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Nesting and Nest Success of the Leatherback Turtle (*Dermochelys coriacea*) in Suriname, 1999–2005

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ABSTRACT. – **Suriname beaches support a major nesting colony of leatherback turtles. During the 1999–2005 nesting seasons, we collected data on nesting ecology and identified individual turtles that nested at Babunsanti (Galibi Nature Reserve), Samsambo, Kolukumbo, and Matapica. We observed 8462 leatherback females, 6933 of which we PIT-tagged. The remaining 1529 females carried PIT tags of a non-Surinamese origin. Because complete coverage of all nesting beaches was not possible over the study period, estimations of minimum annual nesting colony size were made, which ranged from 1545 to 5500 females in Suriname alone. Of the 7394 turtles observed during 1999–2004, 14.8% were seen renesting by 2005. Annual mean internesting period ranged between 9.4 ± 1.0 to 9.6 ± 1.0 days. Annual mean observed clutch frequency was between 1.6 ± 1.0 to 3.1 ± 1.4 and annual minimum estimated clutch frequency between 4.1 ± 1.6 to 4.9 ± 1.8 clutches. Annual mean standard curved carapace length ranged from 154.1 ± 6.7 to 155.6 ± 6.7 cm, and annual mean clutch size ranged from 80.8 ± 18.3 to 88.2 ± 19.5 yolked eggs. Annual average hatch success (including nests with zero hatching) ranged from 10.6% ± 16.4 to 25.8% ± 24.4 at Babunsanti, and from 52.7% ± 29.7 to 56.0% ± 30.8 at Matapica. Remigrants and non-Surinamese turtles were, on average, larger than new females, and remigrants had a higher clutch frequency. In 6 years, the annual proportion of newly tagged females decreased from 89.9% to 40.5% and that of remigrants increased from 0% to 45.6%. However, the annual proportion of turtles with a non-Surinamese PIT tag (10.1% to 17.6%) was relatively stable. Combined with the moderate frequency of intra- and interseasonal nesting exchange between regional beaches, this indicates that although the Suriname/French Guiana leatherbacks form a single rookery, individual females show strong nesting fidelity to one side of the Marowijne Estuary.**

KEY WORDS. – **Reptilia; Testudines; Dermochelydiae; *Dermochelys coriacea*; sea turtle; nesting; PIT tagging; hatch success; population size; conservation; Guianas; Suriname**

Suriname is located on the northeastern Atlantic coast of South America between Guyana to the west and French Guiana to the east. Some of the most important nesting beaches in the world for leatherbacks (*Dermochelys coriacea*) are found in eastern Suriname and western French Guiana, particularly inside and near the mouth of the Marowijne (Maroni) River that separates Suriname from French Guiana (Reichart and Fretey 1993; Girondot and Fretey 1996). These beaches also provide important nesting sites for the green turtle (*Chelonia mydas*) and the Olive Ridley (*Lepidochelys olivacea*), and some hawksbills (*Eretmochelys imbricata*) come to nest (Schulz 1975; Reichart and Fretey 1993; Mitro 2005). It has been estimated that over 40% of the world leatherback population nests in Suriname and French Guiana (Spotila et al. 1996), and these leatherbacks are believed to represent a single nesting population (Pritchard 1971a; Schulz 1975; Girondot and Fretey 1996; Dutton et al. 1999). Other large Atlantic leatherback nesting populations have been reported in Trinidad (Eckert 2001), West Africa (e.g., Gabon) (Billes et al. 2003) and along the Caribbean coast of Central America (Troëng et al. 2004). Most former large leatherback nesting colonies in the Pacific and Indian Oceans have collapsed (Spotila et al. 1996, 2000). The species is listed as Critically Endangered in the World Conservation Union (IUCN) Red List of Threatened Species (IUCN 2000). However, this status has been disputed because of incomplete data—particularly regarding Atlantic populations—and a possible overestimation of the decline in the Pacific populations (e.g., Girondot 2002; Mrosovsky 2003; Rivalan 2003).

The leatherback nesting season in the Guianas typically spans from early April to early August in the rainy season, with a peak in May–June. A second, shorter and less significant nesting season occurs around December (Chevalier et al. 2000). In contrast to the leatherbacks nesting in French Guiana, which have been intensively studied and tagged since 1970 (Pritchard 1971b; Girondot and Fretey 1996; Rivalan 2003), the Surinam leatherback population has, until recently, received relatively little scientific attention. In addition to some tagging done in the late 1960s and early 1970s (Schulz 1975), several short-

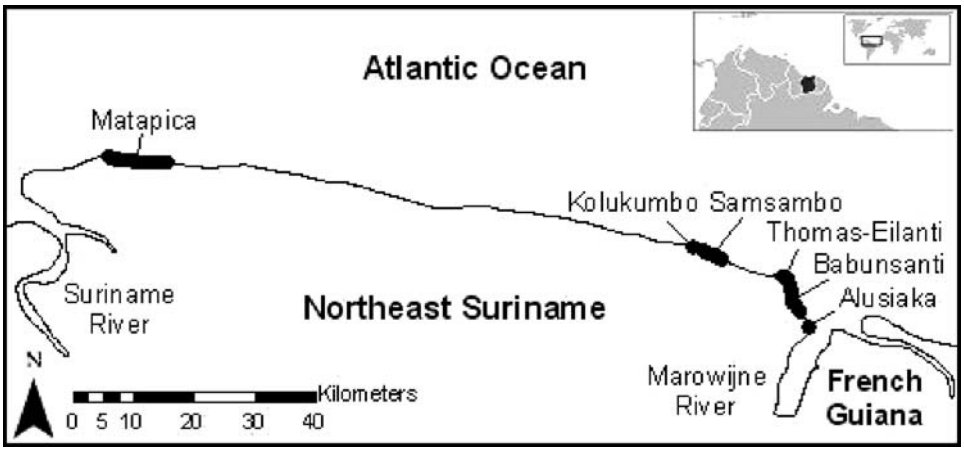

Figure 1. Map of East Suriname with main nesting beaches.

term nest ecology and nest relocation studies have been performed (e.g., Schulz 1975; Mrosovsky et al. 1984; Whitmore and Dutton 1985; Godfrey et al. 1996; Hoekert et al. 2000), and annual nest count data based on track counts in the morning have been collected for most years since 1967 by the Foundation for Nature Conservation Suriname (STINASU) (Schulz 1975; Reichart and Fretey 1993). However, female population size and parameters have not been studied previously.

The annual number of leatherback nests fluctuated highly during the period of observation previous to the present study, but has increased from less than 300 in the late 1960s to peaks of over 11,000 nests in the mid and late 1980s (Reichart and Fretey 1993). Nest data for 1967 to 1975 were corrected for days when no counting was performed (Schulz 1975). However, because survey effort by STINASU field staff strongly differed over years and beaches and because no corrections for missed nestings were made since 1975 (Reichart and Fretey 1993; Dijn 2001, 2003), it can be assumed that, in many years, these nest numbers are underestimates of the true number of nests laid. During the civil war from 1986 to 1989, survey efforts continued at a low level, and during the occupation of the Galibi Nature Reserve (GNR) by local Amerindians from 1990 to 1993, surveys in the GNR stopped altogether (Reichart and Fretey 1993). Moreover, on narrow and shallow-sloping beaches such as Babunsanti, considerable numbers of tracks are obscured by subsequent nesters or washed over by the high tide, especially around spring tides when peak nesting occurs (Girondot and Fretey 1996; Hilterman and Goverse 2002). A reported decline of the French Guiana/Suriname nesting population (Chevalier et al. 1999; Chevalier and Girondot 2000) was largely based on incomplete Suriname nest count data. Likewise, annual nesting colony size estimates for Suriname of 600-2000 females (Spotila et al. 1996) used for listing the leatherback as Critically Endangered were based on dividing highly incomplete nest data by an assumed annual clutch frequency of 5 and do not include any data after 1993.

