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Inter-nesting behavioural adjustments of green turtles to an estuarine habitat in French Guiana

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ABSTRACT: Sea turtles adjust their behaviour according to the conditions of their habitat, thus saving or gaining energy during the energetically costly inter-nesting season. This study aimed to investigate how gravid green turtles *Chelonia mydas* nesting in Suriname and French Guiana have adapted to the unusual habitat of the Maroni River estuary, which has highly turbid and low salinity waters and *a priori* lacks seagrass, one of the main foods consumed by this species. Satellite telemetry was used to assess the behavioural adjustments of 26 adult females in terms of (1) home range and (2) diving behaviour, by recording the movements (location, dive depth, dive duration, surface duration) and environmental conditions (temperature and salinity of the water) experienced by each individual. The turtles exhibited limited movements, occupying a core home range of 512.7 km² and remaining close to the shore (3.8 ± 3.1 km) and the nesting beach (18.6 ± 22.7 km). Dive data showed that individuals spent extended periods at the surface (210 ± 288 min), probably associated with diurnal resting activity. The turtles performed uncharacteristically short and shallow dives (<5 min and <2 m) which could result from lung volume issues linked to positive buoyancy. This species shows a unique ability to tolerate extreme environments in this inter-nesting habitat, where large river outputs generate warm water (~27 to 29°C) and highly variable salinities (range: 1.2 to 35.5 psu). These results highlight the various behavioural adjustments of this population in response to the atypical and estuarine habitat of the Maroni river mouth.

KEY WORDS: *Chelonia mydas* · Guiana coast · Habitat use · Diving behaviour · Satellite tracking

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INTRODUCTION

To compensate for the high energy costs of reproduction, organisms must choose between 2 types of strategies: income breeding, whereby an animal feeds during reproduction, or capital breeding, whereby an animal stops feeding and relies solely on its body reserves (Drent & Daan 1980). Sea turtles are commonly considered as capital breeders, storing fat reserves at their foraging grounds then ceasing to

feed during the breeding–nesting season (Drent & Daan 1980, Goldberg et al. 2013, Perrault et al. 2014), which occurs every 1 to 4 yr (Miller 1997). During this breeding–nesting period, gravid females must meet the high energy costs incurred by multiple activities that occur during the breeding–nesting season; i.e. migrating from the foraging grounds, mating, travelling to and from the nesting beach, incubating the clutch (50 to 150 eggs), laying eggs several times per season depending on the species (Miller 1997, Wal-

lace et al. 2005, Walcott et al. 2012), and migrating back to the foraging areas—all potentially without feeding during at least 2 consecutive months (Schofield et al. 2013, Hays et al. 2014).

To limit the continuous loss of energy during the inter-nesting season, sea turtles have developed multiple strategies to maximize their reproductive output. For example, females have been reported to commonly rest on the seabed during U-shaped dives, as observed in green (Hays et al. 2000), hawksbill (Houghton et al. 2008, Walcott et al. 2013), loggerhead (Sakamoto et al. 1993, Houghton et al. 2002), and leatherback turtles (Reina et al. 2005). 'Assisted resting' has also been reported in Caribbean hawksbill turtles, which wedge themselves under coral reefs on the seafloor substrate during the inter-nesting season. Alternatively, gravid females can rest in mid-waters by controlling their lung volume to achieve neutral buoyancy, thereby limiting their energy expenditure (Minamikawa et al. 1997, Hays et al. 2000). In addition to diving adjustments, female sea turtles can restrict their movements by remaining close to the nesting beach (Stoneburner 1982, Hays et al. 1999, Blanco et al. 2013, Maxwell et al. 2014, Esteban et al. 2015). During the inter-nesting period, females can also show a preference for locations where optimal water temperatures enhance egg development prior to laying (Schofield et al. 2009, Fossette et al. 2012).

While some sea turtle populations have developed strategies to conserve energy during the inter-nesting season, others use specific behaviours to increase their energy reserves. Depending on local habitat conditions and the availability of food resources, gravid females can feed during the inter-nesting season (Hays et al. 2002c, Schofield et al. 2006, Georges et al. 2007). This behaviour has been highlighted for the green turtle in Cyprus (Hays et al. 2002c), where individuals perform shallower dives to forage on a site with seagrass beds, but has not been observed in females nesting in Ascension Island, where the apparent absence of a food supply prevents females from feeding during the inter-nesting season. Strong behavioural plasticity occurs in the case of habitat loss, when some individuals from the same population travel long distances to reach alternative breeding–nesting sites, whilst others remain close to the nesting beach, as recorded in loggerhead (Schofield et al. 2010a), hawksbill (Esteban et al. 2015), olive ridley (Hamel et al. 2008), leatherback (Shillinger et al. 2010) and green turtles (Troëng et al. 2005).

The dispersal and diving behaviour of gravid green turtles has been widely studied in many different

nesting sites and shows strong inter-individual and inter-population variability, but to date, no information is available for the population nesting in the Suriname–French Guiana rookery. This site hosts one of the largest green turtle rookeries on the north-eastern part of the South American coast (Schulz 1975, Chevalier et al. 1998, Baudouin et al. 2015, Chambault et al. 2015), with 869 females and 2228 clutches counted in 2015 in French Guiana (Mast et al. 2016). The waters of the Guianese continental shelf contain large amounts of sediments and suspended materials continuously discharged by the Amazon River (Milliman & Meade 1983, DeMaster et al. 1996), leading to low levels of irradiance (Molleri et al. 2010) and presumably limiting the development of seagrass, one of the main foods consumed by adult green turtles. It is important to mention that although it is widely acknowledged that green turtles consume seagrass, there is no evidence to date of this occurring in Surinamese green turtles; Bjørndal (1982) suggests that they may feed on macroalgae. Located on both sides of the border between Suriname and French Guiana, this rookery is also influenced by the Maroni and the Mana rivers. Their mean discharge rates of 1680 vs. 300 m³ s⁻¹, respectively (Lambs et al. 2007), make the water highly turbid and brackish (Jounneau & Pujos 1988) and bring high volumes of freshwater to the coast, especially during the rainy season (Lambs et al. 2007). This creates unusual estuarine conditions for sea turtles.

