

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Influence of artificial lights, logs and erosion on leatherback sea turtle hatchling orientation at Pongara National Park, Gabon

Stéphanie Bourgeois^a, Emmanuelle Gilot-Fromont^b, Anne Viallefont^b, François Boussamba^c, Sharon L. Deem^{d,*}

^aNational Veterinary School of Alfort, 7, avenue du Général de Gaulle, 94700 Maisons-Alfort, France

^bUnité Mixte de Recherche N°5558 "Biométrie et Biologie Evolutive", University Claude Bernard Lyon 1, 43 Bd. du 11 novembre 1918, 69622 Villeurbanne Cedex, France

^cAventures Sans Frontières, BP 7248 Libreville, Gabon

^dDepartment of Animal Health, Smithsonian National Zoological Park, 3001 Connecticut Avenue, Washington, DC 20008, USA

ARTICLE INFO

Article history:

Received 28 February 2008

Received in revised form

22 September 2008

Accepted 27 September 2008

Available online 12 November 2008

Keywords:

Dermochelys coriacea

Gabon

Hatchlings

Leatherback sea turtle

Orientation

Photopollution

ABSTRACT

The coast of Gabon is one of the most important nesting sites for the endangered leatherback sea turtle *Dermochelys coriacea*. In this study, hatchling orientation was recorded during natural emergences at Pongara National Park, Gabon. This nesting beach is located close to both the capital of Gabon and a developing resort area, Pointe Denis. Under natural conditions most sea turtle hatchlings emerge at night and orient to the ocean by crawling away from dark, high silhouettes landward towards the bright, low seaward horizons. Artificial lights interfere with natural cues and disrupt hatchling orientation. The relative influence of artificial lights, logs and erosion were assessed on the nesting beach in Pongara National Park using a linear mixed model. We found that the attraction to artificial lights was higher than the effect of silhouette cues landward alone, but could be balanced by the simultaneous presence of the moon. Based upon these results, we recommend combining light management in the resort area to reduce the light pollution on the nesting beach and reinforcement of natural cues landward to minimize the effect of the remaining light pollution from the capital.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Under natural conditions most sea turtle hatchlings emerge during the cool hours of night and move along the beach immediately towards the ocean. The primary cues for sea-finding under natural conditions are visual and are mainly associated with light intensity and horizon elevation. Hatchlings have been shown to analyze their visual environment

between a wide cone of acceptance (180°) centered on the horizon (Witherington and Martin, 1996). Hatchlings orient away from high silhouette elevations, which absorb light (Limpus, 1971; Salmon et al., 1992), and towards the brightest region, which under natural conditions will be the ocean (Mrosovsky and Shettleworth, 1968; Van Rhijn and Van Gorkom, 1983). While on the beach, hatchlings find the ocean by crawling towards the lower, brighter seaward horizon

* Corresponding author: Present address: WildCare Institute, Saint Louis Zoo, 1 Government Drive, Saint Louis, MO 63110, USA. Tel.: +1 314 646 4528; fax: +1 314 746 5534.

E-mail addresses: stephbougeois@hotmail.com (S. Bourgeois), fromont@biomserv.univ-lyon1.fr (E. Gilot-Fromont), anne.viallefont@univ-lyon2.fr (A. Viallefont), deem@stlzoo.org (S.L. Deem).

0006-3207/\$ - see front matter © 2008 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2008.09.028

and away from the dark, elevated silhouettes of vegetation and dunes. When these cues conflict, some hatchlings tend to rely on elevation cues over light (Van Rhijn and Van Gorkom, 1983) and move seaward by crawling toward the lowest illuminated horizon. Movement towards the brightest light is favored by hatchlings only when the horizon elevation is similar in all directions (Salmon et al., 1992).

In beaches located close to human populations, hatchling seafinding is often disrupted by artificial lighting (Witherington and Martin, 1996; Salmon, 2003). Hatchlings that are oriented away from the most direct ocean path are “mis-oriented” and hatchlings lacking directed orientation are “dis-oriented” (Verheijen, 1985). Artificial lights can be a super-stimulus that overrides tendencies to orient to other visual cues (Witherington and Martin, 1996). In many cases, the interaction between natural and artificial visual stimuli is competitive: seafinding, disorientation and mis-orientation are graded responses correlated with differences in perceived magnitudes of natural and artificial cues (Tuxbury and Salmon, 2005). The moon usually decreases the impact of artificial light by modulating background illumination and reducing the directivity of the light: directivity being defined as the contrast of irradiance between light sources and background (Verheijen, 1958; Salmon and Witherington, 1995; Tuxbury and Salmon, 2005).

By making the way to the ocean longer, artificial lights are responsible for increased mortality of hatchlings for a variety of reasons including exhaustion, dehydration, increased predation, and human traffic (McFarlane, 1963; Limpus, 1971; Philibosian, 1976; Mann, 1978; Mortimer, 1979; Peters and Verhoeven, 1994; Witherington and Martin, 1996). Additionally, mortality often will occur even if hatchlings reach the ocean after a long wandering because of the consumption of their limited energetic reserves and the high energetic cost of the first 24 h of crawling and swimming (Kraemer and Bennett, 1981). Additionally, it has been demonstrated that the longer hatchlings are disoriented on land, the more difficulty they have to properly orient in the sea when surface waves are absent (Lorne and Salmon, 2007).

