Impact of density-dependent nest destruction on emergence success of Guianan leatherback turtles (*Dermochelys coriacea*)

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Abstract

To assess the impact of nest covering on a leatherback turtle *Dermochelys coriacea* nesting beach in French Guiana, we used field study data and a modelling approach. Field results showed that the covering of a pre-existing nest by a new one causes the destruction of the older nest under some conditions of time and covering area, and almost always causes the destruction of the new nest. We then used field results to parameterize a theoretical model of the nesting beach. This allowed us to obtain a 'critical carrying capacity for the beach': the number of nests deposited for which the number of successful nests is maximum; when this number increases, the number of successful nests decreases. With these results, we then concluded that density-dependent nest destruction plays a role in the functioning of the nesting beach. These results are essential for our understanding of nest-site selection at the scale of the beach and its consequences.

Introduction

The leatherback turtle *Dermochelys coriacea* is one of seven sea turtle species and is accorded the highest conservation priority on the IUCN's Red List (IUCN, 2004). Analysis of published estimates of global population size suggests a reduction of over 70% for the populations in the Pacific Ocean (Pritchard, 1982; Spotila *et al.*, 1996). The species' strongholds have declined drastically in the last decade, with current annual nesting female mortality estimated at around 30% (Sarti *et al.*, 1996; Spotila *et al.*, 2000). French Guiana represents 40% of worldwide leatherback nesting (Spotila *et al.*, 1996), and the beach of Awa:la-Ya:lima:po alone is home to more than 90% of the nesting leatherbacks of French Guiana (Girondot & Fretey, 1996). Since the discovery of the importance of western French Guiana for leatherback reproduction at the end of the 1960s, several protection programmes have been put in place to observe and count the number of nesting females. Since the early 1990s, the results of these surveys have revealed a decline in the annual numbers of laying leatherbacks on the main sites in French Guiana and Suriname (Chevalier & Girondot, 1998). There is an urgent need to understand the current trends in Suriname and French Guiana because the decrease can be very rapid, as has been observed for other nesting beaches, such as those in Malaysia (Chan & Liew, 1996) and Mexico (Eckert & Sarti, 1997).

A seldom considered alternative is that the observed trends are natural fluctuations in population size (Pritchard, 1996). It has been suggested that density-dependent regulation of population size is of major importance in some populations of marine turtles *Chelonia mydas* (Bustard & Tognetti, 1969), *Lepidochelys olivacea* (Eckrich & Owens, 1995) and *D. coriacea* (Girondot *et al.*, 2002). Bustard & Tognetti (1969) studied the effect of high nest density for green turtles *C. mydas*. They used a stochastic model to determine the relationship between the percentage of nests destroyed and the size of the turtle population. They concluded that nest destruction is dependent on population density and provides a mechanism to regulate population size. Girondot *et al.* (2002) tested the same hypothesis on the leatherback population nesting in Awa:la-Ya:lima:po. They improved the model used by Bustard & Tognetti (1969) and examined how density-dependent nest destruction affects the number of successful nests.

A previous study carried out on the beach of Awa:la-Ya:lima:po showed that the proportion of nests producing

hatchlings varies from 10% for 10 000 clutches laid during the nesting season to 4% for 60 000 clutches (Girondot & Tucker, 1998). These observations concur with the intuitive idea that the probability of destruction is higher if the area usable for turtles to lay their nests is more restricted. The choice of a laying site by the female would then have a strong influence on hatching success (Ackerman, 1997). In high-density nesting areas, gravid females could lay in some pre-existing nests. This process creates physical disruptions of the initial nest and chemical changes (temperature, humidity). Several authors have found an increased rate of mortality because of rotation of eggs (Limpus, Baker & Miller, 1979). For *D. coriacea*, a clutch is sensitive to this phenomenon up to 5 h after oviposition (Chan, Salleh & Liew, 1985). Studies on the effect of the rupture of sea turtle eggs are very rare. Hill (1971) showed that nests of *D. coriacea* with some broken eggs have a reduced rate of emergence (13.4 vs. 41.7% for control nests).