This study aims to investigate how gravid green turtles nesting in Suriname and French Guiana have adapted to the biological conditions of this estuarine habitat during the inter-nesting season. Satellite telemetry was used to assess the behavioural adjustments of 26 adult females in terms of home range and diving behaviour, by recording the movements and environmental conditions (temperature and salinity of the water) experienced by each individual. This is the first study to track this specific population of green turtles during the inter-nesting season in an unusual habitat influenced by large rivers, i.e. the Amazon, the Maroni and the Mana rivers.

MATERIALS AND METHODS

Ethics statements

This study meets the legal requirements of the countries where it was carried out, and follows all institutional guidelines. The protocol was approved by the Conseil National de la Protection de la Nature

(CNPN; www.conservation-nature.fr/acteurs2.php?id=11), a branch of the French Ministry for Ecology, Sustainable Development and Energy acting as an ethics committee in French Guiana and Suriname (permit number: 09/618). After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of French Guiana (Cayenne, France), in order to minimize disturbance to the animals.

Satellite tag deployment

During the inter-nesting season, 16 Argos-linked Fastloc GPS tags (MK10, Wildlife Computers) were deployed on adult female green turtles from February to June 2012 on both sides of the Maroni River: at Awala-Yalimapo in the Amana Nature Reserve, French Guiana (5.7°N, 53.9°W, $n = 8$), and in the Galibi Nature Reserve in Suriname (5.4°N, 53.5°W, $n = 8$; see Fig. 1). During the same period in 2014, 10 additional females in the Amana Nature Reserve were equipped with Conductivity-Temperature-Depth-Fluorometer Satellite Relayed Data Loggers (CTD-SRDL; the Sea Mammal Research Institute Instrumentation). The attachment procedure followed the standard methods described in Baudouin et al. (2015). During tag deployment, measurements of the curved carapace length (CCL) were taken, and body mass was then calculated using the method of Hays et al. (2002a). A Platform Terminal Transmitter (PTT) was assigned to each turtle equipped with a tag.

Data collection

Inter-nesting route data were extracted following the procedure described by Baudouin et al. (2015). The Argos-linked Fastloc GPS tags recorded Argos locations and GPS positions of the turtles at 4 h intervals (10% of the locations transmitted). These tags also provided diving data, i.e. maximum dive depths, dive durations and *in situ* temperature data, binned as 4 h period histograms. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m. Maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, every 5 min from 5 to 20 min, and finally every 10 min from 20 to 60 min. *In situ* temperatures were recorded during dives from 20 to 32°C, every 1°C.

The CTD-SRDL tags provided the locations of the turtles via Argos data, and recorded simplified pro-

files of the diving parameters (dive depth, time at depth, dive duration and post-dive surface interval), and oceanographic data in the form of vertical temperature and salinity profiles taken during the ascent phase of the turtles' dives (Boehme et al. 2009). The CTD-SRDL tags were programmed to send summarized dive profiles using the compression algorithm described by Fedak et al. (2001), providing 4 depth records for each dive (instead of the single maximum depth per dive provided by Argos-Fastloc GPS tags). Temperature and salinity data were quality controlled using the procedure described in Roquet et al. (2011), with an estimated accuracy of 0.02°C and 0.05 psu.

Data pre-filtering

The tags were deployed at the beginning of the inter-nesting season, and therefore recorded location data for post-nesting migration. Following the procedure described in Baudouin et al. (2015), a spatial query was performed via ArcGIS version 10.1 (ESRI) to identify the date of migration departure. Only positions corresponding to the inter-nesting season were retained for analysis, as indicated in Chambault et al. (2015).

Using the same approach as Heerah et al. (2013), a Kalman-filtering algorithm was then applied (CLS; Collecte Localisation Satellites) to enhance tag position estimates (Argos and GPS) by accounting for Argos location errors (Patterson et al. 2010, Lopez et al. 2014). The General Bathymetric Chart of the Oceans database (GEBCO, www.gebco.net/; 30 arc-second 1 km grid) was used to discard any locations on land. Positions associated with a speed of $>5 \text{ km h}^{-1}$ (Hays et al. 2004, Schofield et al. 2013) and those with location Class Z (class associated with the raw location before Kalman filtering) were considered insufficiently accurate and were removed.

Data analyses

The 'trackDistance' function from the 'trip' package in R (Luque 2007) was used to calculate distance travelled and elapsed time between locations. Observed speed was then derived from these values. Distance to shore was calculated by finding the shortest distance to the coastline for each turtle location, using the 'dist2Line' function from the 'geosphere' package (Robert 2015). Distance to nesting site, i.e. the location where each turtle was initially tagged, was also calculated for each position.

All statistical analyses were performed using R software version 3.2.2 (R Core Team 2014). Before being submitted to statistical tests, all samples were checked for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test). The results of these tests determined the subsequent use of either parametric or nonparametric tests for sample analysis, with a significance level of $\alpha = 0.05$. Values are means \pm SD.

For the diving variables, we discriminated between benthic and pelagic dives by calculating the difference between the bathymetry at the dive location and the maximum dive depth recorded by the CTD-SRDL for the same location for each dive. Dives with a maximum depth within 1 m of the seabed were classified as benthic dives, and those with a maximum depth beyond 1 m of the seabed were pelagic dives. Data from the Argos-linked Fastloc GPS tags ($n = 16$) were not used due to their coarser resolution (1 dive depth every 10 m). At some locations, depth difference was greater than the bathymetry depth, possibly due to the error generated by the shift between the incorrect Argos positions and the considerable movements of the turtle during the dive.

To obtain an idea of the dive patterns, we calculated the Time of Allocation at Depth (TAD) index by using the 4 inflection points of the summarized profiles provided by the CTD-SRDL tags. Based on the method of Fedak et al. (2001), TAD calculation makes it possible to obtain relevant information about where turtles concentrate their activity within the dives, i.e. V-shaped dives for $0.5 \leq \text{TAD} < 0.75$ (exploratory dives) and U-shaped dives for $0.75 \leq \text{TAD} < 1$ (activity centered at the bottom of the dive, linked to either foraging or resting activity). Following the method of Plot et al. (2015), the average rate of change of depth was fixed at 1.4 m s^{-1} . Bottom time was calculated as the time spent below 80% of the maximum depth (Heerah et al. 2013), and the descent and ascent rates (in m s^{-1}) were also determined. The day hours were set from 06:00 to 18:00 h local time to assess potential diel dive patterns.