Central Africa is a major rookery for leatherback sea turtles (*Dermochelys coriacea*) with a peak of 1500 nests per night over the entire Gabonese coastline (Aventures Sans Frontières, unpublished data). One of the primary leatherback nesting beaches in Gabon is located within the newly established Pongara National Park, located close to the capital city, Libreville. Beach landscapes in the region are deeply modified by the countless logs lost during commercial timber transport, which obstruct the nesting beaches and cause false crawls, nesting below the high tide line and fatal entanglement of females, with approximately 30.5% of the nesting area in Pongara National Park blocked by logs in the 2002–2004 nesting seasons (Laurance et al., 2008). Therefore, the beach environment in Pongara is influenced greatly by logs and by the large source of artificial light from Libreville and from Pointe Denis resort area, within walking distant of the nesting beach. Light pollution from this resort area has grown significantly during the last five years in conjunction with the increase in private bungalows and hotels (Deem et al., 2007). The third particularity of this beach is a continuous erosion

process, which creates major escarpments, deeply impacting the visual environment of newly emerged hatchlings.

Most of the orientation studies are based on experiments in a controlled environment. Here we studied nests in which hatchlings have emerged in natural conditions, on a beach characterized by several natural and artificial visual cues. In a previous study it was suggested that enhancing natural cues could be an efficient conservation strategy, when it is impossible to reduce artificial lights (Tuxbury and Salmon, 2005). The objective of our study was to assess the relative impact of artificial lights, and silhouettes of logs and erosion on leatherback sea turtle hatchling orientation in Pongara National Park, Gabon.

2. Methods

2.1. Study area

Research was conducted at Pongara National Park, Gabon, located 11 km across an estuary from the capital, Libreville. The study site is a 3.5 km beach (00°21.149' N, 009°21.298' E - 00°19.975' N, 009°19.665' E) running north-east to south-west from Pointe Pongara (Fig. 1). The leatherback sea turtle nesting season in Pongara is October to April with peak nesting occurring in December and February (Aventures Sans Frontières, unpublished data). More than 1,800 leatherback nesting events were recorded during the 2003–2004 season by the local NGO, Aventures Sans Frontières.

The nesting zone is a strip of open sand about 10–20 m wide, next to a large extent of savanna that separates the beach from the village of Pointe Denis to the east and from the forest to the south-east. Landward of the high tide line is an area covered by dense vegetation consisting mainly of *Ipomea pescaprae* and *Canavalia maritima* and dispersed low shrubs. This area is continuously modified by a process of erosion, resulting in steep and narrow areas and in vertical escarpments, approximately 0.5 to more than 1.5 m high. Lights from Libreville are visible during the whole night and along the entire beach from the north-east and lights from Pointe Denis are visible from the east between 0.5 and 1.5 km from Pointe Pongara. The landscape varies slightly along the beach. To the north-east, many logs accumulate in the wide sand area and the artificial lights are directly visible behind Pointe Pongara and the savanna. To the south-west, the narrow sand area is delimited by a continuous escarpment resulting from the erosion and low shrubs and artificial lights are directly visible only behind Pointe Pongara.

2.2. Data collection

Data were obtained from natural nests that emerged in March and April 2006. The beach was patrolled every morning and the nests were located by the tracks of hatchlings in the sand. All nests that hatched after sunset and before sunrise with visible tracks, possible to count, were included in the study. The direction of each track was recorded in the periphery of a 10 m diameter circle drawn in the sand around the nest. The direction corresponded to the angle between the track and the straight path to the ocean. Positive values were attrib-

