observed in 2005; 80 turtles were tagged and 11 remigrants were observed in 2006; and 39 turtles were tagged

and 18 remigrants observed in 2007. The number of nests observed during nightly patrols and inferred from morning track counts ranged between 200 and 350 (Table 1).

Unfortunately tag loss was a serious problem, particularly in the early stages of the program. In addition to newly tagged turtles, four turtles tagged in 2002, 20 tagged in 2004, 35 tagged in 2005, 21 tagged in 2006, and nine tagged in 2007 already had holes or scars on their front flippers, representing 5.0%, 30.8%, 41.7%, 26.3%, and 23.7% of those seasons' tagged females, respectively. Fortunately, this number appears to be decreasing, and it is hoped that the continued use of iconel brand tags will improve tag retention.

Additional females were tagged around the island between 2000 and 2007 (Table 2). Interestingly, 14 new females were tagged on Moustique beach in 2007. This beach, located north of Folle Anse, may be a promising new nesting site and warrants increased beach coverage in future seasons. As of 2007, 363 new turtles have been tagged, 58 different remigrants have been observed, and 89 turtles that may have been previously tagged were tagged again.

Temporal and Spatial Distribution of Nesting.—Although nesting surveys were not undertaken year round nor were complete surveys conducted throughout all nesting seasons, data from 2000 to 2004 suggest that the majority of

TABLE 2. Number of Hawksbills tagged on other beaches around Marie-Galante, Guadeloupe.

	2000	2001	2002	2003	2004	2005	2006	2007
Moustique								14
Anse ballet						1		
Petite Anse			2			1		
Feuillère					1	1		
Les Galets	1					1		3