To obtain better information on the minimum size, trends, and parameters of the leatherback nesting population in Suriname and to assess the extent of nesting exchange with French Guiana, a PIT-tagging project was initiated in 1999 under the WWF-Guianas regional marine turtle program. In addition to tagging, data on biometrics, nest survival, hatch success, and sand temperatures were collected. PIT tagging has also been done at Awala-Yalimapo beach in French Guiana since 1998 (Chevalier and Girondot 2000), and on Shell Beach in Guyana since 2000 (Freitas 2003).

This article summarizes the main results of the PIT-tagging program and studies on hatch success in the main nesting period of the 1999–2005 nesting seasons, and aims to pose new estimates of the minimum annual number of nesting females in Suriname.

METHODS

Study Area. — Due to the westward-oriented Guiana Current and northeasterly trade winds, the Surinamese coastline is highly dynamic and subject to successive phases of beach erosion and accretion (Schulz 1975; Augustinus 1978). The coastline is dominated by extensive mudflats, and sandy beaches are found mainly in the eastern part of the country. Total beach length is around 30–40 km but fluctuates over the years (Hilterman et al. in press). In 1999–2005, leatherbacks nested primarily at Babunsanti (Galibi Nature Reserve), Samsambo, Kolukumbo, and Matapica (Fig. 1). Beach topography strongly differs between the beaches (Fig. 2). Babunsanti (including some sections known as "Pruimeboom") is a narrow, sandy beach on the western banks of the Marowijne Estuary, with a length of approximately 6.5 km and dense vegetation reaching up to the spring high-tide line. Samsambo, known as Spit until 2000, was established as a sandbank just west of the Marowijne Estuary in 1995 and developed into a wide, sandy nesting beach of approximately 9 km length in 1998–1999. By 2000, it had lost much of its nesting importance because of the

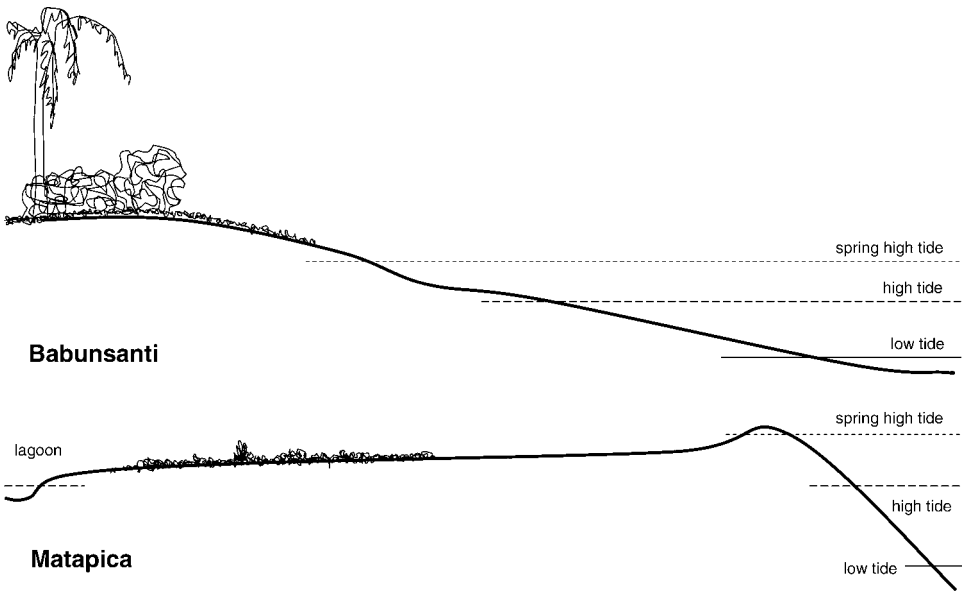

Figure 2. Beach profiles of Babunsanti (Galibi Nature Reserve) and Matapica.

formation of extensive mudflats that made large parts of it inaccessible to leatherbacks. In 2005, however, Samsambo attracted significant numbers of leatherbacks again. Kolukumbo (initially known as "BGW") was formed west of Samsambo in 2000. In the 2001 to 2003 seasons, it was a high and suitable nesting beach, with a length of approximately 1 km. In the 2001 peak nesting season, it had as many as 250 leatherbacks per night. In 2004, Kolukumbo was blocked by a mudflat, and the new beach Marie formed just west of it.

Matapica is a high-energy beach of approximately 10 km length that is exposed to heavy waves and exhibits dramatic short-term alterations. Vertical flood cliffs come and go, and the entire beach moves westward by about 1.5 km per year as a result of erosion on the east side and accretion on the west side (Augustinus 1978). It is steeply sloped and up to 80 m wide. The western end, consisting mainly of nonvegetated open sand mixed with broken shells, is the most newly formed and most visited by leatherbacks. Formerly, when this beach was located more to the east, it was first known as Bigisanti and subsequently as Krofajapasi (Reichart and Fretey 1993). Other nesting beaches are Alusiaka and Thomas-Eilanti in the Galibi Nature Reserve, and Diana Beach and Braamspunt just west of Matapica.

From 1999 to 2002, aerial surveys were conducted along the shoreline of East Suriname at the beginning of the nesting season to monitor the formation of new beaches and assess the nesting status of existing beaches (Goverse and Hilterman 2002; Goverse 2003). From 2003 to 2005, boat surveys by STINASU were used for this purpose. The beaches monitored in a given season depended primarily on the beaches being present, their expected or proven importance for leatherback nesting, presence of a field station or temporary campsite, team size and equipment, and boat availability. Because of its stability, importance for leatherback nesting, and the permanent presence of a field station, Babunsanti is the only beach surveyed in each consecutive nesting season from 1999 to 2005.

Nesting Females. — Nightly tagging surveys were conducted from April to July with a small team of volunteers, but the duration and intensity of the survey period varied among beaches and years (Table 1). In the 1999–2000 seasons, beach coverage was low, and the tagging protocol, set in 2001, was not yet in use. For the 2001–2005 seasons, beach patrolling was done from at least 2 and half hours prior to peak high tide until at least 2 hours after at Babunsanti and Kolukumbo, because nesting there concentrates around high tide. On Matapica, patrolling was adjusted to a different nesting pattern in which a peak in nesting activities occurred when the tide had risen and fallen to one-quarter of the maximum height (L. Katidjo, *pers. comm.*; pers. obs.).

In the Guianas, TROVAN ID100 PIT tags were injected in the muscle of the right shoulder as described by Dutton and McDonald (1994). In the 2001–2005 seasons, scanning (with TROVAN LID500 scanners) and tagging were done at all stages of the nesting process and after tagging, turtles were always rescanned to check for proper tag placement and recording of the tag code. In 1995 and 1996, a limited number of leatherbacks in French Guiana were PIT-tagged in the neck (Chevalier and Girondot 2000), so we also scanned the neck area for all turtles encountered. During the 2001–2005 seasons, in addition to the PIT code, tag status (new or old) and date, we recorded time, the turtle's activity (crawling up the beach, body pitting, digging nest, laying eggs, closing nest-hole, camouflaging, returning to sea), distance of the nesting position to the spring high-tide line, distance traveled from the current water line, location on the transect line or beach section, and the curved carapace length (CCL) and width

Table 1. PIT-tagging effort during the 1999–2005 nesting seasons. Estimated spatiotemporal beach coverage is based on duration of survey period, distance covered, human resources, and nesting intensity on a particular beach. Distances covered are between brackets.