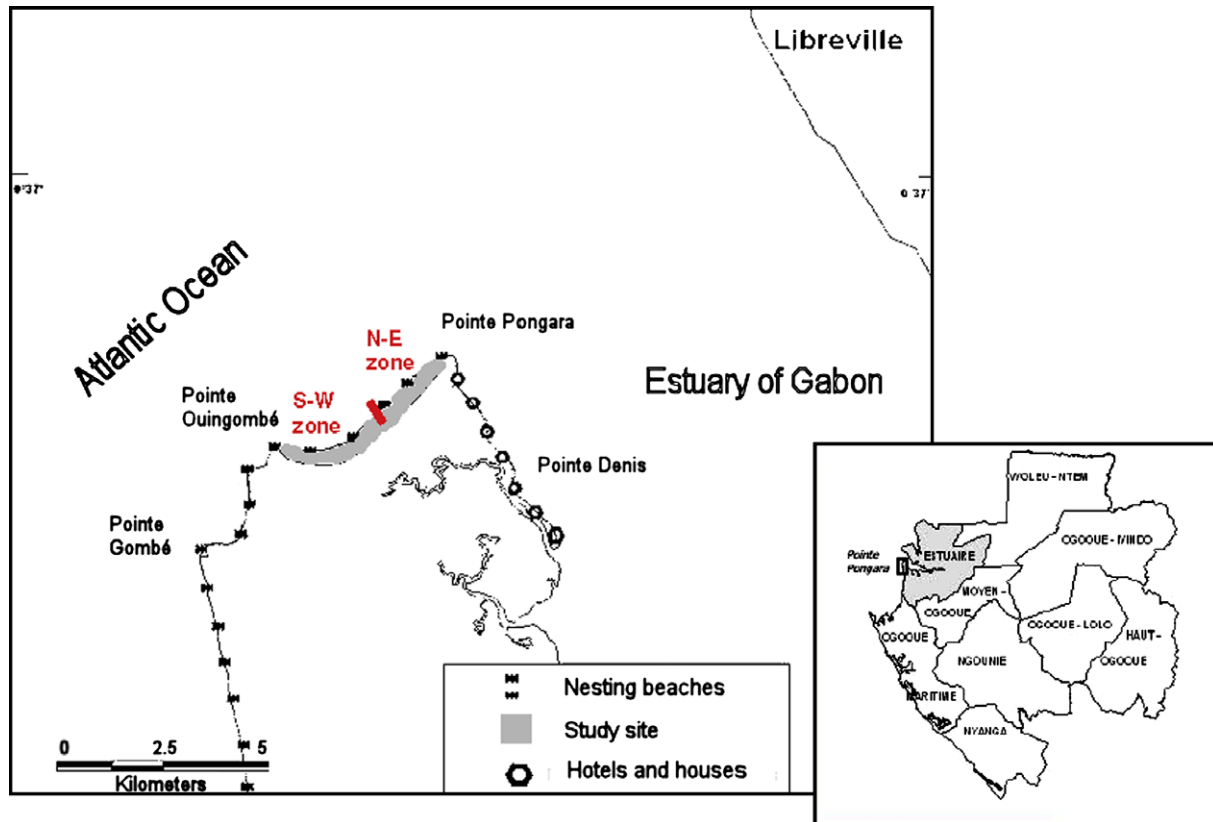


Fig. 1 – Map of the study site in Pongara National Park and its localization in Gabon. The nesting beach (in grey) exposed to light pollution from Pointe Denis (to the east of the beach, marked by open circles) and from Libreville (to the north-east). The break between the north-east and the south-west zones is figured in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

uted to the tracks facing north-east and negative values to the tracks facing south-west of the beach. Fig. 2 provides four examples of hatchling orientation from nests located north-east and south-west of the beach, and that hatched during a night with a large moon or during a moonless night. The direction angles were estimated a posteriori, based on the finding that the tracks were equidistant within a quadrant and knowing the portion of the circle crossed by hatchlings. For example, if 14 hatchlings crossed the circle in quadrant 0–45°, these hatchlings would be given values of 3°, 6°, 9°, ..., 39°, and 42° (Nest 60, Fig. 2). The exception to this was that an estimate of 0° was attributed to the whole group of tracks aggregated around the straight path to the ocean (for example, Nest 74, Fig. 2).

The following parameters were recorded at each nest: date, time of emergence, GPS position, moon phase, distance to the high tide line, drawing of vegetation cover, escarpments in the sand and logs and their distance to the nest. Time of emergence was roughly estimated according to tide, and only used to determine whether the emergence occurred before sunset. Vertical escarpments in the sand resulting from the erosion were recorded, as they played the role of shape cues by creating dark silhouettes landward, as do logs and vegetation. If more than one shape cue was present, we only recorded the one closest to the nest. Vegetation and escarpments were considered as one shape cue since the two were subjectively inseparable at our study site. The horizontal extent of the

shape cue was determined by the angle (in degrees) between the nest and the two points where the shape cue crossed the circle around the nest. The artificial lights were measured at night every 250 m along the beach using a compass to determine the horizontal extent of the artificial lights visible from a nest at turtle-eye level. The extent was evaluated by naked eye, by the angle (in degrees) between the nest and the extreme bright points at the sand level.

Nests were dug up three days later to estimate the accuracy of the tracks counted. The number of live emerged hatchlings was approximated by counting the number of empty shells, minus the number of dead or alive hatchlings in the sand column.

2.3. Data analysis

The location of the nests was tested for random distribution with a Chi-square test. We used logistic regression to determine the relationship between the number of tracks per nest and the number of live emerged hatchlings. The normality of the distribution of the tracks was assessed with a Shapiro-Wilk *W* test for normality. We used logistic regression and ANOVA to determine the variation of the tracks direction and of the candidate explanatory variables (e.g., shape cues and light) along the beach. The GPS North coordinates increase regularly along the beach and were used as a quantitative variable to summarize the location of the nests.