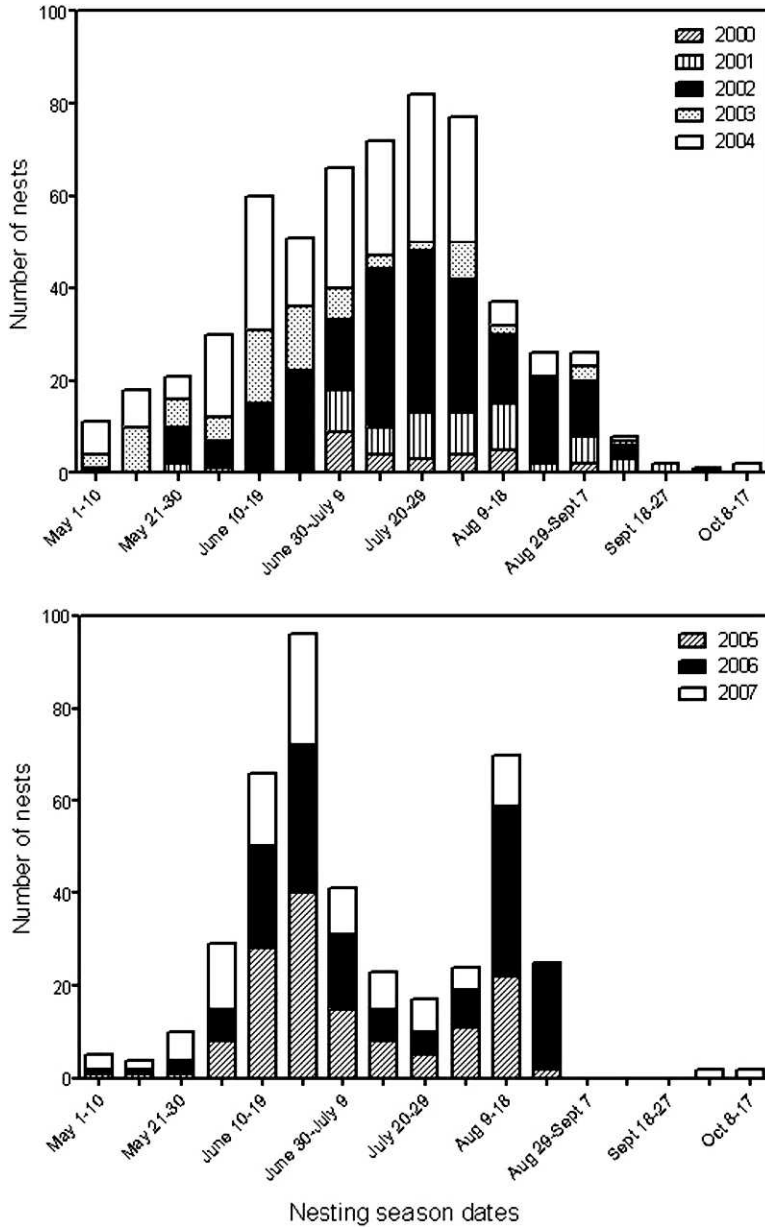


FIG. 2. Frequency distribution of observed Hawksbill nesting on Trois Ilets and Folle Anse for (A) the 2000 to 2004 nesting seasons ($N = 590$ nests) and (B) the 2005 to 2007 seasons ($N = 414$ nests).

females ($N = 590$ nests) nest between May and September (Fig. 2A), with emphasis in July (37.3%, $N = 220$), June (23.9%, $N = 141$), and August (23.7%, $N = 140$). Based on these data, a new survey protocol was established in 2005, whereby intensive beach patrolling is conducted before and after peak nesting. As a result, more nests were seen in June and August during the subsequent nesting seasons (Fig. 2B).

Hawksbills mainly nest in areas with at least some vegetation, and only 39 of 651 observed nests (6.0%) were laid in the open sand. The remainder of the nests were placed in relatively equal proportions in the other three beach zones (low-lying vegetation: 31.8%, $N = 207$; forest border: 36.6%, $N = 238$ and forest: 25.6%, $N = 167$). Nest placement among the beach sections was generally lower on Folle Anse (likely a function of survey intensity) and in particular

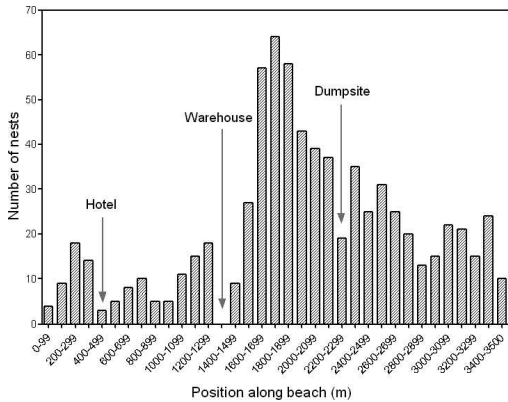


FIG. 3. Distribution of nests along the beach in 2002 and 2004–2007 ($N = 734$ nests). Folle Anse comprises 0–1,300 m and Trois Ilets extends from 1,500–3,500 m running in a north–south direction. The location of the warehouse, the open air dumpsite and the hotel are indicated. The beaches are bounded by the town of St. Louis to the north and by forest and a sugar refinery to the south.

on the areas adjacent to a hotel. On Trois Ilets there was decreased nesting in the center near an open air dumpsite located behind the littoral forest and to the south where the beach trails off into heavily treed areas (Fig. 3).

Carapace and Clutch Measurements.—Carapace measurements were obtained for 91.4% of all newly tagged females over the eight seasons. Mean CCLmin was 87.9 ± 4.2 cm (range: 74–99 cm, $N = 310$). There were no significant differences in CCLmin among the nesting seasons (ANOVA: $F_{7,302} = 1.18$, $P = 0.8$; Table 1).

The observed and estimated clutch frequencies were relatively low in all nesting seasons (mean OCF = 1.7 ± 0.3 and mean ECF = 2.0 ± 0.4 , $N = 8$ seasons). During the most comprehensive survey year (2002), OCF and ECF were the highest at 2.3 and 2.7 clutches, respectively. This variable is related to survey intensity and even during the most intensively monitored season, Folle Anse beach was only patrolled until midnight starting on 25 June. Therefore, the high proportion of one-time nesters may be a sign of turtles whose subsequent (or previous) nests were not observed. As a preliminary estimate, three clutches/turtle should be considered the minimum number of nests for this rookery. A more robust value will emerge when more rigorous surveys are undertaken.