	Babunsanti (ca. 6.5 km)	Samsambo (ca. 9 km)	Kolukumbo (ca. 1 km)	Matapica (ca. 10 km)	Estimated coverage (%)
1999*	May 8–Jul 30 (2 km)	No tagging	No tagging	No tagging	< 5
2000*	May 7–Aug 5 (2 km)	Apr 30–Jun 5 (2.5 km)	No tagging	Jun 30–Jul 24 (2 km)	15
2001	Apr 19–Aug 10 (4.5 km)	May 2-May 21 (2.5 km)	Jun 19, 20; Jul 4, 6, 22 (1 km)	May 15–Jun 15 (3 km)	40
2002	Apr 8–Aug 5 (4.5 km)	No tagging	May 6–Aug 5 (1 km)	Apr 26–Jul 15 (3.5 km)	75
2003	Apr 23–Jul 31 (4.5 km)	No tagging	May 9–Jul 14 (1 km)	No tagging	65
2004	Apr 17–Jul 20 (4.5 km)	No tagging	No tagging	No tagging	35
2005	Apr 17–Jul 23 (4.5 km)	May 12**; June 25, 26** (500 m)	No tagging	May 21, 25, 26 (3.5 km)	35

* In 1999–2000, only females that were in the stage of digging their nest or laying eggs were tagged, restricting the number of females tagged.
** Morning visits.

(CCW). Minimum (or standard) CCL was measured alongside the vertebral ridge, CCW was measured at the widest point as described by Bolten (1999). The average individual size for turtles measured more than once during the season was used for further calculations, turtles with obvious carapace deformities were excluded from analyses involving size. Females were checked for flipper tags and briefly examined for fisheries-related injuries. These were categorized as machete or net wounds and scars, fish hooks in flesh or propeller damage and (partly) cut-off limbs.

For the most intensively monitored seasons (2001–2005), we calculated several parameters based on the collected PIT-tag data. Observed internesting period (OIP) was defined as the number of days between 2 consecutive observed nesting attempts. In calculating the mean OIP, we excluded OIP values of less than 6 or greater than 11 days as these values indicated either aborted nesting attempts (false crawls) or missed nestings (Miller 1997; Reina et al. 2002).

Observed clutch frequency (OCF) was defined as the number of nesting attempts observed during the nesting season for an individual (Steyermark et al. 1996). The minimum estimated clutch frequency (ECF) was calculated for turtles that were observed nesting at least twice by dividing the number of days in between the first and last nesting dates by the mean OIP, adding one for the first oviposition. We used only the individuals with a first nesting date of at least 60 days prior to the end of the survey period, thereby avoiding the possibility that the turtle finished nesting after the end of the fieldwork period (Reina et al. 2002). This method does not correct for unobserved clutches before the first observation and after the last observation and ECF will therefore be an underestimation.

We defined 3 categories of females: 1) newly tagged turtles that were previously untagged and PIT tagged by us; 2) non-Surinamese turtles that had been previously PIT-tagged in French Guiana or Guyana but were new to Suriname; and 3) remigrants that were previously newly tagged or non-Surinamese females that returned to nest in a subsequent year to the one in which we originally observed them. The category of non-Surinamese turtles may also include some erroneous codes, caused by writing errors (Godfrey 2003). Turtles originally tagged in Suriname but later observed nesting in French Guiana are not included in our data set. We calculated mean annual values for the different parameters such as OCF, ECF, intraseasonal beach fidelity, and carapace size, and compared them across the groups of newly tagged, non-Surinamese, and remigrant females in the 2002–2005 seasons (prior to 2002, sample size of remigrants was too small). We assumed the same capture probability for turtles from each of the 3 categories of females. Because different beaches had different monitoring efforts over the years, we analyzed OIP, OCF, and ECF for the combined beaches and Babunsanti separately.

Nest Numbers. — Track counts were done by field staff of STINASU at Matapica, the Galibi Nature Reserve, Samsambo, and Kolukumbo, mostly in the early morning. Based on the shape of the crawl and other visual signs resulting from the nesting attempt, a distinction was made between what was believed to be a nest (eggs deposited) and false crawl (no eggs deposited), and both were recorded. STINASU track counts throughout the years showed that of all leatherback nesting attempts, generally between 9% and 12%, resulted in false crawls (STINASU unpubl. data; J. Mitro, *pers. comm.*). Annual counting effort in 1999–2005 strongly varied, and not all beaches and beach sections were regularly surveyed. On relatively moderate-density nesting beaches with a high and wide profile such as Matapica, track counts are a good indicator of actual nesting activity (Hilterman and Goverse 2002). On high-density nesting beaches such as Kolukumbo and

narrow beaches such as Babunsanti they are not, because crawls and nests are covered up and obscured by subsequent nesters and washed over by the high tide (Girondot and Fretey 1996; pers. obs.). For Babunsanti, we found that for those days with PIT data and track count data on the same beach sections, the number of nesting attempts as obtained from PIT tagging was, on average, 20%–40% higher than the STINASU track counts (nests and false crawls) (Hilterman and Goverse 2006; IUCN NL unpubl. data). Moreover, numbers obtained from PIT surveys were incomplete. Based on the 1987 nesting season in which Awala-Yalimapo beach in French Guiana was patrolled the entire night, it was estimated that with the current tagging protocol even on the monitored beach sections each night, at least 20%–30% of the females can nest unobserved (Rivalan 2003). This is in line with our records on the number of crawls of missed turtles at the onset of and during tagging surveys at Babunsanti and Kolukumbo (IUCN NL, unpubl. data), but because those records naturally do not include missed nestings that were not observed, the real proportion of missed females is higher.

All this implies that, on average, at least 40% of the tracks were no longer visible or were overlooked during track counts, hence, nest numbers based on uncorrected track counts are underestimations. By combining, for the Marowijne beaches, the nest count data of STINASU with data obtained during the PIT-tagging surveys, we derived more accurate estimates of minimum nest numbers in the 2001–2005 seasons, assuming that on PIT surveys, 20% of the nestings were missed, and with track counts, 40% are missed at Babunsanti and 20% at Samsambo, where less wash-over of tracks occurs.

1) For beach sections on Babunsanti and Kolukumbo with nightly PIT-tagging patrols for most of the season, we used the following equation: $N_{pit} = [(1 - F)\ P/(1 - S_{pit})]$, where N_{pit} = Number of nests based on nightly PIT patrols, F = decimal fraction of false crawls, P = nightly observations, S_{pit} = decimal fraction of nestings missed. Gaps of 1–5 days were filled using the average of 3 days before and 3 days after (Schulz 1975).

2) For beach sections with no tagging patrols but nest count data for most of the season, the equation $N_{count} = [C/(1 - S_{count})]$ was used, where N_{count} = number of nests based on track counts, C = track count (excluding false crawls) and S_{count} = decimal fraction of nests missed. Gaps of 1–5 days were filled as described under 1).

3) For beach sections with only several reliable data points, Lagrange interpolation (Press et al. 1992) was used to estimate the number of nests for missing days, using nest distribution on the best-monitored section as a reference.

4) For beaches or beach sections that were not or only very occasionally visited and had no reliable data points a rough estimate was made based on the little information there was, such as information from fishermen that "on average 5–10 leatherbacks are nesting there each night." We then used the lower number as a daily average for the 2 peak months of May and June and half that number for April and July, taking into account our previous experience on leatherback nesting at those beaches.