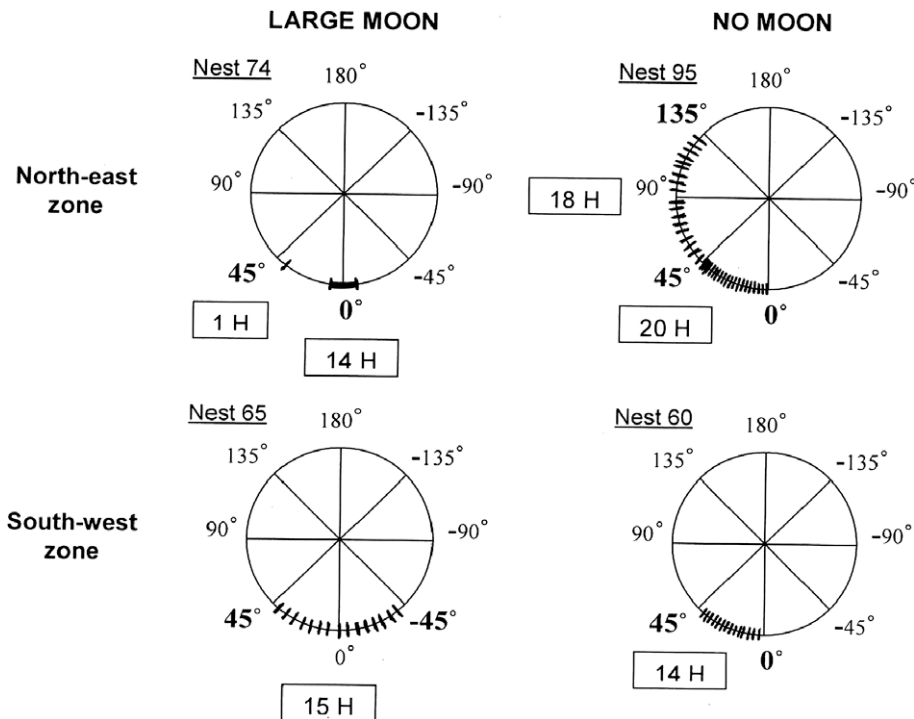


Fig. 2 – Examples of hatchlings orientation direction around four nests, located north-east and south-west of Pongara beach, during a night with a large moon or during a moonless night. A 10 m diameter circle was drawn in the sand around the nest, after the emergence. Positive values were given to the tracks facing north-east; negative values to the tracks facing south-west (the ocean was located at 0°). The number of hatchlings (H) that have crossed the circle in each quadrant was counted to estimate individual direction angles. A log was located at 180° near nest 74.

To assess the influence of artificial lights, shape cues and moon size on hatchling orientation, the direction of individual tracks was modeled using a linear mixed model. The mixed model permitted the use of individual tracks while correcting for the lack of independence between individuals from the same nest. Four candidate explanatory variables were introduced as fixed effects:

- LIGHT: the extent of the artificial lights, transformed in a binary qualitative variable (0: width less than 100°, 1: width more than 100°).
- POSI: the position of the shape cue around the nest, transformed in a qualitative variable with four modalities (0: absence of shape cue, 1: shape cue located seaward, 2: shape cue located north-east of the nest, between the nest and Libreville, 3: shape cue located landward, 4: shape cue located south-west of the nest. The modality 1 was then suppressed as it concerned only one nest).
- MOON: the phase of the moon cycle, transformed in a binary variable (0: more than 7 days from the full moon, 1: less than 7 days from the full moon).
- SHAPE: the horizontal extent of the shape cue, measured by the angle between the nest and the two points where the shape cue cross the circle around the nest. It was tested as a quantitative variable.

NEST is a random effect that assesses variation among nests from which hatchlings emerged.

The perception of the light and moon intensity can be modulated by the characteristics of each nest (e.g., location

on the beach, time of emergence, and weather). To test the variability of the effect of these two explanatory variables, we added interaction between NEST and LIGHT or MOON. These interaction terms are the random variation of the light or moon effect among nests.

Interactions between the fixed effects were also tested. The interactions moon \times position and moon \times artificial lights were included in the model to determine if the influence of the artificial lights varied with the nest environment (e.g., logs, erosion, and vegetation) and to explore the cues conflict competition hypothesis (Tuxbury and Salmon, 2005).

The residuals from the model assess intra-nest variation between hatchlings. They were modeled to figure the dispersion of the tracks from one nest, which usually increases when the mis-orientation increases, by using a weight function. The standard deviation of the weighted residuals is proportional to the fitted value raised to a power. The model was built using a forward selection and comparisons between models were done using the corrected Akaike information criterion (AIC) (Burnham and Anderson, 2002). Statistics were performed using the software R (R Foundation, version 2.3.1).

3. Results

3.1. Descriptive analysis

In total, 726 tracks from 41 nests uniformly scattered along the beach ($\chi^2 = 7$, $ddl = 6$, $p = 0.321$) were included in the study.

Seven nests were excluded because it was estimated that the time of emergence was after sunrise and four nests because the misorientation made it impossible to count the tracks. The number of tracks per nest was not significantly correlated to the number of live emerged hatchlings ($r^2 = 0.08$, $F = 2.38$, $p = 0.134$). The mean number of live emerged hatchlings was 41.8 ± 16 per nest, while the mean number of tracks counted was 17.7 ± 6.9 , but the accuracy of the track count was up to 100% when the tracks were dispersed. Overlapping tracks in the direction of the ocean, predation closer than 5 m from the nest, wind, rain and sand type can explain the low number of tracks observed. The distribution of the variable “direction of the tracks” was not normal (Shapiro–Wilk: $W = 0.835$, $p < 0.001$).

The extent of the shape cues in the nest environment increased significantly along the beach from north-east to south-west ($r^2 = 0.24$, $F = 12.65$, $p < 0.001$), while the extent of the artificial lights decreased (Fig. 3a and b). Based on this result, we divided the beach in two zones: the north-east zone, where the extent of the artificial lights was more than 100° and the south-west zone, where the extent was less than 100° . The break between these two zones was located at $00^\circ 24.468'$ N (Fig. 1), which corresponds to the point where the forest gallery begins to block the lights from Pointe Denis, and where the lights from Libreville decrease due to a change in the beach orientation. The mean direction of the tracks was significantly different between the two zones (12.4° and 25.7° , $F = 14.79$, $p < 0.001$), with a higher value in the north-east zone (Fig. 4).