It has been shown that the existence of decaying eggs on the surface of the sand, as well as in the nest, could facilitate nest localization by predators (Brown & MacDonald, 1995). Therefore, the second nest laid on the top of a pre-existing nest may increase the possibility of predation for the first one (Allen *et al.*, 2001). Several studies indicate that the eggs are very vulnerable to predation by insects [Phoridae and Sarcophagidae (Acuna-Mesen & Hanson, 1990; Trauth & Mullen, 1990); Sarcophagidae (McGowan *et al.*, 2001a,b)]. However, the level of impact is unknown. Moulis (1997) described a reduction of 15% of hatchling emergence for some *Caretta caretta* nests infested by *Solenopsis invicta*, compared with non-infested nests. On Awa:la Ya:lima:po beach, the high concentration of leatherback eggs attracts different animals such as dogs, birds *Coragyps atratus*, ghost crabs *Ocypode quadrata* and mole crickets *Scapteriscus didactylus* that prey on both eggs and hatchlings (Fretey & Lescure, 1998; Maros *et al.*, 2003).

All these factors could interact synergistically to increase the predation levels of the two nests (Wilmers *et al.*, 1996; Parris, Lamont & Carthy, 2002), as well as having an effect on the hatchling sex ratio. They could create a variation of hydric and thermal conditions that could cause a subtle difference (1–2 °C) in the temperature of egg incubation during the thermosensitive period, which could then create a considerable difference in the sex ratio of the hatchlings (Mrosovsky & Yntema, 1980; Girondot, Fouillet & Pieau, 1998). Kaska *et al.* (1998) noted that predation can have an effect on sex ratio: partial predation, on the top of the nest, will particularly affect the females. On the other hand, predation during hatching will mainly affect the juveniles that hatch last, i.e. those that emerge from the eggs at the bottom of the nest (males).

For all these reasons, the impact of density-dependent nest destruction is important in considering the problem of nest-site selection by leatherback females. If density-dependent nest destruction occurs at the scale of the nesting beach, there are direct and indirect consequences of the nest-site choice on offspring fitness. It is then important to understand the nest-site choice process by nesting females in this population, from an evolutionary point of view.

In this study, we first assessed the potential impact of nest destruction on the emergence success of covered and covering nests. We used two destruction rates (25 and 50%) and three destruction times (8, 25 and 38 days after the clutch has been laid). Second, we incorporated these parameters into a model similar to that of Girondot *et al.* (2002), and we compared the outputs of these two models. We then demonstrated how using these experimental parameters could greatly improve the performance of the model and modify the conservation strategies.

Materials and methods

Field study

Study site

The Amana Nature Reserve is located in north-western French Guiana, on the inshore plain of coastline between the Organabo and Maroni rivers. In general, the beaches of this area change very quickly, although the beach of Awa:la-Ya:lima:po (53°56′99W/5.44′62N), where the study was carried out, has been the most stable for the past 20 years and has one of the highest nesting densities in the region (Fretey & Lescure, 1998). The major laying season at Awa:la-Ya:lima:po extends from March to the end of August, including a peak in June, with some sporadic clutches outside this period (Chevalier & Girondot, 1998).

Transplantation to the open-air hatchery

On Awa:la-Ya:lima:po beach, the leatherback nests used for our study were transplanted to an open-air hatchery between 1 April and 24 May 2002 (authorization no. 1516 1D/1B/ENV of 27 August 2001, DIREN Guyane), in order to reduce variations in various environmental conditions along the beach (predation, temperature). We relocated nests laid below the high tide line because these nests would have been destroyed by the tide. The eggs were then transferred to the open-air hatchery as soon as possible after laying (3 h maximum), at the same depth as in the original nest. The time zero of T incubation was recorded once the nest was completely covered.

Different laying situations in the open-air hatchery (Fig. 1)

In order to determine the effects of a leatherback clutch being laid on a pre-existing clutch, we measured the hatching success (percentage of eggs having produced hatchlings at the end of incubation) for three situations (S1–S3).