Nest Success. — In the first half of the 2001–2004 seasons at Babunsanti and 2001–2002 seasons at the westernmost 3 km of Matapica, we marked the nests of females encountered while laying their eggs or that were in a late stage of digging their nest. Exact location of each clutch was triangulated (except for nests at Matapica in 2001) from the nearest 2 20-m interval stakes along a 3-km transect line, and a small plastic tag with nest number was placed in the sand on top of each clutch as a nest-marker. Three days after first hatchling emergence at the surface, or 73 days in case of nonemergence or unnoticed emergence, the nests were excavated and nest contents analyzed. Hatch success was determined by dividing the number of empty shells by the total number of eggs (sum of empty shells, pipped eggs, and all unhatched eggs), yolkless eggs not included. In calculating emergence success, the number of dead hatchlings inside the nest was subtracted from the number of empty shells. The categories for unhatched egg contents are similar to those from Whitmore and Dutton (1985) and are described in detail in Hilterman and Goverse (2002). Successful nests were defined as nests from which hatchlings had emerged. Across-beach nest location was estimated to the nearest 0.5 m from the spring high-tide line (SHTL). For determining nest-site selection and the effect of nest location on hatch success, the beaches were divided into 3 zones based on their morphology. At Babunsanti, the low zone was defined as more than 0.5 m below the SHTL, the mid zone between 0.5 m below and 0.5 m above the SHTL, and the high zone at more than 0.5 m above the SHTL. At Matapica, this was below the SHTL, between the SHTL and 2 m above the SHTL, and more than 2 m above the SHTL, respectively.

Hatchling size was recorded in the 2002 season for 10 randomly chosen newly emerged hatchlings from 36 randomly chosen in situ nests at Matapica and from 10 randomly chosen nests at Babunsanti.

Data Analysis. — Data were tested for normality and homogeneity of variance and subsequently means were compared using 1-way analysis of variance (ANOVA) followed by a post-hoc Bonferroni multiple comparison test, 2-tailed two independent-samples or paired-samples *t*-test, Kruskal-Wallis or Mann-Whitney U test. Means are given ± standard deviation (SD). Regression analysis was used to determine relationships between nesting parameters. For comparing proportions, we used a Chi-square test (Sokal and Rohlf 1987).

RESULTS

Nesting Females. — During 1999–2005, we observed 8462 leatherback females nesting at least once, 7938 of which nested during the 2001–2005 seasons (Table 2). PIT

Table 2. The number of newly PIT-tagged, non-Surinamese, and remigrant turtles observed during the nesting seasons 1999–2005. The annual spatial and temporal tagging effort varied between years (see Table 1).

Nesting season	Newly tagged	Non-Surinamese	Remigrants
1999	62	7	0
2000	385	70	0
2001	2455	448	24
2002	1831	401	51
2003	1473	365	397
2004	294	90	261
2005	433	148	487

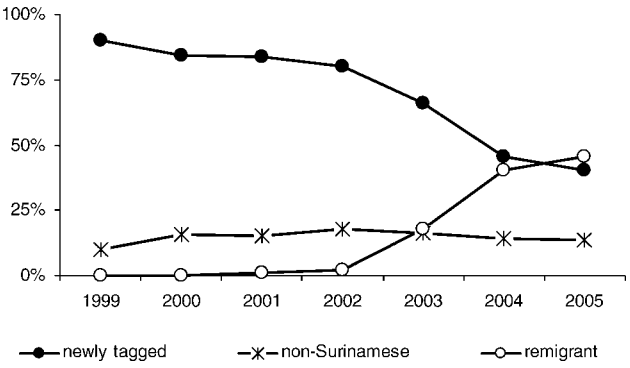

Figure 3. Proportion of newly tagged, non-Surinamese, and remigrant turtles nesting in the 1999–2005 seasons.

tags were applied to 6933 untagged individuals; the remaining 1529 carried TROVAN PIT tags of a non-Surinamese origin (Fig. 3), most of which had been placed in French Guiana (P. Rivalan, *pers. comm.*). Of the 6933 new tags, 59.7% were applied at Babunsanti, 34.0% at Kolukumbo, 5.2% at Matapica, and 1.1% at Samsambo.

In the 2002 season, 16.9% of the nesting females had injuries that showed evidence of being fisheries related. In the 2003 season, at least 18.3% had such injuries, and in 2005, this was 9% (no data for 2004). In the 2000–2003 seasons, 37, 43, 15, and 17 dead leatherbacks, respectively, washed ashore on the beaches under survey. In 2005, 6 dead leatherbacks stranded on Babunsanti. In 2001 and 2003, 501 females were observed stuck on the mud flat in front of Samsambo and Kolukumbo in the early morning after nesting, when the tide was retreating. They generally struggled for about 30–60 minutes, got covered with mud, and finally rested. However, all of these turtles—except for one—released themselves at the first subsequent high tide, and we observed several of them at later nesting attempts.

Nesting Frequency. — OIP, OCF, and ECF were calculated from the tag data of the 2001–2005 seasons (Table 3). OIP data of the 2001–2005 seasons indicated that, on average, 6.9% to 12.1% of the nesting attempts resulted in false crawls. No significant difference existed between mean values of OIP or ECF for the combined beaches and Babunsanti separately for any of the years (Mann-Whitney, $p > 0.5$). However, mean OCF was in 2001 slightly higher for Babunsanti (1.7 ± 1.0, $n = 2227$) than for the combined beaches (Mann-Whitney, $p < 0.01$), and in 2002, when mean OCF was highest at Kolukumbo (2.4 ± 1.6, $n = 1594$), significantly lower for Babunsanti (1.9 ± 1.4, $n = 633$) than for the combined beaches (Mann-Whitney, $p < 0.01$). We compared mean OCF, ECF, and the proportion of one-time observed nesters between the categories of newly tagged, non-Surinamese, and remigrant females (Table 3). Mean OCF was in all 4 years (both for the combined beaches and for Babunsanti alone) significantly higher for the remigrants than for newly tagged and non-Surinamese turtles (Kruskal-Wallis, $p < 0.001$). Mean ECF was also higher for the remigrants than for newly tagged and non-Surinamese turtles in all 4 seasons, but this difference was only significant in 2003 and 2005 (Kruskal-Wallis, $p < 0.01$). A significant relationship existed between the turtle category and the proportion of females observed only once in all seasons 2002–2005 (Chi-square, $p < 0.001$); their proportion being highest in the category of non-Surinamese turtles followed by the new turtles, and lowest for the remigrant turtles in all 4 years.

Remigration. — Of all observed females in the 1999 to 2004 nesting seasons, 1093 (14.8%) were seen renesting in Suriname in a subsequent season (Table 4). Of these, 1.0% had a remigration interval of 1 year, 67.5% of 2 years, 15.4% of 3 years, and the remaining 16.0% had a remigration interval of 4 or 5 years. 126 females were observed in 3, and 1 in 4 different nesting seasons. We have no information on the number of turtles that remigrated to nest in French Guiana. We observed 31 turtles with flipper tags from French Guiana (thus tagged before 1998), 5 turtles with flipper tags from Trinidad, and 3 turtles that had been PIT-tagged in Guyana in a previous season (A. Arjoon, *pers. comm.*). Three PIT-tagged turtles that nested in Suriname were subsequently encountered off the coast of Nova Scotia, Canada (James 2004; M. James, *pers. comm.*), and we observed 3 other females with flipper tags from Nova Scotia, 1 of which had previously been PIT-tagged at Babunsanti and returned to nest in Suriname with an interval of 2 years. Two turtles PIT-tagged in Suriname in 2001 were observed renesting in 2003 in Guyana (A. Arjoon, *pers. comm.*).