3.2. Explanatory model

Each of the models, including one, two or all three variables LIGHT, MOON and POSI as fixed terms were better than the null model ($\Delta AIC > 4.82$ with one variable, 11.12 with two variables and 36.96 with three variables), whereas the variable SHAPE did not improve the models ($\Delta AIC < -4.10$). The models were much improved when adding the interaction term $LIGHT \times POSI$ ($\Delta AIC = 24.12$) and the interaction term $LIGHT \times MOON$ ($\Delta AIC = 5.51$). All models including residuals modeling vastly outperformed those with residuals independent of the fitted value ($\Delta AIC = 300.26$). Similar improvements were obtained when fitting LIGHT and MOON as random terms ($\Delta AIC = 220.91$). Among all the tested models, the dependence of hatchling direction on the factors is best modeled as follows:

$$TRACK_{ij} = \beta_0 + \beta_1.LIGHT + \beta_{2k}.POSI_k + \beta_{3k}.LIGHT \\ : POSI_k + \beta_4.MOON + u_{0i} + u_{1i}.LIGHT + u_{2i}.MOON \\ + a.(TRACK_i)^b$$

where $TRACK_{ij}$ is the direction of the hatchling j from the nest i (in degrees), β are the coefficients of the fixed terms (k is the value of the variable POSI) and u are the coefficients of the random effects. The coefficients a and b are used to calculate the intra-nest residuals from the mean fitted value of the nest i .

The model is a linear mixed model, which includes a fixed part (1st line) and a random part (2nd and 3rd lines). The fixed part represents the mean effects of the moon, the artificial lights and the shape cues on hatchling orientation. The ran-

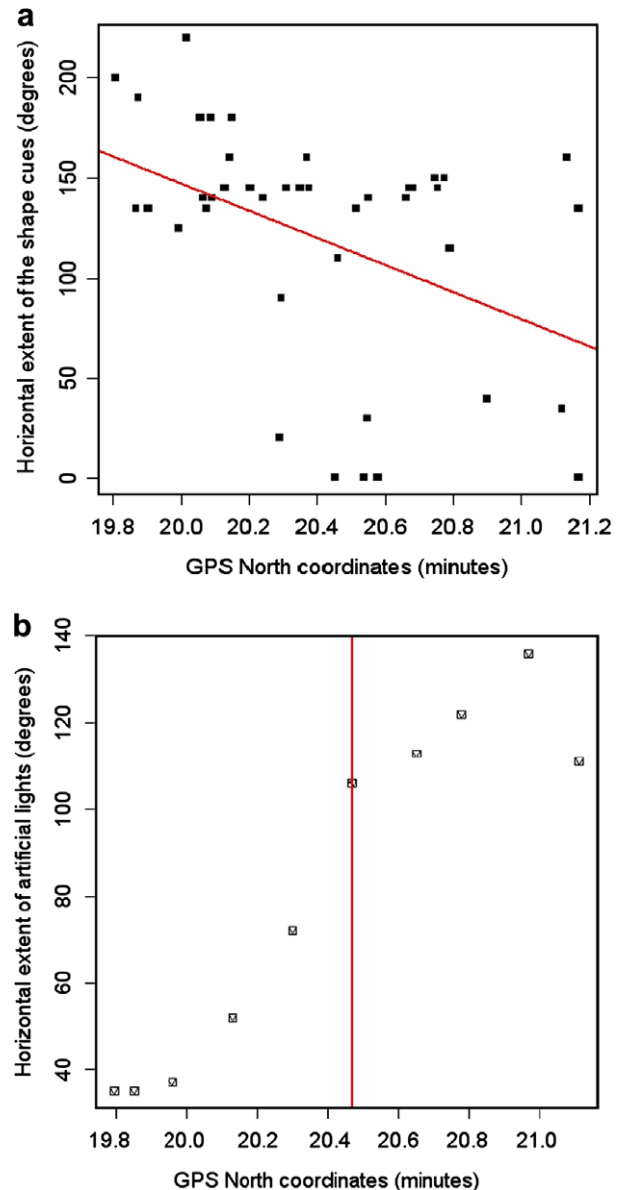


Fig. 3 – Extent of shape cues (logs, vegetation and erosion) (a) and artificial lights (b) along the nesting beach in Pongara National Park, Gabon. The horizontal extent was determined by the angle (in degrees) between the nest and the two points where the shape cue crossed the circle around the nest (a) or between the nest and the extreme bright points (b). The GPS north coordinates decrease from north-east to south-west along the beach. The red line indicate the break between the two zones based on the extent of artificial lights (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dom part assesses inter-nest variability (random effects) and intra-nest variability (residuals).

3.3. Model interpretation

The increase of artificial lights in the north-east zone of the beach had a significant influence on hatchling orientation

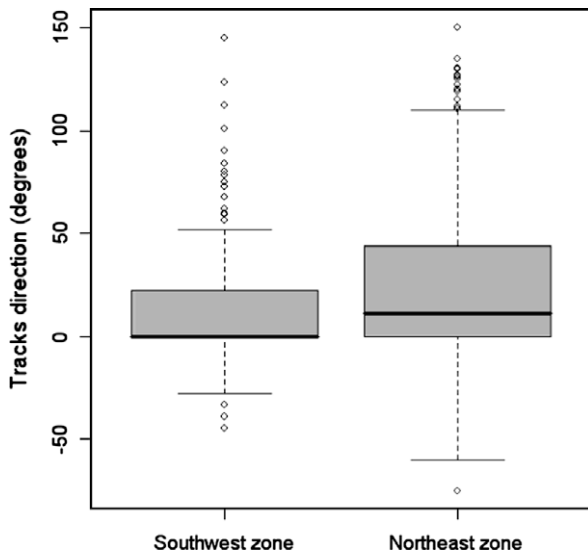


Fig. 4 – Boxplot of the direction of leatherback hatchling tracks in the north-east and south-west zones of the nesting beach in Pongara National Park, Gabon. 50% of the tracks are in the box; median, upper and lower quartile as well as minimum and maximum values are drawn.