Home range estimation

In order to display residency patterns, both the Argos and GPS positions were used to estimate home ranges by mapping kernel density distributions (Worton 1989). Although GPS locations are more accurate than Argos locations for the quantification of home ranges (Schofield et al. 2010b), the low number of GPS locations transmitted (10%) made it

impossible to base the kernel calculation on GPS data alone. To minimize autocorrelation in spatial analyses, median daily locations were generated for each turtle (Schofield et al. 2010b, 2013, Revuelta et al. 2015). A kernel density analysis was then carried out for each year of tag deployment using the 'kernelUD' function from the 'adehabitatHR' package in R (Calenge 2006). As kernel density cannot always be calculated using the least square cross-validation method (Seaman & Powell 1998), the smoothing parameter was set using the default approach, i.e. the ad hoc method (Calenge 2006). Ninety percent density contours were used to represent the broad home range, and 50% density contours were used to indicate the core area. The corresponding area (expressed in km^2) was then calculated within each kernel contour.

Nesting events and basking identification

Nesting events were identified using direct observation during nocturnal surveys rather than evidence of haul-outs from tracking data. This choice is explained by the lack of precise resolution from the Argos ($>1500 \text{ m}$) and GPS locations ($<100 \text{ m}$) and the potential inaccuracy of the GEBCO database in such coastal habitat, making the identification of nesting events unreliable if based on tracking data alone. Daily nocturnal patrols were therefore performed from February to July during each year of tag deployment (2012 and 2014) on Awala-Yalimapo beach (Amana Nature Reserve) to observe the entire nesting season of green turtles in this rookery. Each observed female was scanned to identify a Passive Integrated Transponder (PIT). If the individual was not tagged, a PIT was inserted in the top right triceps muscle. The GPS location of the animal, time, PIT number, beach location (sand, bank, vegetation or water) and behaviour (rise, first sweep, digging, second sweep, laying, filling or U-turn) were systematically recorded for each individual throughout the nesting periods. To avoid any possibility of false nesting events affecting the results, only laying behaviour was retained for analysis.

The haul-out information recorded by the wet/dry sensor of the tags was also used to identify surface resting/basking behaviour. The Fastloc-GPS tag sensor enters haul-out state after 20 consecutive dry minutes, and exits haul-out state if it remains wet for 30 s or more. For CTD-SRDL tags, a haul-out was recorded when the saltwater switch dry time exceeded 10 min, and the end of the haul-out was

registered after a submersion time of at least 40 s. Any haul-outs that were recorded during the daytime were considered as Extended Surface Times (ESTs; Hochscheid et al. 2010), the latter being considered as evidence of surfacing/resting behaviour, as green turtles nest exclusively by night on this site (D. Chevallier unpubl. data).

RESULTS

Capture-mark-recapture data

A total of 475 female green turtles were observed nesting at Awala-Yalimapo beach (French Guiana) from 30 January to 12 July 2012; 669 were observed during the same period in 2014. The average inter-nesting interval between 2 consecutive clutches was 12.8 ± 1 d in 2012 ($n = 2329$) and 12.6 ± 1.4 d in 2014 ($n = 2160$). The activity peak occurred in April of both years, with 2329 nesting events recorded in 2012 and 2160 in 2014. Nocturnal patrols recorded an average 2.4 ± 1.6 nesting events per turtle during the tracking period (range: 1 to 5; Table 1).

General tracking data

The inter-nesting data recorded from the tags covered the period from February to July in 2012 and 2014. The tag instruments transmitted for an inter-nesting tracking duration ranging from 4 d (#115458) to 95 d (#130766; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m555p235_supp.pdf) for an average of 254 ± 144 locations (5.4 ± 1.7 locations d^{-1}). Only 1 of the 16 turtles equipped during the inter-nesting season in 2012 (#115459) did not transmit any location data during the inter-nesting season. The CCL of these green turtles varied from 103 to 133 cm (mean: 115.5 ± 5.8 cm; #130776 vs. #130773) and their body mass ranged from 130.8 to 238.1 kg (mean: 177 ± 16.5 kg; #130776 vs. #130773).

Displacement and home range

Total distance travelled varied from 28 km (#115458) to 2627 km (#130766; Table 1). Gravid green turtles travelled over longer distances in 2014

Table 1. Horizontal movements of the 25 gravid green turtles *Chelonia mydas* tracked in 2012 and 2014. PTT: turtle ID. Values are mean \pm SD

PTT	Instrument	Nesting events	Distance (km)	Distance to shore (km)	Distance to nest (km)	Speed (km h ⁻¹)
115445	MK10	3	928	6.9 \pm 7.2	24 \pm 29	1.6 \pm 1.3
115446	MK10	1	1323	3.7 \pm 2.8	8.1 \pm 5.1	1.1 \pm 1.1
115447	MK10	1	764	2.3 \pm 2.0	8.4 \pm 4.6	0.8 \pm 0.9
115448	MK10	1	727	2.2 \pm 1.7	7.6 \pm 3.8	0.8 \pm 0.9
115449	MK10	1	547	2.9 \pm 2.4	14 \pm 11	0.8 \pm 0.9
115450	MK10	1	881	2.7 \pm 2.2	11 \pm 3.1	1.1 \pm 1.1
115451	MK10	5	871	4.5 \pm 4.7	14 \pm 14	0.9 \pm 1.1
115452	MK10	1	523	3.1 \pm 4.2	11 \pm 5.1	0.9 \pm 1.1
115453	MK10	1	479	2.9 \pm 2.1	9.9 \pm 3.0	0.7 \pm 0.8
115454	MK10	1	812	2.4 \pm 2.0	8.6 \pm 4.8	1.1 \pm 1.1
115455	MK10	1	486	4.3 \pm 3.0	13 \pm 7.3	1.0 \pm 1.0
115456	MK10	2	688	2.4 \pm 2.3	14 \pm 16	1.2 \pm 1.1
115457	MK10	1	362	2.7 \pm 1.8	5.9 \pm 1.8	0.8 \pm 0.9
115458	MK10	1	28	0.6 \pm 0.5	2.8 \pm 1.9	1.1 \pm 0.9
115460	MK10	2	305	2.7 \pm 2.2	7.8 \pm 6.0	1.3 \pm 1.1
130766	CTD-SRD	4	2627	16.0 \pm 26.0	96 \pm 110	1.5 \pm 1.2
130767	CTD-SRD	5	533	1.6 \pm 2.0	5.2 \pm 8.3	0.9 \pm 1.0
130768	CTD-SRD	5	849	1.5 \pm 1.6	12 \pm 11	0.9 \pm 0.9
130769	CTD-SRD	5	570	5.1 \pm 5.4	18 \pm 17	1.0 \pm 1.0
130770	CTD-SRD	2	345	3.0 \pm 2.6	6.0 \pm 3.9	0.9 \pm 1.1
130771	CTD-SRD	4	671	5.3 \pm 3.8	18 \pm 16	1.2 \pm 1.1
130773	CTD-SRD	5	535	2.5 \pm 2.4	6.6 \pm 4.9	0.9 \pm 0.9
130776	CTD-SRD	2	680	2.9 \pm 2.6	84 \pm 56	1.5 \pm 1.4
131354	CTD-SRD	4	1578	8.8 \pm 18	35 \pm 59	1.4 \pm 1.3
131355	CTD-SRD	1	286	3.8 \pm 4.4	26 \pm 18	1.0 \pm 0.9
		2.4 \pm 1.6	736 \pm 510	3.8 \pm 3.1	18.6 \pm 22.7	1.1 \pm 0.2