Nesting Beach Fidelity. — Nesting-site fidelity was noted in the 2001–2003 seasons, when we surveyed at least 2 beaches simultaneously. In 2001, 47 turtles (4.8% of turtles observed at least twice) were seen nesting on at least 2 different beaches throughout the season. However, because Babunsanti was the only beach covered over the entire season, other shifts between beaches may have been missed. In the 2002 season, 145 turtles (11.1% of turtles observed at least twice) were seen nesting on at least 2 different Suriname beaches. Of these, 119 turtles (82.1%) moved between Babunsanti and Kolukumbo, and 26 turtles (17.9%) moved between Babunsanti/Kolukumbo and Matapica. In 2003, 101 turtles (8.4% of turtles observed at least twice) moved between Babunsanti and Kolukumbo.

Table 3. The mean observed clutch frequency (OCF), estimated clutch frequency (ECF), proportion of females observed only once (% one-time nesters) and mean observed internesting period (OIP) for all observed females and (except for OIP) for the categories of newly tagged, non-Surinamese, and remigrant females in 2002–2005 (all beaches combined). Means are given with SD.

Nesting season	Turtle category	OCF	ECF	% one-time nesters	OIP
2001	all females	1.6 ± 1.0 (n = 2927)	4.5 ± 2.0 (n = 568)	66.7	9.6 ± 1.0 (n = 725)
2002	all females	2.3 ± 1.5 (n = 2283)	4.9 ± 1.8 (n = 623)	46.4	9.6 ± 1.0 (n = 1635)
	newly tagged	2.4 ± 1.5 (n = 1831)	4.9 ± 1.8 (n = 508)	39.2	—
	non-Surinamese	2.0 ± 1.4 (n = 401)	4.7 ± 1.8 (n = 89)	54.1	—
	remigrant	3.6 ± 2.1 (n = 51)	5.5 ± 2.3 (n = 26)	19.6	—
2003	all females	3.1 ± 1.4 (n = 2235)	4.5 ± 1.9 (n = 948)	46.4	9.5 ± 1.0 (n = 1286)
	newly tagged	2.0 ± 1.3 (n = 1473)	4.2 ± 1.7 (n = 576)	49.1	—
	non-Surinamese	1.8 ± 1.3 (n = 365)	4.6 ± 2.1 (n = 110)	61.5	—
	remigrant	3.0 ± 1.8 (n = 397)	5.3 ± 2.1 (n = 262)	23.2	—
2004	all females	1.6 ± 1.0 (n = 645)	4.1 ± 1.8 (n = 140)	63.6	9.6 ± 1.0 (n = 181)
	newly tagged	1.4 ± 0.7 (n = 294)	4.0 ± 1.8 (n = 51)	69.4	—
	non-Surinamese	1.4 ± 0.9 (n = 90)	3.9 ± 2.3 (n = 14)	76.7	—
	remigrant	1.9 ± 1.2 (n = 261)	4.2 ± 1.7 (n = 75)	52.5	—
2005	all females	1.9 ± 1.3 (n = 1068)	4.7 ± 2.1 (n = 296)	55.3	9.4 ± 1.0 (n = 461)
	newly tagged	1.6 ± 0.9 (n = 433)	4.2 ± 1.8 (n = 94)	63.6	—
	non-Surinamese	1.3 ± 0.8 (n = 148)	4.4 ± 1.8 (n = 16)	77.7	—
	remigrant	2.3 ± 1.5 (n = 487)	5.0 ± 2.2 (n = 186)	40.1	—

Rivalan (2003) reported 320 individuals (10.9% of observed females in Suriname; or 6.1% of observed females in French Guiana/Suriname) that nested in both Suriname and French Guiana in the 2001 nesting season. In 2002, an intraseasonal shift between a Surinamese and French Guianese beach was made by 245 turtles (10.7% of observed females in Suriname; or 5.4% of observed females in French Guiana/Suriname) (P. Rivalan, *pers. comm.*).

We compared the proportion of turtles making an intraseasonal beach exchange for the groups of newly tagged, non-Surinamese, and remigrant turtles for 2002–2003, the 2 years with adequate coverage of more than 1 beach and a large enough group of remigrants. The outcome was inconclusive because the 2 years showed opposite results. Of the 1220 observed remigration events (by 1093 individuals), 80.3% occurred on the same beach on which the former nesting occurred. For instance, the 2 remigrants that were observed at Matapica in 2005 had both originally been tagged on this beach and 1 of them, tagged in 2000, nested at Matapica for the third subsequent season.

Carapace Size. — During the 2001–2005 seasons, the CCL and CCW were measured on 62.9% to 97.5% of the nesting females. CCL ranged from 128 to 184 cm and CCW from 97 to 135 cm. Annual mean CCL ranged from 154.1 ± 6.7 cm (n = 1840) to 155.6 ± 6.7 cm (n = 629) cm and mean CCW from 113.2 ± 5.0 cm (n = 801) to 114.5 ± 4.9 cm (n = 383). The mean CCL of the group of females that were first measured in 2001, 2002, or 2003 and were measured again in a later season, had significantly increased from 155.9 ± 6.7 cm to 157.3 ± 6.2 cm (paired samples t-test, 2-tailed, n = 736, $p < 0.0001$). Mean CCL of newly tagged individuals was significantly smaller than that of non-Surinamese turtles and remigrants in all years (ANOVA, $p < 0.001$), the difference between newly tagged and remigrant females ranging from 3.2 to 4.4 cm (Table 5).

Nesting Patterns. — The estimated minimum annual number of leatherback nests in Suriname ranged from 6600 to 31,000 over the 1999–2005 nesting seasons (Table 6). At Matapica, leatherbacks generally nested above the SHTL in the open sand of the mid- and high beach zones (85% of the nests in 2002), whereas at Babunsanti, they nested more often in the open sand of the mid- (25%–33%

Table 4. Observed remigrants (expressed in numbers and as proportion of original cohort for a particular year of first observation) for females observed nesting in Suriname during the 1999–2004 seasons. Only the first subsequent year in which an individual turtle returned is presented, 126 individuals were observed in 3 different and 1 in 4 different nesting seasons. Note that beach coverage was incomplete in all of the years and varied between the years and beaches, and that turtles may have returned on a non-Surinamese beach.

Year first observed	Observed no. individuals	2000	2001	2002	2003	2004	2005	Observed no. remigrants
1999	69	0	22	3	2	1	0	28 (40.6%)
2000	455	—	2	45	19	7	2	75 (16.5%)
2001	2927	—	—	3	363	114	54	534 (18.2%)
2002	2283	—	—	—	6	130	49	185 (8.1%)
2003	2235	—	—	—	—	1	269	270 (12.1%)
2004	645	—	—	—	—	—	1	1 (0.2%)

Table 5. Mean curved carapace lengths (in cm) for the categories of newly tagged, non-Surinamese, and remigrant turtles in 2002–2005. Means are given with SD.

Turtle category	2002	2003	2004	2005
Newly tagged	154.0 ± 6.7 ($n = 742$)	153.2 ± 6.7 ($n = 1074$)	154.0 ± 6.8 ($n = 287$)	153.0 ± 6.7 ($n = 400$)
Non-Surinamese	157.3 ± 6.9 ($n = 165$)	157.3 ± 7.0 ($n = 233$)	156.4 ± 5.6 ($n = 84$)	155.9 ± 6.7 ($n = 130$)
Remigrants	158.4 ± 6.9 ($n = 34$)	157.0 ± 6.5 ($n = 314$)	157.2 ± 6.5 ($n = 256$)	156.7 ± 6.5 ($n = 459$)

of nests) and low beach zone (39%–59% of nests). The mean distance traveled by turtles from the actual water line to the nesting position in 2001 was 7.1 ± 4.8 m at Babunsanti and 23.0 ± 17.1 m at Matapica; in 2002 this was 5.6 ± 4.4 m at Babunsanti and 16.3 ± 8.3 m at Matapica. For both years, the difference in distance traveled was highly significant (*t*-test, 2-tailed, $p < 0.001$). At Babunsanti and Kolukumbo, 96.8% to 99.6% of the nesting occurred around high tide at night between 1900 and 0700 hrs, whereas at Matapica, only between 76.1 and 86.1% of the nesting occurred between 1900 and 0700 hrs.