(Table 1). The direction of the tracks was 38.6° farther from the straight path to the ocean than in the south-west zone ($p = 0.023$). This effect is exactly balanced in the presence of a shape cue landward (-38.4° , $p = 0.039$). All along the beach, the mean direction of the tracks in the presence of a shape cue landward was around $16\text{--}17^\circ$ from the ocean during nights with less than half moon and around 4° from the ocean during nights with more than half moon ($p = 0.009$). A shape cue in the opposite direction of artificial lights vastly increased the angle between the tracks and the straight path to the ocean in the south-west zone (74.6° , $p = 0.001$), whereas

the influence is almost null in the presence of artificial lights in the north-east zone (2.5° , $p = 0.036$). The effects of a shape cue between the nest and the artificial lights on the entire beach ($p = 0.762$ and $p = 0.212$), and landward in the south-west zone ($p = 0.374$), were not significant. The standard deviation between nests of the influence of the artificial lights in the north-east zone was 24.6° and the standard deviation between nests of the influence of the moon in the entire beach was 15.9° . The standard deviation of the intra-nest residuals was $10.84 \times (\text{fitted direction})^{0.333}$. The variance due to the random effects was decomposed as follows:

- 89.1% of inter-nest variability (56.2% due to the variable effect of artificial lights, 23.4% due to the variable effect of the moon and 9.5% due to other “nest” effects).
- 10.9% of intra-nest variability between hatchlings.

4. Discussion

4.1. Impact of artificial lighting, logs and erosion on hatchling orientation

In this study we assessed the relative influence of artificial lights, logs and escarpments resulting from the erosion on leatherback hatchling seafinding ability in situ. We showed that leatherback hatchling orientation was deviated towards the direction of artificial lights all along the study site. However, artificial lights tended to cause higher deviation in the north-east zone (zone of high artificial light and few silhouette cues) than in the south-west zone. Additionally, we found that the dispersion of the tracks within a nest increased proportionally to the mis-orientation, even if this result is probably partly due to the method that we used to estimate the direction angles, which underestimated the variability in the direction to the ocean. The position along the beach of logs

Table 1 – Summary of the final selected model for the effects of artificial lights, shape cues and moon size on the direction of leatherback hatchlings tracks in Pongara National Park, Gabon. The model is a linear mixed model, with fixed and random effects (LIGHT, extent of artificial lights; POSI = 2, shape cue located north-east of the nest; POSI = 3, shape cue located landward; POSI = 4, shape cue located south-west of the nest; MOON, phase of the moon cycle). Intra-nest residuals are proportional to the fitted value raised to a power. Degrees of freedom (df) as well as t-test value are given for each parameter; p-value that are statistically significant at the 5% level are bolded.

Variables	Coefficients	df	t-Test	p-Value
<i>Fixed effects</i>				
Intercept	6.319	685	0.589	0.556
LIGHT	38.637	32	2.394	0.023
POSI = 2	-3.967	32	-0.304	0.762
POSI = 3	10.308	32	0.901	0.374
POSI = 4	74.581	32	3.568	0.001
MOON	-12.706	32	-2.805	0.009
LIGHT:POSI = 2	-29.455	32	-1.275	0.212
LIGHT:POSI = 3	-38.404	32	-2.156	0.039
LIGHT:POSI = 4	-72.053	32	-2.191	0.036
<i>Random effects</i>				
Intercept	10.127			
LIGHT	24.611			
MOON	15.875			
Residuals	$10.839 \times (\text{fitted})^{0.333}$			

and escarpments had an influence on leatherback hatchling orientation, but their horizontal extent was not a significant factor. The small width of the nesting beach at Pongara probably results in a horizontal shape cue threshold being met everywhere along the beach. The positive influence on leatherback hatchling seafinding is large when logs or escarpments in the sand are located landward, whereas the logs often had a negative influence when located in the opposite direction of the artificial lights or seaward. In fact the leatherback hatchling tracks from nests with a log placed seaward could not be accurately recorded because hatchlings tended to walk in countless circles, unable to escape.

Our results agree with the cues competition hypothesis, which considers that sea turtle hatchling orientation depends on the relative perception of natural and artificial cues (Tuxbury and Salmon, 2005). Disorientation occurs when artificial light is a stronger stimulus than natural cues. Our model showed that the influence of the logs and escarpments resulting from the erosion was variable and dependent on the level of artificial lights. Moreover, the moon modulates the ambient light level and decreases the directivity of artificial lights. According to the model, the attraction to artificial lights is higher than the positive effect of shape cues landward alone, but can be balanced when a positive effect of the moon occurs.

Salmon and Witherington (1995) considered that orientation is disturbed when the modal direction is deviated from ocean direction from more than 30° or the dispersion is more than 90°. Fitted values given by the model showed that disruption of orientation can potentially occur in all the nests located in the north-east zone, even if the risk is lowered by the presence of a shape cue landward or during nights with more than half moon. Misorientation occurred in the south-west zone only when a shape cue was located in the opposite direction of artificial lights. The north-east zone is the zone where the risk of disruption of orientation is higher, because it is the most open area (e.g., without logs, erosion process and vegetation) and because artificial lights are more visible.