(867.4 ± 714.6 km) than the females tracked in 2012 (648.2 ± 310.6 km). In 2014, 2 individuals (#130766 and #131354) performed large loops towards the French Guianese and the Brazilian coasts, whereas the 8 other turtles mostly remained close to the shoreline during the inter-nesting season (Fig. 1). The distance to shore ranged from 0.6 ± 0.5 km (#115458) to 16 ± 26 km (#130766), with turtles remaining on average within 3.8 ± 3.1 km from the coastline (Fig. 1, Table 1). The green turtles remained within 18.6 ± 22.7 km of the nesting site (range: 2.8 to 96 km; #115458 vs. #130766, respectively). The average travel speed was 1.1 ± 0.2 km h⁻¹ (range: 0.7 to 1.6 km h⁻¹; #115453 vs. #115445, respectively; Table 1).

A daily average of 5.5 ± 3.6 locations was retained to perform the kernel analysis. There was clear inter-annual variability in the habitat used by turtles: in 2012, the broad home range (90% kernel estimator) measured 351.3 km² and the core home range (50% kernel estimator) covered only 89.9 km² (Fig. 2A), whereas the 10 gravid females tracked in 2014 used

a much broader home range (up to 42 times larger than in 2012) with a 90% kernel contour that covered 15 050 km², concentrating their activity within a 1620.8 km² area (Fig. 2B).

Diving behaviour

Data from Argos-Fastloc GPS tags

The 15 Argos-linked Fastloc GPS tags deployed in 2012 provided 5522 records of maximum dive depths and 5305 records of dive durations. Maximum dive depths differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$), and varied from 0 to 150 m, with 80% of the dives performed in the upper 10 m (Fig. 3A). Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$) and ranged from 30 s to 70 min, with 35% of the dives lasting up to 5 min (Fig. 3B).

The number of ESTs recorded by the Argos-Fastloc GPS tags varied from 1 to 6 per individual (#115447,

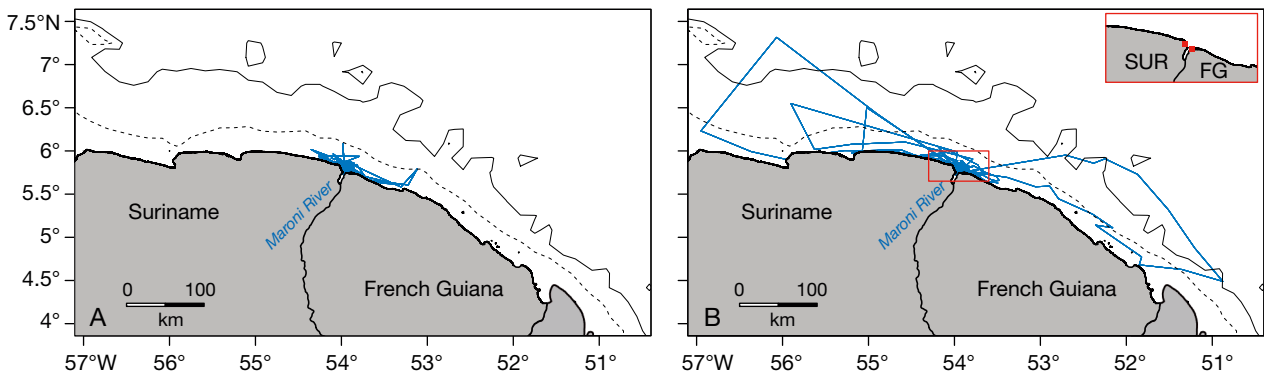


Fig. 1. Trajectories of the gravid green turtles *Chelonia mydas* tracked in (A) 2012 ($n = 15$) and (B) 2014 ($n = 10$). The 2 tagging sites are presented in the red rectangle in B (SUR = Suriname and FG = French Guiana)

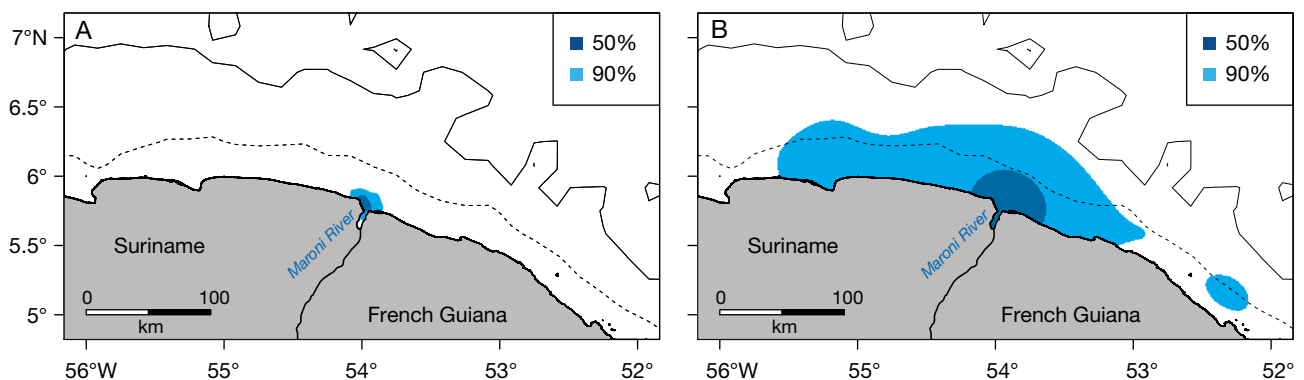


Fig. 2. Kernel density contours (90% in turquoise; 50% in dark blue) of (A) the 15 green turtles *Chelonia mydas* tracked in 2012 and (B) the 10 turtles tracked in 2014