Nest Success. — We were able to retrieve 100% of the marked nests at Babunsanti in 2002–2003, and 91–92% in 2001 and 2004; the lower retrieval in 2001 and 2004 was likely due to incorrectly recorded nest coordinates, and possibly poaching. Of the marked nests at Matapica, we retrieved 98% in 2002 and 74% in 2001. The 3 nests not found in 2002 were located very low on the beach and lost to beach erosion. The low retrieval in 2001 was because the marked nests had not been triangulated. Not all excavated nests were used for determination of in situ hatch success; nests that had hatched but were mixed with other nests or (partially) dug up by other turtles or raccoons, or were poached, were excluded from further analysis (2.5%–6% of excavated nests).

Hatch success was significantly higher at Matapica than at Babunsanti in both the 2001 and 2002 seasons (Mann-Whitney U, $p < 0.001$), the hatch success at Babunsanti (including unhatched nests) being less than half that of Matapica (Table 7). Depredation by the mole cricket (*Gryllotalpa* sp. and *Scapteriscus* sp.) was significantly higher at Babunsanti than at Matapica (Mann-Whitney, $p < 0.001$). Embryonic mortality of nonpredated eggs was also higher at Babunsanti (Mann-Whitney, $p < 0.05$). There was a weak correlation between distance to the SHTL and hatch success at Babunsanti, with the further the nests were below the SHTL, the lower the hatching success was (e.g., in 2003: $n = 188$, $r^2 = 0.128$, $p < 0.001$). However, nests below the SHTL can still hatch. Nest failure at Babunsanti was highest at distances of more than 2 m below the SHTL, although even some of these nests did hatch.

Nest and Hatchling Characteristics. — Clutch size (Table 8) ranged from 23 to 147 yolked eggs and 0 to 223 yolkless eggs. There was a positive correlation between CCL and clutch size ($r^2 = 0.35$, $F = 10.8$, $n = 297$, $p < 0.001$) for the pooled data of the 2002 to 2004 seasons as well as the separate seasons. No data from 2001 were included because turtle size was not recorded for most of the marked nests. Incubation period ranged from 56 to 74 days (2001–2004) at Babunsanti and 59 to 73 days at Matapica (2001–2002). Mean incubation period (Table 8) was significantly longer at Matapica than at Babunsanti in 2001 and 2002 (*t*-test, 2-tailed, $p < 0.01$).

Mean hatchling straight carapace length in the 2002 season was 59.1 ± 2.0 mm ($n = 10$ nests) at Babunsanti and 59.5 ± 2.0 mm ($n = 36$ nests) at Matapica, average weight was 44.7 ± 3.5 g (Matapica, n = 34 nests).

DISCUSSION

Nesting Females. — For the Guianas, with a large nesting colony spread over many highly dynamic and often remote and high-density nesting beaches, it is not possible to monitor 100% of the nesting areas, and despite a maximum tagging effort on some of the beaches, many females are not observed. By combining our PIT-tag data with intensity and duration of beach coverage and with nesting density, and assuming a within-country beach exchange for a maximum of 12% of females, we estimated the minimum number of nesting females in Suriname in

Table 6. Estimate of the minimum number of nests in the Galibi Nature Reserve (Babunsanti, Alusiaka, Thomas-Eilanti), Samsambo, Kolukumbo-Marie, and Matapica in the 1999–2005 nesting seasons.

Beach	1999	2000	2001	2002	2003	2004	2005
Galibi Nature Reserve	2500 (b,c)	8283 (b,c)	12,800 (a,b)	2600 (a,b)	5600 (a,b)	2300 (a,b)	4650 (a,b)
Samsambo	12,000 (b,c)	1985 (b,c)	2000 (b,c)	450 (b, c)	1500 (b, c)	450 (d)	3000 (b)
Kolukumbo	—	2200 (b,c)	12,500 (a,c)	7500 (a)	2300 (a)	850 (d)	350 (d)
Marie	—	—	—	—	400 (b,d)		
Matapica	2000 (b)	2169 (b)	3700 (b)	2243 (b)	2645 (b)	3000 (b)	2000 (b)
Total estimated nest number	16,500	14,637	31,000	12,793	12,445	6600	10,000

(a) estimate based on nightly observations during PIT tagging surveys; (b) estimate based on STINASU nests counts (Mohadin 1999; Dijn 2003; Dijn, *pers. comm.*; Mitro 2005) (c) Lagrange interpolation; (d) rough estimates based on occasional visits.

Table 7. Average hatch success (H%) and proportion of nests and eggs affected by mole cricket (MC) and ghost crab (GC) predation for the 2001–2004 nesting seasons. Emergence success was generally 1%–1.5% lower than hatch success at both Babunsanti and Matapica (Hilterman and Goverse 2003, 2004). Means are given with SD.

	Beach	2001	2002	2003	2004
H% (hatched nests only)	Babunsanti	21.6 ± 17.7 (n = 72)	34.9 ± 22.1 (n = 117)	28.0 ± 21.6 (n = 149)	28.7 ± 22.1 (n = 42)
	Matapica	58.3 ± 25.4 (n = 56)	63.7 ± 24.2 (n = 95)	—	—
% of nests that failed to hatch	Babunsanti	51.7	25.9	20.7	36.4
	Matapica	9.7	14.4*	—	—
% of nests affected by MC	Babunsanti	94.6	93.0	90.4	92.4
	Matapica	79.0	76.9	—	—
% of eggs per nest predated by MC	Babunsanti	41.4 ± 20.4 (n = 149)	37.4 ± 20.7 (n = 158)	33.1 ± 20.2 (n = 188)	35.3 ± 20.9 (n = 66)
	Matapica	13.7 ± 17.4 (n = 62)	11.2 ± 14.1 (n = 108)	—	—
% of nests affected by GC	Babunsanti	—	2.5	1.6	0
	Matapica	75.8	38.9	—	—
% of eggs per nest predated by GC	Babunsanti	1.2 ± 2.7 (n = 149)	0.1 ± 0.5 (n = 158)	0.1 ± 0.7 (n = 188)	0 (n = 66)
	Matapica	6.3 ± 6.5 (n = 62)	2.5 ± 4.7 (n = 108)	—	—

* Includes 3 nests that were not retrieved because they were lost by beach erosion.

the 2001 season at 5500 (Hilterman and Goverse 2002), at least 3000 in 2002–2003 (Hilterman and Goverse 2003, 2004), 1545 in 2004 (Hilterman and Goverse 2005), and at least 3250 in 2005 (Hilterman and Goverse 2006).