4.2. Applicability of the mixed model

The influence of artificial lights, shape cues and moon on leatherback sea turtle hatchling orientation was examined using individual tracks while correcting for the lack of independence inside a nest with a mixed model. It is uncommon to study sea turtle hatchling orientation using individual tracks. Both experimental and in situ studies are usually conducted by considering group orientation (Mrosovsky, 1970; Mrosovsky and Shettleworth, 1975; Godfrey and Barreto, 1995; Salmon and Witherington, 1995; Peters and Verhoeven, 1994). The overlapping tracks, which bias the count, especially when many hatchlings are going straight to the ocean, did not allow us to estimate the percentage of tracks in several directions, as in Peters and Verhoeven (1994), and led to an overestimation of the proportion of misoriented hatchlings. The distribution of the tracks around the nest, which often consisted in one group seaward and several dispersed individuals in other directions, was not appropriate for measuring modal direction and dispersion as recommended by Witherington and Martin (1996). A linear mixed model al-

lowed us to test the influence of several factors on a large sample. We measured individual direction of misoriented hatchlings, without having to estimate the proportion of misorientation. The distribution of the direction of the tracks was not normal, because of the attribution of the angle a posteriori, and the choice to attribute the same value of 0° to all the tracks aggregated close to the straight path to the ocean. We believe that this bias does not affect the validity of the linear mixed model. The residuals are symmetrical and homoscedastic, which should ensure validity of the tests.

Another application of the mixed model is to assess the variability of tested and non-measured effects in a study in situ and to distinguish inter- and intra-nest variability. Both intra- and inter-nest variability were expected and confirmed by the model. Intra-nest variability is the dispersion of individual tracks between individuals emerging from the same nest and is known to increase when the orientation is disrupted (Salmon and Witherington, 1995). Inter-nest variability is mostly explained by the model as the variable effect of artificial lights and moon on hatchling orientation and is not surprising for an in situ study. Most of the studies on sea turtle hatchling orientation are based on the release of a few hatchlings by an observer, who can record the environmental parameters at the time of the experiment. In our study we used hatchlings from nests that had emerged prior to our presence (during the previous night), at different times and dates and located in the whole beach, including upper, middle and lower beach. Thus, the level of artificial lights and moon can have a different effect on each nest. The distance to the high tide line, as well as a strong rain can reduce the visibility of artificial lights from a nest, whereas a cloudy sky can dim the background illumination produced by the moon. Therefore, emergence may have occurred at a time of night and a place less affected by these variables, possibly explaining why hatchlings from some nests were well-oriented, despite their location on a part of the beach with high artificial light pollution.

A part of the inter-nest variability is not explained by the tested factors and must be a result of non-measured effects. This may be explained by cooperation between hatchlings that emerge together. Several emergences were observed on this beach, all with a large number of hatchlings emerging together at one time. Carr and Hirth (1961) considered that cooperation exists during emergence and could be pursued on the way to the ocean. However, this aspect of hatchling seafinding has been poorly documented. The pattern of repartition of the tracks in Pongara, with a group of tracks aggregated and a small number of dispersed individuals seems in favor of this hypothesis; the dispersed individuals could have emerged later or sooner than the majority of the clutch.

4.3. Conservation implications

During the study period (2006), the influence of artificial lights was often counteracted by the presence of logs and escarpments resulting from erosion, especially in the southwestern zone. However, artificial and natural cues are precariously balanced. We have observed the logs and erosion on this beach oscillating over a number of years (Deem, unpublished data), whereas artificial lights are increasing with the rapid

coastal development of the region. For example, during the 2006–2007 nesting season we documented an unprecedented number of mis-oriented female and hatchling leatherback sea turtles that walked into the savanna away from the ocean (Deem et al., 2007). This we hypothesized was a direct impact from the significant new coastal construction and increased artificial lights (Deem et al., 2007). These mis-oriented leatherback females and hatchlings are at risk of death due to exhaustion and dehydration, and hatchlings are at risk of increased predation by crabs, dogs, birds and other predators.

Conservation actions must be taken to lessen the impact of artificial lights on this critically important nesting beach for leatherback sea turtles. Although it is impossible to completely eliminate artificial light pollution on this beach due to the influence of Libreville, our results highlight that immediate action must be implemented to minimize the impact. This might be accomplished by both reducing lights and reinforcing the natural cues landward. Increasing the number of dark and elevated silhouettes landward of the beach should significantly improve hatchling orientation (Tuxbury and Salmon, 2005). Our study showed that the shape cues visible on this beach (e.g., escarpments in the sand, vegetation and logs) help to orient hatchlings to the ocean, even when artificial lights are visible. Therefore at this site, actions that could be undertaken include enhancing the vegetation cover, with low shrubs similar to those present in the south-west part of the beach, or using logs present on the beach to build a barrier along the beach-savanna interface. Logs should be used carefully, because of their ecological impact. Results from this study demonstrate that such measures would be less effective in the extreme north-east part of the beach, especially when the moon is not visible. Therefore, the level of artificial lights should be reduced by controlling as many lights as possible. Conservation NGOs are working to demonstrate ways to minimize light directed towards the nesting beach and to bring motion-detector operated lights in Gabon, to minimize the time of lighting. Such actions will be most effective in reducing light pollution from Pointe Denis, which have a high impact because of their proximity to the nesting beach. Additionally, although time intensive it may be prudent to maintain patrol teams each nesting season, as it proved of great value this past season to aid females and hatchlings towards the ocean (Deem et al., 2007). These conservation actions are warranted to preserve this critical leatherback sea turtle nesting beach. The importance of Pongara National Park for the leatherback females that nest here and the hatchlings that start life here is irreplaceable.