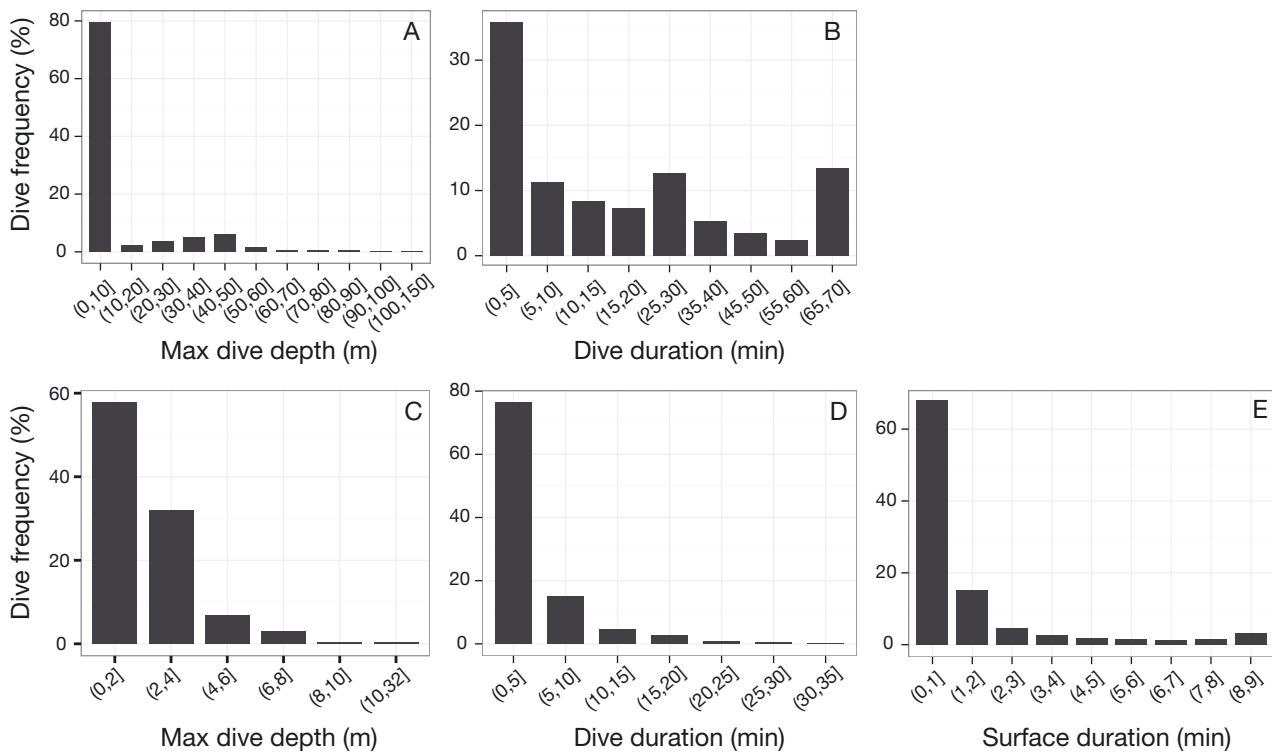


Fig. 3. Diving variables recorded by the (A,B) Argos-Fastloc GPS tags and (C–E) CTD-SRDL tags showing maximum dive depth (A,C), dive duration (B,D), and post-dive surface interval (E) for all individual green turtles *Chelonia mydas*. The bins differ from those described in the 'Materials and methods' section as they were combined for a better visual representation

#115452, #115457 vs. #115455), with an average of 1.7 ± 1.0 per female, and mostly occurred late in the afternoon, at 17:00 h. The possible inaccuracy of the bathymetry extracted in this coastal region (~ 1 km resolution) made it impossible to differentiate between terrestrial and surface basking. Unfortunately, the Argos-Fastloc GPS tags did not provide any information regarding EST duration.

Data from the CTD-SRDL tags

The 10 CTD-SRDL tags deployed in 2014 provided reliable data for 1237 summarized dive profiles. Average maximum dive depth was 2.6 ± 2.1 m, ranging from 1 to 32.5 m, and 59% of the dives were performed within the upper 2 m (Fig. 3C). Maximum dive depths were significantly different between individuals (Kruskal-Wallis rank sum test, $p < 0.001$). The maximum dive depth did not differ significantly between day and night (2.5 ± 1.5 vs. 2.8 ± 2.7 m; Mann-Whitney *U*-test, $p = 0.5723$).

Dive durations varied from 30 s to 35 min and lasted on average 4.0 ± 4.7 min, with 79% of the dives lasting < 5 min (Fig. 3D). Dive durations dif-

fered significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$). Dive duration was not significantly different between day and night (3.8 ± 4.7 vs. 4.2 ± 4.9 min; Mann-Whitney *U*-test, $p = 0.4819$).

Post-dive surface duration ranged from 0.06 s to 8.1 min, for an average duration of 1.3 ± 1.9 min. Seventy percent of the post-dive surface intervals lasted < 1 min, and differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$) (Fig. 3E). Surface duration did not differ significantly between day and night (1.33 ± 1.87 vs. 1.42 ± 2.02 min; Mann-Whitney *U*-test, $p = 0.3993$).

The average TAD was 0.71 ± 0.15 , indicating mainly V-shaped dives. However, other dive shapes were also performed by the green turtles, as 43% of the dives were associated with a TAD ranging between $0.75 \leq \text{TAD} < 1$ (resting U-shaped dives), and 47% were associated with a TAD between $0.5 \leq \text{TAD} < 0.75$ (exploratory V-shaped dives). Bottom time lasted on average 2.5 ± 4.0 min, ranging from 0 to 34.1 min, meaning that the turtles spent 52.3% of the diving time at the bottom. Average descent rate was 0.21 ± 0.20 m s^{-1} while the average ascent rate was 0.03 ± 0.03 m s^{-1} . Of the 1237 summarized dives

retained for the analysis, 62% were benthic dives and 38% were pelagic, showing a difference between bathymetry and maximum dive depth >1 m (Fig. 4).