We found the annual proportion of turtles with a non-Surinamese PIT tag (10.1% to 17.6% of the females) to be much lower than could be expected, considering that from 1998 to 2003, 7325 leatherback females were PIT-tagged in French Guiana (no data available for 2004 and 2005) and when assuming that the leatherbacks nesting on the beaches of Suriname and French Guiana are a single large nesting population with a high nesting exchange between beaches (Pritchard 1971a,b; Girondot et al. 2007). Moreover, the actual percentage of non-Surinamese turtles may be lower because this group also includes some erroneous codes, for instance, in 2001, the origin of 4% of the PIT tags could not be ascertained. The strong decrease of the proportion of newly tagged turtles (from 89.9% to 40.5%) and the similar increase of remigrants (from 0% to 45.6%) in only 6 years time, and the moderate frequency of intra- and interseasonal nesting exchange between beaches suggest that—at least on the time scale of the present study—individual females tend to be relatively faithful to one side or other of the Marowijne Estuary. This idea was also expressed earlier by Schulz (1975), but because beach coverage was incomplete, the data on nesting exchanges may be either under- or overestimates and, thus, have to be interpreted with caution.

The significantly smaller CCL of newly tagged females indicates that they were on average younger (Zug and Parham 1996; Price et al. 2004) than remigrants and non-Surinamese females, and that this group may indeed for large part consist of (relatively) new nesters. Newly tagged females also showed a different nesting behavior than remigrants, with a lower mean OCF and ECF, and a higher proportion of females observed nesting only once. These results are in line with findings at Playa Grande, Costa Rica, where significant morphological and reproductive differences between first-time nesters and remigrants were reported (R. Reina, *pers. comm.* in Nieto et al. 2003).

Our data indicate that remigrating leatherbacks tend to be relatively faithful to their previous nesting beach and it

Table 8. Mean clutch size and incubation periods for the marked nests in the 2001–2004 nesting seasons. Means are given with SD.

	Beach	2001	2002	2003	2004
Clutch size (yolked eggs)	Babunsanti	87.5 ± 17.4 (n = 149)	85.1 ± 18.7 (n = 158)	86.6 ± 18.4 (n = 188)	88.2 ± 19.5 (n = 66)
	Matapica	83.1 ± 18.8 (n = 62)	80.8 ± 18.3 (n = 108)	—	—
Number of yolkless eggs	Babunsanti	26.3 ± 13.5 (n = 149)	31.9 ± 18.1 (n = 158)	31.6 ± 20.9 (n = 188)	29.1 ± 17.1 (n = 66)
	Matapica	29.7 ± 20.6 (n = 62)	32.4 ± 23.7 (n = 108)	—	—
Incubation period (days)	Babunsanti	60.9 ± 2.5 (n = 18)	64.8 ± 3.2 (n = 86)	62.6 ± 3.0 (n = 104)	63.2 ± 1.2 (n = 130)
	Matapica	62.7 ± 1.8 (n = 39)	67.3 ± 2.2 (n = 89)	—	—

appears that turtles are more likely to make an interseasonal shift if a beach has disappeared or become unsuitable (e.g., when Kolukumbo was no longer a suitable nesting beach in 2004, the leatherbacks that previously nested there were forced to select a new beach). The question of which turtles colonize the newly formed beaches remains unanswered. The lower ECF and larger difference between OCF and ECF for leatherbacks in Suriname and French Guiana than reported for leatherbacks elsewhere (e.g., Dutton et al. 1992; Reina et al. 2002) are most likely a result of unobserved nestings (Tucker 1989; Steyermark et al. 1996). Our OCF data are similar to those reported for Awala-Yalimapo in the 2001–2003 seasons (Briane et al. in prep.); however, our mean ECF values are higher. This may partly be due to a different methodology of calculating ECF and partly to a higher beach coverage in Suriname. For the 1988 season, Fretey and Girondot (1989) calculated the mean number of nests per female during a nesting season at 7.52, and using stopover duration methodology, this was even as high as 9.6 (Rivalan et al. 2006). In both cases, nesting frequency was corrected for unobserved nestings before and after the survey period, but they do not take into account the nesting exchange between Suriname and French Guiana and the different nesting behavior of new females. Even when considering incomplete beach coverage, the high proportion of one-time observed nesters (46%–67% of females) in both Suriname and French Guiana (Briane et al. 2007) remains largely unexplained. If these females were merely "unfaithful visitors" from other nesting beaches (in French Guiana or Suriname) rather than "true one-time nesters" (Girondot et al. 2007), they should have been observed on other monitored beaches. Our finding that the non-Surinamese turtles have a higher proportion of one-time observed nesters than the newly tagged and remigrant turtles supports this hypothesis. However, the non-Surinamese turtles make up only 10%–17% of the annual number of turtles, and in the 2002 season (highest beach coverage), most of the Suriname one-time observed nesters were not observed at Awala-Yalimapo either (P. Rivalan, *pers. comm.*). Even if they would have nested on other, unmonitored (French) beaches than Awala-Yalimapo, we believe that the one-time nesting phenomenon may partially be explained by other factors than nesting exchange and monitoring effort, such as the proven different nesting behavior of new females. Alternatively, one could expect that new nesters have a higher tendency of nesting exchange between beaches, but we found no evidence for this. As estimated clutch frequencies calculated in most studies exclude the one-time observed nesters, they may be overestimations for the mean clutch frequency of the population as whole, especially where there is, like in the Guianas, also some nesting exchange between beaches in the region.

Remigration rates demonstrated in our study are rough and preliminary. Dutton (2002) reported a minimum of 69% survival in the 5 years after tagging for leatherback females at St. Croix. The observed return rates of tagged turtles in Suriname of 41% for the 1999 cohort and 16% for the 2000 cohort were similar to those found in French Guiana for the 1999–2000 cohorts (Rivalan 2003). These are certainly underestimates, in view of the high proportion of unobserved females on a regional scale, the lack of information on females renesting in French Guiana, and because some beaches were no longer surveyed after the year(s) of tagging. However, incidental captures by coastal driftnet fisheries in and around the Marowijne Estuary were high (Chevalier 2000; Kelle 2001), which was also reflected by the high numbers of dead leatherbacks stranded in the study area as well as on Awala-Yalimapo, where 54 strandings were reported in 2001 (Godfrey 2001). In 2002, more severe fisheries regulations were enforced in Suriname (Dijn 2003), which will certainly have reduced the number of incidental captures. The high incidence of fresh fisheries-related injuries found on females nesting in 2002–2005, however, indicates that the driftnet fisheries still pose a serious threat to nesting leatherbacks in the Guianas and may be a serious cause of mortality.

Nest Success. — Egg-predation by highly abundant mole crickets, and related effects such as increased attraction of bacteria and fungi (Mo et al. 1990), appear to be the main causes for a lower hatch success observed at Babunsanti than at Matapica. The type of sand (consisting of course shell parts), beach morphology, a better drainage capacity, and the continuous replenishment of sand at Matapica may also provide a better environment for the developing eggs (Hilterman and Goverse 2003). Furthermore, Babunsanti is subject to regular inundation by brackish water, which may further reduce hatch success. The mean proportion of yolked eggs per nest that were predated by mole crickets at Babunsanti (37.4%–41.4%) was higher than at Matapica (11.2%–13.7%) and also than reported by Maros et al. (2003) in a smaller-scale study at Awala-Yalimapo (18%). The lower hatch success at Babunsanti in 2001 than in subsequent years may be a result of the extremely high nesting density for that year, as bacterial and fungal contamination of eggs broken by other nesting females can conceivably affect the newly deposited eggs as well (Girondot et al. 2002; Tiwari et al. 2006) but may also reflect the type of nest marking used in that year. In 2001, some nests were located with the help of a probe stick. A small-scale study in 2002 confirmed earlier findings by Hill (1971) that probing for eggs, as has been done on a large scale for marking nests in earlier hatch success studies in Suriname (e.g., Hoekert et al. 2000), significantly lowers hatch success, regardless of whether eggs were observed to be pierced or not (Hilterman and Goverse 2003). Hence, hatch-success values found in those earlier studies can be assumed lower than natural. Hatch success of leatherback nests was much lower than that of green turtle nests on the same beaches, which was around 85% on Bigisanti (Whitmore and Dutton 1985) and on Babunsanti and Matapica

(Hilterman 2001). The longer incubation periods at Matapica as compared to Babunsanti reflect the lower sand temperatures on this beach (Goverse et al. 2006). However, because only clutches laid during the first, cooler half of the season were marked and followed on both beaches, average incubation periods over the entire season might be shorter. Average hatch success for the successful nests at Matapica (58.3%–63.7%) compared well to that for leatherbacks on St. Croix, where the annual mean ranged from 56.9% to 76.4% over the 1982–1995 nesting seasons (Boulon et al. 1996) and was 52.7% in 2006 (Garner et al. 2006); but because those numbers exclude nests that were relocated to protect them from inundation or erosion, results may be positively biased.