S1: The nest was transplanted at time $T0$ and did not undergo destruction (control nest at time $T0$).
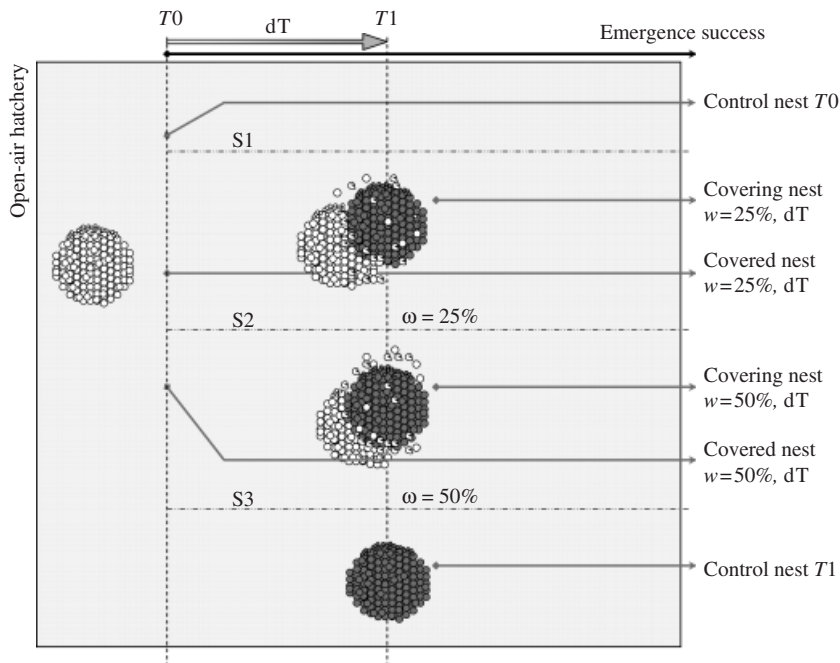
Figure 1 Diagram of the open-air hatchery study. The first transplantation (*T*0) is in white with three situations (S1–S3). After a time, dT (8, 25 or 38 days), there is a second transplantation (grey, *T*1) modelling destruction by covering with different destruction rates (ω), 25 and 50%. At the end of each of the three dT, there are six nests in situation S1 (control of the nests transposed at *T*0), six nests in situation S1 (control of the nests transposed at *T*1), six nests in situation S2 (containing a nest transposed at *T*0, 25% of which was covered by a nest transposed at *T*1) and six nests in situation S3 (containing a nest transposed at *T*0, 50% of which was covered by a nest transposed at *T*1).

S2: The nest was transplanted at time *T*0 and underwent artificial destruction by a second nest after dT days of incubation (dT is the destruction time). This second nest was dug to simulate the laying of a female over 25% of the pre-existing nest (destruction rate, $\omega = 25\%$ of the surface). Eggs were destroyed and left in the nest.

S3: The nest was transplanted at time *T*0 and underwent artificial destruction by a second nest after dT days of incubation. This second nest was dug to simulate the laying of a female over 50% of the surface of the pre-existing nest (destruction rate, $\omega = 50\%$). Eggs were destroyed and left in the nest.

In order to differentiate the eggs of covered and covering nests at the end of incubation, the shells of the peripheral eggs of the covering nest were stained with a yellow vital stain (the colouring effect on the hatching success was previously tested and is not significant).

Experimental design

We attempted to determine the impact of covering on the rate of emergence of the two nests (covering and covered nests), depending on the time when the covering nest was laid. The total duration of the incubation of leatherback eggs in French Guiana is 60–75 days (Rimblot *et al.*, 1985). For this study, we used three different dT values (8, 25 and 38 days).

A first transplantation phase took place from 1 April to 9 April 2002. We transferred six nests from the beach to the open-air hatchery on each of the nine nights: two nests corresponding to situation S1, two others to situation S2 and the last two to situation S3. Nests were randomly assigned to dT (8, 25 or 38 days) or control without destruction (*n* = 54 nests).

A second transplantation phase began when the incubation of the eggs had reached their assigned dT. We then transferred six nests per night, as described above: two nests for situation S1, therefore corresponding to the control, two others on the top of the two nests transposed at *T*0 and corresponding to situation S2 and, finally, the last two that were placed on the top of the two nests transposed at *T*0 and corresponding to situation S3 (*n* = 54 nests).