The number of ESTs varied between 3 and 29 per individual (#131355 vs. #130767), with an average of 13.6 ± 9.5 per female during this period. EST duration ranged from 10 min (#130767 and #130771) to 1920 min (#131355), with an average duration of 210 ± 288 min.

Temperature and salinity data

During the 2012 inter-nesting season, the Argos-Fastloc GPS tags recorded 2169 temperature values ranging from 24 to 33°C, for an average temperature of $28.4 \pm 1.1^\circ\text{C}$. Eighty-six percent of the dives were performed in warm waters with temperatures between 27 and 29°C (Fig. 5); there were also inter-individual differences in the mean temperature (Kruskal-Wallis rank sum test, $p < 0.001$). A slight increase was observed in water temperature throughout the tracking months, with the coolest values in April (mean: $28.2 \pm 1.2^\circ\text{C}$) and the warmest in June ($29.0 \pm 0.9^\circ\text{C}$).

During the 2014 inter-nesting season, 57 of the CTD profiles analysed recorded a total of 516 temperature and salinity values. Salinity ranged from 1.2 to 35.5 psu (mean: 24.6 ± 10.3 psu), and temperatures varied from 25.3 to 28.4°C ($26.8 \pm 0.5^\circ\text{C}$) (Fig. 6). All

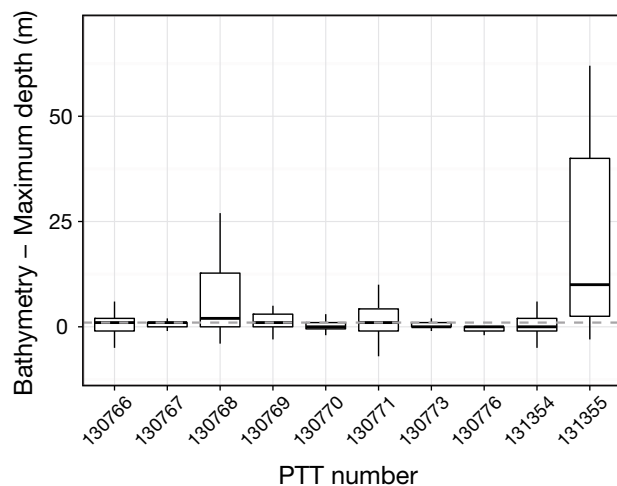


Fig. 4. Depth difference between bathymetry and maximum dive depth data from the 10 CTD-SRDL tags of each individual green turtle *Chelonia mydas* equipped in 2014. Dashed line: limit between benthic (depth difference ≤ 1 m) and pelagic dives (depth difference > 1 m)

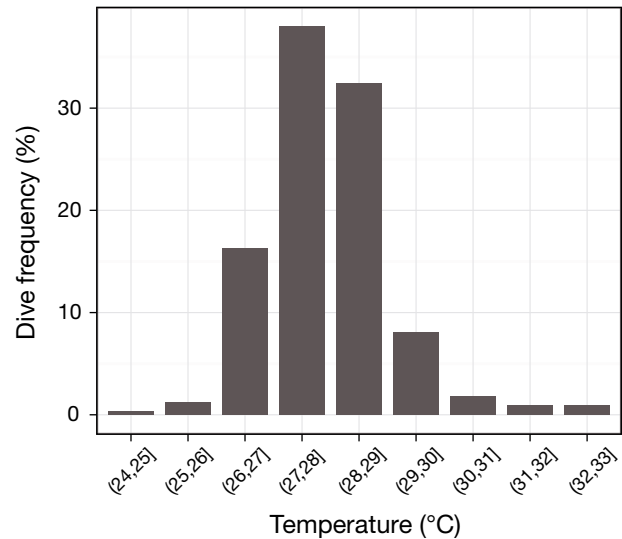


Fig. 5. *In situ* temperatures recorded by the 15 Argos-linked Fastloc GPS tags deployed on green turtles *Chelonia mydas* in 2012

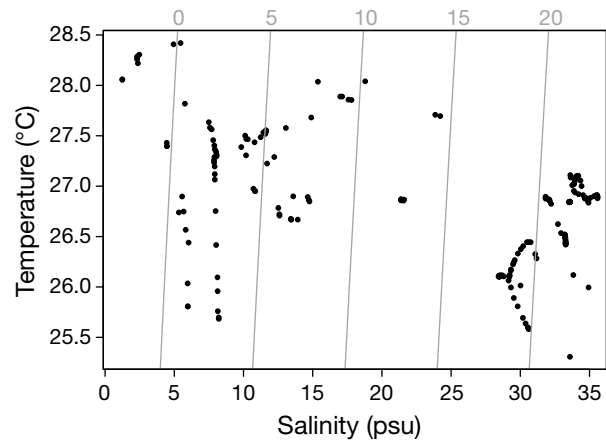


Fig. 6. Temperature–salinity diagram for the 10 individual green turtles *Chelonia mydas* fitted with a CTD-SRDL tag in 2014. Grey lines and numbers: isopycnal lines and values

turtles used a broad range of oceanographic structures, especially in terms of salinity (Fig. 6).

DISCUSSION

This tracking of green turtles from Suriname and French Guiana during the inter-nesting season provides the first data to describe their inter-nesting events, habitat use, dispersal and diving behaviour. These results highlight the various behavioural adjustments of this population in response to the atypical and estuarine habitat of the Maroni river mouth.

Inter-nesting events

Direct observation (nocturnal patrols) showed the inter-nesting interval to be 12.8 ± 1 d in 2012 ($n = 2329$) and 12.6 ± 1.4 d in 2014 ($n = 2160$) (range: 5 to 18 d), which is within the range recorded for other green turtle populations in the Atlantic (range: 10 to 14 d; Carr et al. 1974, Hays et al. 2002b), Caribbean (9 to 13 d; Bjorndal & Carr 1989, Esteban et al. 2015), and Pacific (10 to 15 d; Blanco et al. 2013). Because the turtles were equipped with transmitters on both sides of the Maroni river mouth, we can be certain that they were nesting on both the Surinamese and French Guianese beaches. However, the number of nesting events per female may be underestimated as the nocturnal patrols were only performed on the beaches of French Guiana, which may explain the long inter-nesting interval for some individuals. Simultaneous direct observation of individuals on both sides of the river mouth therefore appears to be a crucial source of additional information for tracking data, and annual monitoring on the Surinamese side is also necessary in order to paint a clear picture of the inter-nesting period.