Mean clutch size in 2004 (159 ± 29 eggs; range: 113–276, $N = 64$ nests) was significantly larger (t -test: $t_{149} = 4.78$, $P < 0.0001$) than mean clutch size in 2002 (137 ± 26 eggs; range: 65–184, $N = 86$ nests). To address the possibility that eggshell counts postemergence were not accu-

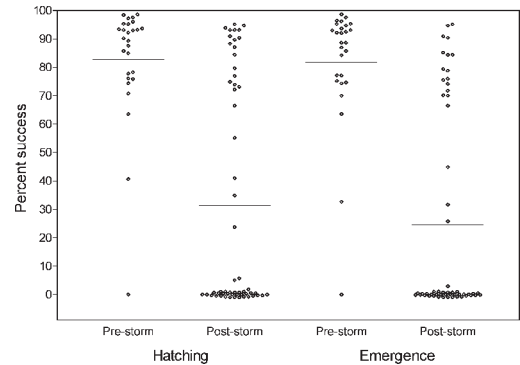


FIG. 4. Hatching and emergence success for nests excavated prior to 7 September (prestorm; $N = 27$ nests) and after 17 September (poststorm; $N = 57$ nests) on Trois Ilets in 2004. Dots represent individual nests and horizontal lines represent mean values. The large majority of failed clutches were composed of late-stage embryos.

rate measures of clutch size, five nests were excavated within 12 h of laying in 2002, and the eggs were counted and reburied; and then that number was compared with the estimate obtained by counting eggshells following emergence. The eggshell based estimates were a mean of 2.6 ± 1.5 eggs different from the initial count, suggesting that methodology was not responsible for the observed difference. There was also a significant positive relationship between mean clutch size and CCLmin (linear regression: $R^2 = 0.12$, $P < 0.0001$, $N = 78$ turtles and 144 nests) for 2002 and 2004 combined.

Mean hatching and emergence success were high in 2002 ($85.6 \pm 13.4\%$, and $81.9 \pm 17.5\%$, respectively, $N = 86$ nests). In 2004, hatching and emergence success were high for nests that hatched prior to the storm of 7 September ($82.4 \pm 21.2\%$ and $81.8 \pm 21.5\%$, respectively, $N = 27$ nests). For nests that hatched after the storm ($N = 57$), both hatching ($30.2 \pm 39.8\%$) and emergence ($24.4 \pm 36.5\%$) success dropped precipitously because a large number of clutches were inundated or washed away by the storms (Fig. 4)

Interesting and Remigration Intervals.—The median of the observed interesting interval (OII) was 15 days ($N = 87$) with smaller peaks around 30 ($N = 13$) and 44 ($N = 6$) days, probably reflecting unobserved nesting. When values larger than 20 days were excluded, mean OII for 2000–07 was 14.6 ± 1.2 days (range: 11–18, $N = 250$). When values larger than 20 days were included after being divided either by 2, by 3 when values > 39 days, by 4 when values > 52 days, or by 5 when values > 70 days, mean OII was 14.8 ± 1.3 days (range: 10–19, $N = 342$).

A total of 58 tagged remigrants were observed as of October 2007. Four of these females were seen in three different seasons within the eight-year period and one turtle was seen in four different years. This individual is particularly interesting because she twice nested in consecutive seasons (2003–04 and 2006–07). Four other remigrants were also observed nesting in successive seasons. At this early stage, remigration interval for this population is 2.24 ± 0.47 years, which is within the range of other published estimates (Mortimer and Bresson, 1999; Richardson et al., 1999). An additional 89 turtles showed scars indicative of previous tags, but were not able to be identified and therefore not included in the calculation.

Nesting Beach Fidelity.—There is sporadic nesting on almost all the beaches along the coast of Marie-Galante, but the majority of Hawksbills nest on Trois Ilets and Folle Anse. In 2002, most turtles appeared to lay all of their clutches on the same beach within a nesting season, but 11 females were seen nesting on both Trois Ilets and Folle Anse. However, because the beaches are so close, they are often considered as one. More interestingly, two females were observed nesting on both Trois Ilets and Les Galets, a beach frequented primarily by Green Turtles. Les Galets is located on the eastern side of Marie-Galante, almost directly across from Trois Ilets (Fig. 1).