As the first nests (transposed at *T*0) approached expected emergence, we placed a wire mesh around every nest, in order to count the number of hatchlings when they emerged (they were released immediately afterwards into the sea). This was repeated for the nests simulating destruction.

When hatchling emergence was observed, the relevant nest was then dug by hand 48 h after the last hatchling emerged, in order to determine the emergence success and the rate of nest predation. During the digging, the number of shell fragments and unhatched eggs were recorded in order to establish hatching success. The nests exceeding 75 days of incubation were classified as having failed. These nests were dug by hand and all the parameters concerning nests and eggs were recorded as described above. Upon nest excavation, any sign of predation (especially by mole crickets) was recorded and the remaining contents were analysed.

Statistical analyses

Generalized linear models (GLMs) were used for the analysis of emergence success for covered and covering nests. Two models (covering and covered nest) with first-order interactions were fitted:

$$G(\text{emergence success}) = \text{adult size} + \text{clutch size}$$
$$+ \text{number of yolkless eggs}$$
$$+ \text{yolked eggs preyed}$$
$$+ \text{destruction time} + \text{destruction rate}$$
$$+ \text{interactions} + \text{error}$$

where G is a link function and where destruction time and destruction rate were treated as factors. Error distribution was assumed to be binomial, and the logit link function was used. The significance of factors and interactions was tested. However, a non-significant term was retained if this interaction with another factor was significant. The final model was attained when all the variables retained were statistically significant ($P < 0.05$):

$$G(\text{emergence success}) = \text{destruction time} + \text{destruction rate}$$
$$+ \text{interactions} + \text{error}$$

Moreover, we used this model to obtain the percentage of deviance explained by each variable when compared with the null model (Martínez, Serrano & Zuberogoitia, 2003). All calculations were performed using GLMStat, version 5.7. The final model was used to modify the modelling of the nesting process in the model described below.

Modelling of the nesting process

The modelling of the nesting process is based on the same principle as the one used in Girondot et al. (2002). For each day of the 1994 nesting season (from 1 March to 31 August), we know the number of nests laid on the beach. Each individual nest is plotted under a uniform distribution on a rectangular beach representing the effective area xy of the beach of Awa:la-Ya:lima:po. After the location of the nest has been randomly generated, we test to see whether it covers a pre-existing nest containing living embryos or not. In Girondot et al. (2002), the impact of recovery was modelled by a very simplistic process: the covered nest was totally destroyed and the covering one underwent no effect. To evaluate more accurately the effect of destruction, we consider now that nests that have undergone destruction have an emergence success that is equal to the emergence success of the corresponding control nest, multiplied by the effect of destruction. Therefore, if the destruction effect is strong, the value of the multiplication factor is close to 0, and if the effect is weak, it is close to 1. The effect of destruction is calculated with the statistical model obtained (see previous paragraph) for a given destruction rate and time and for covered (c) and covering nests (k). The covered nest is destroyed with the probability k, and the covering one with the probability c. After all the nests of the day have been laid on the beach, every nest containing living embryos is aborted with the daily probability of nest failure d (destruction by all biotic or abiotic factors, excluding covering). Then, for every nest still containing living embryos, we test to see whether incubation has ended (nest counted as hatched), and the next day is simulated using the same process. When the entire nesting season has been simulated with this process, nests still containing living embryos continue their incubation until hatching or abortion.

At the end of the simulated nesting season, the number of females having covered none or at least one nest containing living embryos for each day is known. We use Fisher's exact test to compare these values with the observed number of females having covered none or at least one nest containing living embryos (resulting from daily counts on the beach of Awa:la-Ya:lima:po). We then obtain a value of likelihood associated with the parameter set (d; xy) used for the simulation of the nesting season. We use a simplex method to find the (d; xy) values that maximize the likelihood. With these values, we then estimate the number of nests still containing living embryos at the end of their incubation (hatched nests) or destroyed before. These parameters are evaluated for a given total number of nests deposited on the beach during the season.

Results

Destruction effect in the open-air hatchery

For the nests that were destroyed, the emergence success (*Es*) was corrected by

$$Es(\%) = \frac{H}{Y(1 - \omega)} 100$$

where H is the number of hatchlings leaving or departed from the nest and Y is the number of eggs containing yolk.