Habitat use

Despite the high inter-annual variability of the habitat, kernel analysis indicated that the turtles spent most of their time in a relatively small area measuring 512.7 km^2 (50% contour). Although this core range was significantly larger than the 50% contour for East Pacific green turtles (3 km^2 ; Blanco et al. 2013), the French Guiana turtles concentrated their activity close to the nesting beach (range: 2.8 to 96 km, mean: 18.6 ± 22.7 km). This mirrors habitat use by green turtles in Florida (6 to 11 km; Hart et al. 2013). Gravid green turtles may therefore reduce the energy costs of locomotion by limiting their movements, as their home range is dictated by their metabolic rate (Slavenko et al. 2016).

Our estimation of home range should, however, be interpreted with caution, as the kernel densities were obtained from both Argos and GPS data. In some cases, the estimated Argos position can be some km away from the true location (Rutz & Hays 2009). This explains the high number of locations on land (32%) that had to be discarded from the analysis. The use of Argos-Fastloc GPS tags made it possible to increase the accuracy of the location estimations, which is crucial when dealing with resident animals whose movements occur on a very small scale. Argos loca-

tions had to be included in the kernel analysis, as the unique surfacing behaviour of green turtles (brief and slanting) resulted in the transmission of a very low number (7%) of GPS locations. The low number of GPS positions could also be explained by the GPS sampling interval, which was fixed to 4 h. Although a shorter sampling interval would have increased the number of GPS locations recorded, it would have also reduced the lifespan of the tag. This would have been counterproductive, as our objective was to record both the inter-nesting and migration periods for each tracked individual.

The associated habitat was characterized by low salinity and highly turbid waters resulting from the large river outputs that are continuously discharged onto the Guiana continental shelf (Jounneau & Pujos 1988, Froidefond et al. 2002). Close to the Maroni and Mana rivers, the Kaw estuary, located 250 km southeast of the rookery, has a wide range of salinities (range: 0.1 to 19 psu) that vary according to the combined effect of rainfall (2000 to 4000 mm yr^{-1} ; Lambs et al. 2007) and tides (Jounneau & Pujos 1988, Lam-Hoai et al. 2006). Négreil & Lachassagne (2000) reported that the salinity of the Kaw estuary dropped to 0.1 psu during the rainy season (April to July), similar to the salinity values recorded by tags on the turtles in our study. The green turtles were tracked from the beginning of the long rainy season (April to June), and the resulting data confirms that they crossed highly contrasted ecosystems in terms of salinity, varying from oligohaline (<5 psu) to ultrahaline habitats (>35 psu). Such results are consistent with the highly variable water properties recorded in the Maroni estuary (salinity range: 0 to 20 psu) due to the high rainfall (mean: 2000 to 2500 mm; data from Météo-France) and the flow of the river during this period (mean discharge: $1680 \text{ m}^3 \text{ s}^{-1}$; Jounneau & Pujos 1988, Artigas et al. 2003). *Chelonia mydas* therefore shows a high tolerance to a wide range of environments in French Guiana, as observed in the loggerhead turtle in southwest Florida (salinity range: 0 to 40 psu; Foley et al. 2006) and the Kemp's ridley turtle in the Gulf of Mexico (Metz 2004).

The water temperatures experienced by tracked green turtles (mean: 26 to 28°C) were similar to those recorded by the olive ridley sea turtles tracked over the Guiana shield (26.2 to 27.8°C; Plot et al. 2012). The temperature range appeared to be slightly wider for the green turtles (range: 23 to 33°C) than that recorded by their conspecifics from the Atlantic (range: 27 to 28°C; Hays et al. 2002b) and Pacific oceans (range: 27 to 29°C; Blanco et al. 2013). The higher temperatures observed in French Guiana

could be explained by the warmer freshwater of the Maroni and Mana rivers (Nikiema et al. 2007), especially during the period of maximum river discharges from May to June (Artigas et al. 2003). Indeed, the highest temperatures recorded in 2012 (29 to 33°C) were mostly located at the mouth of the river, close to the Surinamese nesting beach. Furthermore, the high temperature values recorded in our study are consistent with the samples taken by Négrel & Lachassagne (2000) in the Maroni estuary (range: 23.8 to 33.4°C).

Distance to shore

All 25 females tracked in this study remained close to the shore throughout the inter-nesting season, i.e. within 3.8 ± 3.1 km of the coastline. Similar patterns were observed in green turtles nesting in Tortuguero, Costa Rica, which stayed within 30 km of the coastline (Troëng et al. 2005). The females tracked in the present study remained essentially close to their rookery (20.5 ± 44.4 km), showing strong nest-site fidelity. This has been highlighted for green turtles in the Atlantic (Hart et al. 2013) and Pacific oceans (Blanco et al. 2013). By remaining close to their nesting site, gravid green turtles are probably saving energy for oviposition. However, some inter-individual differences were observed (range: 2.8 to 96 km), particularly for one turtle that travelled over 368 km from the nesting beach (#130766). Similar extensive movements during the inter-nesting season have been recorded in loggerhead turtles in the Mediterranean Sea (Schofield et al. 2010b), as some females may leave the vicinity of the rookery without necessarily nesting on alternative sites. In contrast, some females do show a lack of nest-site fidelity and nest on alternative sites, as observed in green and hawksbill turtles from the Lesser Antilles in the Caribbean (Esteban et al. 2015). The associated travel speeds of the turtles tracked in our study (1.1 ± 0.2 km h⁻¹, range: 0.7 to 1.6 km h⁻¹) were close to those reported by Troëng et al. (2005) (mean: 0.9 ± 1.0 km h⁻¹) and to those recorded in the green turtle population of Ascension Island (mean: 1.5 km h⁻¹, range: 0.9 to 3.5 km h⁻¹; Carr et al. 1974).