In December 2004, a dead Hawksbill washed ashore on Marie-Galante with tags from Barbados. She had been tagged on the west coast of the island on 27 June 2003 by the Barbados Sea Turtle Project (J. Horrocks, pers. comm.). In April 2005, a turtle was observed nesting on Trois Ilets that had originally been tagged on 3 August 2001 in the waters off Monito Island, Puerto Rico (C. Diez, pers. comm.). She was seen again nesting on Trois Ilets in June 2007. Two turtles tagged in Guadeloupe were also fished and killed in the waters off Nicaragua; one in 2003 and one in 2006.

DISCUSSION

It is impossible to overemphasize the importance of publishing updated survey numbers for endangered marine turtles, indeed for endangered species in general. Even in the early stages of monitoring, it appears that Guadeloupe, with a minimum nesting population of approximately 200 females on Trois Ilets and Folle Anse, hosts one of the largest Hawksbill nesting populations in the Caribbean after Mexico, Cuba, Puerto Rico, and Barbados (Garduño-Andrade et al., 1999; Moncada et al., 1999; Diez and van Dam, 2001; Beggs et al. 2007). Moreover, these numbers do not include

turtles nesting on the rest of the Guadeloupean archipelago and on the smaller islands of Saint-Martin and Saint-Barthélemy, indicating that data from Guadeloupe are critical for developing a more robust demographic picture of Caribbean Hawksbills.

Females were larger (mean CCL_{min} = 87.9 cm) than their counterparts from the Pacific (e.g., Malaysia: 82.3 cm [Chan and Liew, 1999]; Australia: 81.6 cm [Dobbs et al., 1999]) and Indian Oceans (e.g., Seychelles: 85.0 cm* [Hitchins et al., 2004]; Oman: 76.8 cm* [Ross, 1981]; Saudi Arabia: 71.2 cm [Pilcher, 1999]). Size seems to vary less among Caribbean populations (Barbados: 89.6 cm [J. Horrocks, pers. comm.]; Costa Rica: 88.8 cm* [Bjorndal et al., 1985]; U.S. Virgin Islands: 87.6 cm [Hillis, 1990]), with the notable exceptions of Brazil (97.4 cm [Marcovaldi et al., 1999]) and Mexico (99.4 cm* [Garduño-Andrade, 1999]; * = conversion from straight carapace length measures to curved carapace length measures following van Dam and Diez, 1998). The correlation between carapace length and clutch size has been found in other Hawksbill studies (Limpus et al., 1983; Bjorndal et al., 1985; Hitchins et al., 2004) but only appears to account for a small proportion of the explained variance here (12% in this study). In general, biometric data on nesting females in Guadeloupe are similar to those for other Caribbean regions, but there are some observations that appear unusual, particularly clutch size and remigration interval.

There was a significant (22-egg) difference between mean clutch sizes in 2002 and 2004. Although variation is expected from season to season, it is not usually significant (Hoyle and Richardson, 1993; Marcovaldi et al., 1999; Moncada et al., 1999). Throughout the 2004 season, 14 clutches were excavated and the eggs counted the morning after they were deposited. The mean of this sample was 173 ± 24 eggs, which suggests that clutches were, in general, especially large that year. In fact, one clutch contained 276 eggs, 12 eggs more than the clutch of 264 from Seychelles previously reported as being the largest worldwide (Hitchins et al., 2004). Additionally, mean clutch size of females observed nesting in 2002 and in 2004 was significantly larger in 2004 (2002: 140 ± 15 eggs and 2004: 159 ± 13 eggs; Kamel and Mrosovsky, 2006a). Why females produced many more eggs during that season is entirely up for debate; perhaps better foraging opportunities led to this increased reproductive output.