Control nests

The emergence success of control nests for every dT (8, 25 and 38 days) was not significantly different (ANCOVA; $P = 0.96$, ddl = 1 and Fig. 2). The mean of emergence success for all control nests was 19.17% ($n = 37$; SD: 19.11%). The predation rate by mole crickets for every dT was not significantly different (ANOVA; $F = 0.93$, ddl = 2, $P = 0.40$), with a mean of 18.49% ($n = 37$; SD: 1.37%).

Covered nests (see Table 1, model A)

It is important to note that the emergence success was corrected to take the destruction rate into account. The destruction rate of covered nests has a significant effect on the incubation success of the remaining eggs (Table 1; $P = 0.0152$) and represents 55.95% of the model deviance. The more the nest has been destroyed, the more the egg incubation has failed. In fact, emergence success was 4.95% (SD: 7.92), 8.79% (SD: 10.80) and 14.43% (SD: 15.15) for destruction rates of 50, 25% and control nests, respectively (Fig. 2). This effect seems to be higher when destruction occurs earlier, although it was not significant (Table 1; $P = 0.1834$). However, their interaction (destruction time destruction rate) was almost significant ($P = 0.0819$).

The overall predation rate by mole crickets at dT = 8 was 30.70 and 36.91% ($\omega = 25$ and 50%, respectively), at

dT = 25 was 40.66 and 49.59% (ω = 25 and 50%, respectively) and at dT = 38 was 30.68 and 35.07% (ω = 25 and 50%, respectively). The destruction rate has a very significant effect on the predation rate by mole crickets (ANOVA; $F = 11.90$, ddl = 2, $P = 0.0001$). But there was no effect between destruction rates 25 and 50% (Tukey test *post hoc* comparison). The destruction time had no effect on the predation (ANOVA; $F = 2.22$, ddl = 2, $P = 0.13$).

Covering nests (see Table 1, model B)

The selected model for emergence success accounted for 57.12% of the original deviance (Table 1). Significant factors and interactions were the same as on the covered nest model but the destruction rate had a very significant effect on the emergence success of the covering nest (Table 1; $P < 0.0001$, representing 83.15% of the model deviance).

The emergence success was very small for a destruction rate of 50% (Es = 1.31%; SD: 3.02) and 25% (Es = 0.99%; SD: 2.92) compared with control nests (Es = 24.16%; SD: 21.88; see Fig. 2). The interaction (destruction time - destruction rate) was highly significant (Table 1; $P = 0.0016$). In brief, a nest that was laid on another nest containing living embryos has an almost negligible emergence success rate.

The overall predation rate by mole crickets at dT = 8 was 39.21 and 39.49% (ω = 25 and 50%, respectively), at dT = 25 was 35.04 and 28.77% (ω = 25 and 50%, respectively) and at dT = 38 was 31.35 and 26.42% (ω = 25 and 50%, respectively). The destruction rate has a very significant effect on the predation rate by mole crickets (ANOVA; $F = 11.39$, ddl = 2, $P = 0.0003$). But there was no effect between destruction rates 25 and 50% (Tukey test *post hoc* comparison). The destruction time had no effect on the predation (ANOVA; $F = 2.31$, ddl = 2, $P = 0.12$).

Parameter estimation

The values obtained with the final GLM model for c and k are described in Fig. 3. In contrast to the conclusions drawn by Girondot *et al*. (2002), the covering nest is almost always destroyed, except in cases where dT is high and ω is small. The destruction of the covered nest is not as systematic as assumed in Girondot *et al*. (2002). With the exception of cases where ω is high and dT is low, the effect of destruction is weak on the covered nest.