Diving behaviour

The dives performed in 2014 by the green turtles during the inter-nesting season were shallow (59% of dives <2 m) and short (79% of dives <5 min). Similar behaviour has been observed in East Pacific green

turtles tracked from Costa Rica (69% <5 m; 72% between 2 and 10 min; Blanco et al. 2013), and also in the leatherback population using the same Awala-Yalimapo nesting site in French Guiana (59% <5 m, 60% <6 min; Fossette et al. 2007). Such behaviour indicates that the gravid turtles studied are mainly influenced by the bathymetry of the inter-nesting habitat. The GEBCO database shows bathymetry to be below 5 m at the mouth of the Maroni River, where the turtles spend most of their time. The dive durations were much shorter than those recorded in Ascension Island green turtles, which mainly rested during the inter-nesting season (mean: 22.1 vs. 7.3 min while migrating; Hays et al. 1999). Additionally, green turtles must reach an optimal depth of 19 m to achieve negative buoyancy for resting after fully inflating their lungs at the surface (Hays et al. 2000). The short, shallow dives of the French Guianese green turtles in the very shallow habitat of the Maroni River mouth could therefore be linked to short-term resting activity caused by lung volume issues. Low visibility could also explain the very short duration of dives, causing turtles to return frequently to the surface to find their way using air-borne chemosensory cues (Endres & Lohmann 2013, Endres et al. 2016).

Alternatively, the short dives observed in French Guiana could be linked to foraging activity, as also observed in Australian green turtles (Hazel et al. 2009). However, the high river outputs lead to low levels of irradiance (Seminoff et al. 2002), probably resulting in a lack of seagrass in this inter-nesting habitat. If the turtles feed during the inter-nesting period, such conditions could encourage them to feed on other resources such as invertebrates, macroplankton or macroalgae (Bjorndal 1982). The foraging ecology of *Chelonia mydas* varies greatly among geographical regions (Buttemer & Dawson 1993, Heithaus et al. 2002, Hatase et al. 2006, Amorocho & Reina 2007, Burkholder et al. 2011, Blanco et al. 2013) and is particularly diverse in estuarine habitats, where this species has been observed to consume mainly animal matter, i.e. crustaceans, molluscs, polychaetes and cnidarians (González Carman et al. 2012, Santos et al. 2015). Jellyfish are also particularly abundant on the French Guiana continental shelf (Fossette et al. 2009), providing an alternative source of nutrition that may enable this green turtle population to adapt to the local conditions of this habitat. However, a visual investigation would be required to confirm this assumption, as was previously carried out on green and loggerhead turtles in the Mediterranean Sea (Hays et al. 2002b, Schofield et al. 2006). Other devices such as jaw sensors could

also be used in future studies to investigate if green turtles feed during the inter-nesting season in French Guiana (Fossette et al. 2008).

Gravid green turtles are known to commonly alternate between different activities at sea during this period, i.e. travelling, resting or foraging (Cheng et al. 2013), and change between different dive shapes, i.e. U (resting/foraging dives), V (exploratory dives) or S (energy-saving swimming); see Hochscheid et al. (1999) for further information. This was reflected in our results, where 43% of the dives were U-shaped and 47% were V-shaped. To confirm the occurrence of these different activities, it would be necessary to deploy acceleration data loggers, as used by Cheng et al. (2013), and perform isotopic analyses, oesophageal lavages and gut content analysis to assess the types of prey consumed during the inter-nesting season (Hatase et al. 2006, Amorcho & Reina 2007).

Multiple extended surface intervals were identified by the tags, and may be associated with a resting activity for prolonged periods (mean: 210 ± 288 min). Unlike East Pacific green turtles, the daytime surfacing behaviour of the females tracked in our study suggests basking at the surface. Such behaviour can be beneficial for thermoregulation (Sapsford & van der Riet 1979, Hochscheid et al. 2010), avoidance of aggressive males or potential predators (Swimmer 2006), delay of algal or fungal infestations and even enhancement of immune response (Boyer 1965, Swimmer 2006). Although some visual investigation is needed, such extended periods of hauling out could be associated with terrestrial basking on a persistent sandbank located in the core area of the green turtles (D. Chevallier unpubl. data). Two tags recorded extremely long periods of hauling out (>1300 min, ~ 22 h). These unusual basking events were occasional, and could be caused by turtles becoming trapped in the mud, the shrubby vegetation, or the decomposing wood accumulated on the beach in piles that can be several meters high. This phenomenon was observed for one female (#131355) in 2014 (D. Chevallier unpubl. data). Indeed, the multiple mudbanks along the shores of French Guiana and Suriname (Allison & Lee 2004, Anthony et al. 2010, 2015, Péron et al. 2013), are generated by the sediment discharges from the Amazon River, and this dynamic ecosystem leads to continuous erosion and accretion processes. The basking behaviour described in this study may be related to resting activity and an uptake of solar radiation by individuals for thermoregulation (Whittow & Balazs 1982, Hochscheid et al. 2010, Van Houtan et al. 2015).

Conservation implications

Satellite tracking of the green turtle population nesting in Suriname and French Guiana made it possible to locate and quantify the habitat used by this species during the inter-nesting season. The survival of this endangered species is at risk given its limited dispersal close to its nesting beaches and the life-threatening risk of illegal fishing along the Guiana coast (Charuau 2002, DEAL Guyane 2013). An evaluation of their home range is essential to obtain a reliable picture of core activity areas and identify hotspots for the protection of this endangered species (Scott et al. 2012, Schofield et al. 2013, Pendoley et al. 2014). The high energetic costs of reproduction and nesting activities make the green turtle particularly vulnerable during the breeding–nesting period, especially in highly turbid waters such as those of the Maroni River, where visibility is significantly reduced (Metz 2004). Although there is some inter-annual variability, the limited core home ranges found in this study (i.e. the areas where turtles concentrate their activity) may facilitate the implementation of adequate measures on a regional scale. Such measures include recording the location of illegal fisheries by the National Navy, the French National Agency for Hunting and Wildlife (ONCFS) or the Amana Nature Reserve, thus enabling us to focus on conservation efforts in this critical habitat. Indeed, the home range estimation derived from this study closely overlaps with a major fishing ground unit (Levrel 2012, Chevallier 2013). We therefore recommend further study to evaluate the interactions between gravid green turtles and fisheries, and thus permit the delineation of a Marine Protected Area that would cover the core area of this endangered species. Given the nesting peak of this population (i.e. from April to June) and the location of its habitat (at the natural border between Suriname and French Guiana), an open dialogue is crucial if we hope to redefine international fishing practices and ensure the conservation of this endangered species.

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