Unfortunately, the 2004 nesting season also permitted a quantitative assessment of the impact hurricanes can have on clutch survivorship. In the absence of disturbances from such

storms, hatching and emergence success are generally high (approximately 80% in both years); something that is seen throughout the Caribbean (Barbados: $89.5 \pm 19.8\%$ [Horrocks and Scott, 1991]; U.S. Virgin Islands: 80.9% [Hillis and Mackay, 1989]; Antigua: 72.6% [McIntosh et al., 2003]; Mona Island: 78.1% [Diez et al., 1996]). However, storms can greatly reduce clutch survivorship (approximately 25% in this study) because Hawksbills, like other sea turtle species, are sensitive to inundation (Bustard and Greenham, 1968; McGehee, 1990). Interestingly, although not quantified, sensitivity to inundation appears to vary across developmental stages (S. Kamel, pers. obs.). Clutches laid shortly before the storms occurred had hatch and emergence rates similar to prestorm nests; however, clutches composed of late-stage embryos did not survive the inundations (Fig. 4).

Three turtles returned to nest in successive seasons, an observation that is uncommon in this species (but see Pilcher, 1999). In the Seychelles, a one-year remigration interval was observed for three of 203 Hawksbills over 25 years; in Mexico, it was observed for three of 151 females over an eight-year period (Mortimer and Bresson, 1999; Garduño-Andrade, 1999). In Guadeloupe, five annual nesters were observed over eight nesting seasons perhaps indicating that these turtles forage close to their nesting grounds.

If this is indeed the case, we would expect to find turtles tagged on Marie-Galante foraging in the waters around the archipelago in the coming years.

Evidence is also accumulating that these Hawksbills travel long distances between foraging and nesting grounds, as the tag returns from Nicaragua (about 2,500 km away) demonstrate. Additionally, the Hawksbill tagged in Puerto Rican waters and seen nesting on Trois Îlets lends support to a recent study that used mtDNA control region sequences (LeRoux et al., 2007) to estimate that Guadeloupe's stock contribution to Puerto Rico's foraging grounds was $22.0 \pm 19.6\%$. Because Hawksbills are thought to exhibit strong fidelity to natal beaches (Bass et al., 1996; Richardson et al., 1999), it appears that this turtle originated from Guadeloupe, returning there to nest while foraging near Monito Island (some 500 km away). The presence of the Hawksbill from Barbados is somewhat problematic because LeRoux et al. (2007) reported that haplotype frequencies from Guadeloupe turtles were significantly different from those in Barbados and Antigua. mtDNA reconstructs female dispersal patterns, so a significant difference between two areas implies that there is limited,

if any, interchange. LeRoux et al.'s (2007) study is intriguing because the authors found no significant differences between Guadeloupe females and populations from Belize and the U.S. Virgin Islands, both of which are further away from Guadeloupe than are Barbados and Antigua. It is well known, though, that mitochondrial genes do not all evolve at the same rate. Thus, different gene trees may produce dissimilar phylogenetic patterns for the same group, which is why researchers eventually incorporate information from numerous mitochondrial and nuclear genes. It is possible that further analyses will change the hypothesis of matrilinear relatedness currently posited by the control region gene tree and undo the paradox. It is also possible that additional data will support the current hypothesis, in which case we will have to search further for explanations of migratory patterns in these turtles.

In terms of the threats facing this population, poaching is declining as a result of increased beach patrols. Eggs are not highly sought after although the turtles are still killed for their meat. It appears that in Guadeloupe, incidental capture in fishing gear is a major mortality source with 156 Hawksbills (including juveniles, subadults and adults) washing up dead since 2004 (Delcroix, 2008). The current sea turtle conservation program hopes to implement measures to reduce this turtle by-catch. Deforestation along coastal areas is another problem in Guadeloupe. Most Hawksbills nest in vegetated areas and it has been shown that temperatures in the forest at Trois Îlets are in the male-producing range (Kamel and Mrosovsky, 2006b). Removal of this forest could have implications for the population sex ratio and preservation of this habitat is being strongly advocated. Although long-term monitoring is necessary to accurately assess trends in nesting numbers, initial observations of Hawksbills nesting on Marie-Galante are encouraging and are hopefully a sign of increasing numbers in the wider Caribbean region.

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