Outputs of the experimental parameter model

The total number of viable nests at the end of their incubation and the proportion of viable nests over the total number of nests during the nesting season were obtained with a yearly number of nests laid on the beach from 10 000 to 200 000 (step 8000). Figure 4 shows the results of these simulations with the values of c and k used by Girondot *et al*. (2002) (hereafter referred to as the theoretical parameter model). In this case, the values of d and xy that
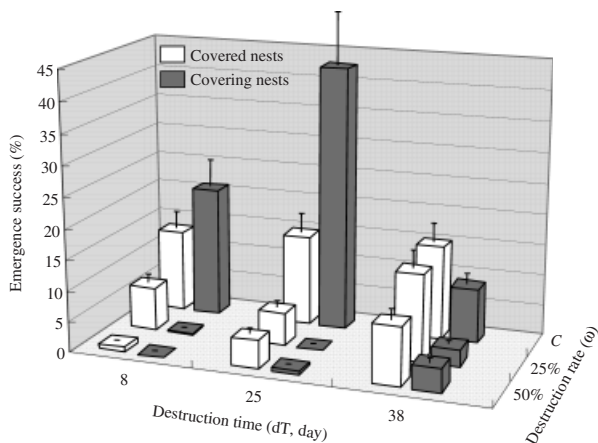

Figure 2 Percentages of emergence success (SE) (corrected) versus the destruction time (dT) and the destruction rate (ω) for *Dermochelys coriacea* in an open-air hatchery. The covered and covering nests are in white and green, respectively. *C* represents the control nests.

Table 1 Generalized linear model (GLM) for the emergence success of covered nests (A) and covering nests (B) of leatherback turtle *Dermochelys coriacea* in Guiana

	Estimate	Deviance	d.f.	F ratio	Probability > F	%
A. Covered nest						
Model		114.7	3	3.764	0.0162	18.13
Constant	−1.761					
dT	1.441e−3	18.48	1	1.819	0.1834	16.12
Dest	−6.718	64.17	1	6.317	0.0152	55.95
dT × Dest	0.1564	32.06	1	3.156	0.0819	27.95
B. Covering nest						
Model		688.3	3	20.19	< 0.0001	57.12
Constant	−0.7277					
dT	−2.206e−2	0.1259	1	1.217e−2	0.9126	0.02
Dest	−28.89	572.3	1	55.35	< 0.0001	83.15
dT × Dest	0.6525	115.8	1	11.2	0.0016	16.82

The percentage of deviance accounted for by each variable and by the model (compared with a null model) are shown (%).
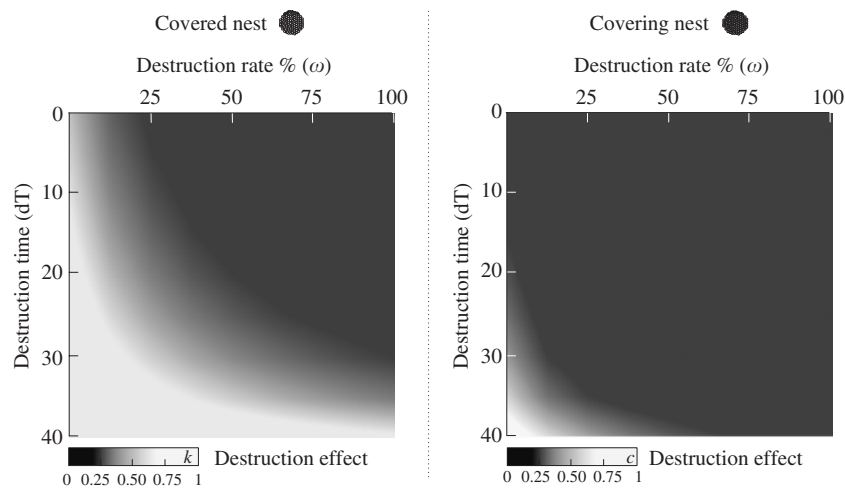
Figure 3 Destruction effect according to destruction rate and destruction time. Surface colour represents model (generalized linear model analysis). Destruction effect is represented by k and c for covered and covering nests, respectively.