Recent hatch rates at Matapica are higher than those found at Bigisanti (50%) (Schulz 1975) and Krofajapasi (52.4%) (Whitmore and Dutton 1985), which are previous names for the same, westward-moving beach Matapica. A possible explanation is that the nests marked in 2001 and 2002 were situated on the accretion end of the beach, whereas previous studies were done on "older" beach sections. Despite the generally lower nest numbers at Matapica compared to the Galibi beaches, more hatchlings are produced at Matapica in most years. Assuming a mean clutch size of 85 yolked eggs and a mean emergence success of 20% at Babunsanti and 50% at Matapica, 3000 nests on Matapica would produce as many hatchlings as 7500 nests on Babunsanti. The lower hatch rates for Babunsanti are probably applicable to other beaches in and close to the mouth of the Marowijne River, such as Awala-Yalimapo, and may have a significant impact on population recruitment (Chevalier et al. 1999). Matapica, and probably other dynamic oceanic beaches in the Guianas (e.g., Kolukumbo, Pointe-Isère-French Guiana), are very important for leatherback hatchling recruitment, and we strongly recommend that they receive more attention for research and conservation considerations in both Suriname and French Guiana.

At Babunsanti, most leatherback females nested in the open sand area below the spring high-tide line (SHTL). Eckert's (1987) finding that beach slope is positively related to the distance traveled by the turtle to the initial nesting position, was confirmed for the Suriname leatherbacks: females nesting at Matapica crawled, on average, 3 times further than at Babunsanti. At Babunsanti, the SHTL is relatively clear and uniform, and at least 80% of all nests are seriously inundated twice a day for at least 3 or 4 periods of several days during their incubation, and nests situated at more than 4 m below the SHTL are inundated at almost each consecutive high tide. However, at Matapica, the SHTL is highly variable (although generally situated at the transition of the beach slope and beach flat), and the swash zone stretches over the entire beach flat in some areas. Therefore, up to 85% of the nests at Matipaca, including those above the SHTL, are washed over by seawater twice a day for at least 1 period of several days during their incubation. Suriname leatherback nests that were subject to tidal inundation or erosion were formerly considered "doomed" (Schulz 1975; Whitmore and Dutton 1985) and since 1964 at Bigisanti and 1969 at the Galibi beaches, were either legally harvested (during an open season) for human consumption or translocated to a position higher on the beach or to a man-made hatchery (Schulz 1975; Reichart and Fretey 1993). It was, however, demonstrated in the present study as well as previous ones (e.g., Mrosovsky 1983; Whitmore and Dutton 1985; Hoekert et al. 2000) that leatherback nests can tolerate relatively high levels of inundation, and hatch success can still be reasonable despite a nest location below the spring tide line. Because of this, and because it may affect natural sex ratios (Mrosovsky and Yntema 1980), the relocation of "doomed" nests was abandoned in 2002 (Dijn 2003); since then, only nests directly threatened by beach erosion at Matapica are, under certain circumstances, relocated to a higher position on the beach.

Historically, egg collection by local Amerindians at the Marowijne Estuary beaches has been excessive (Reichart and Fretey 1993), particularly of green turtle and Olive Ridley eggs. During the study period, poaching of leatherback nests was a major problem in 1999–2001, when at least 26% were poached (Mohadin 2000; Dijn 2001). In 2002–2003, better law enforcement was in place, and poaching was reduced to about 1% of the leatherback nests (Dijn 2003; Mitro 2005). However, in 2004 and 2005, it had increased again (pers. obs.; Hilterman and Goverse 2006).

Nesting Population Status. — The PIT-tagging data collected on the Suriname nesting beaches Babunsanti, Samsambo, Kolukumbo, and Matapica in the 1999–2005 seasons undoubtedly demonstrate the present status of Suriname as a major leatherback rookery. By PIT-tagging, much larger numbers of females were shown than could have been expected from nest counts alone, particularly because the latter are incomplete and highly underestimate the real number of nests for most years. PIT-tagging data (i.e., nightly observations) also helped to improve nest number estimates because during track counts as performed by STINASU field staff, many nests were overlooked on narrow and sometimes high-density nesting beaches such as Babunsanti and Kolukumbo. However, if we used the approach of multiplying the minimum number of females estimated in the 2001–2005 seasons with a generally accepted minimum ECF of 5.5 (Tucker 1989; Steyermark et al. 1996), nest number estimates would be higher than those estimated based on nightly observations for all years except for 2001: namely 30,250, 16,500, 16,500, 8500, and 17,875 for the 2001–2005 seasons, respectively. We believe an overall mean ECF of 5.5 for Suriname is more likely to be accurate than the average of 4.5 found in the present study or an ECF of 7.5–9.6 estimated for French Guiana (Fretey and Girondot 1989; Rivalan et al. 2006), given some nesting exchange with French Guiana and the different nesting behavior of new females. The PIT-tag data show that earlier estimates of

the annual female population size for Suriname of 600-2000 turtles (e.g., Spotila et al. 1996) are much too low.

If we look at Suriname nest number data for the past 3 decades (Schulz 1975; Reichart and Fretey 1993; Mohadin 2000; Dijn 2001, 2003; Girondot et al. 2007) and compare these to nest count data and nest number estimates since 1999, we can assume that most of the earlier nest numbers are likely to be underestimates. These estimates were for most years either uncorrected nests counts, or for years with no data, such as 1990–1993 when the Galibi Nature Reserve was blocked by rebellious Carib villagers (Reichart and Fretey 1993), nest number estimates extrapolated from those at Awala-Yalimapo (Chevalier and Girondot 2000). In the 1990s, the annual number of females in French Guiana was estimated to vary from 1300 to 5500 (Rivalan 2003), and thus similar to the minimum annual number of nesting females (at least 1500 to 5500) we estimated for Suriname alone. The higher number of females observed in Suriname in the 2001–2003 nesting seasons (2927, 2283, and 2235, respectively) than identified at Awala-Yalimapo (2311, 1272, and 1373, respectively) (Rivalan 2003) were probably a result of a higher beach coverage in Suriname. Some nesting exchange between Suriname and French Guiana does occur, but this does not seem a very frequent event, with only 6.1 and 5.4% of all observed females in Suriname/French Guiana making an intraseasonal shift between these countries in 2001 and 2002, respectively.

We believe that the number of females nesting in Suriname has been largely underestimated in the past 2 decades (notwithstanding large annual fluctuations), and we support the idea that the Suriname/French Guiana nesting population is at least stable (Girondot et al. 2007). However, the apparent high incidence of fisheries-related injuries on leatherbacks is a serious reason for concern. To better understand the conservation status of this important population, a next step should be to group the French Guiana/Suriname tagging data and expand it on a wider regional scale.

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