Acknowledgements

We thank the conservateur of Pongara National Park, Mrs. N'Safou Loembé and the government of Gabon for allowing us to conduct this study, the NGO Aventures Sans Frontières, especially Mr. Guy-Phillippe Sounguet, for their help in the field and the Wildlife Conservation Society, especially Dr. Lee White and Mr. Romain Calaque for logistical support. The authors thank two anonymous referees for helpful comments. This study served as a veterinary thesis for S.B. at the National Veterinary School of Alfort, France. Financial sup-

port came from Cleveland Metroparks Zoo, Smithsonian National Zoo, a grant from the Académie d'Agriculture de France and from the French ministry of agriculture and fisheries.

REFERENCES

- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference – A Practical Information-theoretic Approach. Springer-Verlag, New-York.
- Carr, A.F., Hirth, H., 1961. Social facilitation in green turtle siblings. *Animal Behaviour* 9, 68–70.
- Deem, S.L., Boussamba, F., Nguema, A.Z., Sounguet, G.P., Bourgeois, S., Cianciolo, J., Formia, A., 2007. Artificial lights as a significant cause of morbidity of leatherback sea turtles in Pongara National Park, Gabon. *Marine Turtle Newsletter* 116, 15–17.
- Godfrey, M.H., Barreto, R., 1995. Beach vegetation and seafinding orientation of turtle hatchlings. *Biological Conservation* 74, 29–32.
- Kraemer, J.E., Bennett, S.H., 1981. Utilization of post-hatching yolk in the loggerhead sea turtles, *Caretta caretta*. *Copeia*, 406–411.
- Laurance, W.F., Fay, M., Parnell, R.J., Sounguet, G.P., Formia, A., Lee, M.E., 2008. Does rainforest logging threaten marine turtles? *Oryx* 42, 246–251.
- Limpus, C.J., 1971. Sea turtle ocean finding behaviour. *Search* 2, 385–387.
- Lorne, J.K., Salmon, M., 2007. Effects of exposure to artificial lighting on orientation of hatchlings sea turtles on the beach and in the ocean. *Endangered Species Research* 3, 23–30.
- Mann, T.M., 1978. Impact of developed coastline on nesting and hatchling sea turtles in Southeastern Florida. *Florida Marine Research Publication* 33, 53–55.
- McFarlane, R.W., 1963. Disorientation of loggerhead hatchlings by artificial road lighting. *Copeia*, 153.
- Mortimer, J.A., 1979. Ascension Island: British jeopardize 45 years of conservation. *Marine Turtle Newsletter* 10, 7–8.
- Mrosovsky, N., 1970. The influence of the sun's position and elevated cues on the orientation of hatchling sea turtles. *Animal Behaviour* 18, 648–651.
- Mrosovsky, N., Shettleworth, S.J., 1968. Wavelength preferences and brightness cues in the water-finding behaviour of sea turtles. *Behaviour* 32, 211–257.
- Mrosovsky, N., Shettleworth, S.J., 1975. On the orientation circle of the leatherback turtle, *Dermodochelys coriacea*. *Animal Behavior* 23, 568–591.
- Peters, A., Verhoeven, K.J.F., 1994. Impact of artificial lighting on the seaward orientation of hatchling loggerhead turtles. *Journal of Herpetology* 28, 112–114.
- Philibosian, R., 1976. Disorientation of hawksbill turtle hatchlings, *Eretmodochelys imbricata*, by stadium lights. *Copeia*, 824.
- Salmon, M., 2003. Artificial night lighting and sea turtles. *Biologist* 50, 163–168.
- Salmon, M., Witherington, B.E., 1995. Artificial lighting and seafinding by loggerhead hatchlings: evidence for lunar modulation. *Copeia* 4, 931–938.
- Salmon, M., Wyneken, J., Fritz, E., Lucas, M., 1992. Seafinding by hatchling sea turtles: role of brightness silhouette and beach slope as orientation cues. *Behaviour* 122, 56–57.
- Tuxbury, S.M., Salmon, M., 2005. Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation* 121, 311–316.

-
- Van Rhijn, F.A., Van Gorkom, J.C., 1983. Optic orientation in hatchlings of the sea turtle *Chelonia mydas* III. Sea-finding behaviour: the role of photic and visual orientation in animals walking on the spot under laboratory conditions. *Marine Behavior and Physiology* 9, 211–228.
- Verheijen, F.J., 1958. The mechanisms of the trapping effect of artificial light sources upon animals. *Archives Néerlandaises de Zoologie* 13, 1–107.
- Verheijen, F.J., 1985. Photopollution: artificial light optic spatial control systems fail to cope with Incidents, causation, remedies. *Experimental Biology* 44, 1–18.
- Witherington, B.E., Martin, R.E., 1996. Understanding, assessing and resolving light-pollution problems on sea turtle nesting beaches. Florida Marine Research Institute Technical Report TR-2, 73p.