maximize the likelihood of the simulations [$-\ln(L) = 19.74$] are $d = 3.1\%$ ($\text{SE} = 0.019$) and $xy = 7340\,\text{m}^2$ ($\text{SE} = 27.535$). For 90 000 nests laid on the beach, there is a maximum number of nests still containing viable eggs at the end of their incubation (3600 nests). These are the same results as those found in Girondot *et al.* (2002), where this value is defined as the 'maximum carrying capacity of the beach' (the maximum number of nests deposited on the beach for which an increasing hatchling production is still observed). When we use the values of c and k evaluated from the experiments (hereafter referred to as the experimental parameter model), the shape of the curve is completely different. In this case, the values of d and xy that maximize the likelihood of the simulations [$-\ln(L) = 19.83$] are $d = 1.9\%$ ($\text{SE} = 0.026$) and $xy = 7970\,\text{m}^2$ ($\text{SE} = 103.367$). The number of nests still containing viable eggs at the end of their incubation reaches a maximum value at 5000 nests for 60 000 nests deposited. We defined this value as the 'critical capacity of the beach', which represents the highest possible production of the beach. When the annual number of nests deposited on the beach increases, the number of viable nests sharply decreases and reaches 2500 nests for 200 000 nests laid.

The shape of the curves representing the proportion of nests still containing viable embryos at the end of their incubation is roughly the same for the experimental and theoretical parameter models, but with one important difference (Fig. 5): although density-dependent nest destruction was observed (a higher rate of destruction associated with a larger number of nests), this effect was greater in the experimental model. The proportion of viable nests remaining at the end of incubation was 0.22% (experimental parameter model) and 0.11% (theoretical parameter model), with 10 000 nests deposited on the beach. This proportion is lower in the experimental parameter model than in the theoretical parameter model after 140 000 nests. At the critical capacity of the beach (60 000 nests), the proportion of viable nests in the experimental model was almost twice as high as the value in the theoretical parameter model (0.08 and 0.05%, respectively).
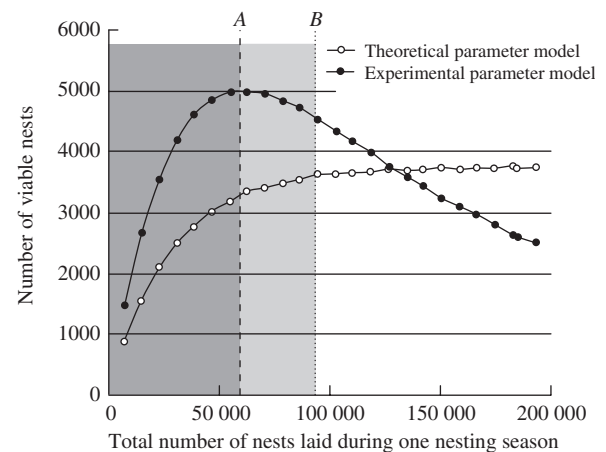

Figure 4 Number of viable nests versus total number of nests on the beach for the theoretical parameter model (Girondot *et al.*, 2002) and the experimental parameter model. A and B represent the 'maximum carrying capacity of the beach' for the experimental parameter model and the theoretical parameter model, respectively.

Discussion

Worldwide, leatherback turtle *D. coriacea* populations on many nesting beaches have been in serious decline (Spotila *et al.*, 1996, 2000). Although survival of adults has been shown to be crucial to the long-term viability of turtle populations (Brooks, Brown & Galbraith, 1991), all life stages should be considered in efforts to stabilize or restore declining populations (Marchand & Litvaitis, 2004). Among the many factors known to affect recruitment, it is thought that density dependence is the primary regulator of population size (Eckrich & Owens, 1995; Girondot *et al.*, 2002). In Sandy Croix nesting population (Virgin Islands), nest success is supposed to be a significant factor governing leatherback population dynamics (Dutton *et al.*, 2005).

GLM analysis makes it possible to demonstrate the significant effects of several factors on emergence success: the destruction rate for covered and covering nests, and the

interaction between destruction time and destruction rate for the covering nest. The main effect of nest covering is to rotate or destroy eggs, causing parasites and bacteria to appear and resulting in non-destroyed egg failure. Therefore, when the surface rate of covering increases, the number of eggs destroyed increases as well. We propose that this effect could explain the significant effect of the destruction rate, especially at the beginning of the incubation when eggs are highly sensitive to incubation condition. Thus, when the destruction time increases, given that the destruction rate is not too great, the effect of covering could be diminished on covering nests because the covered nest contains eggs that are less sensitive to the development of bacteria after their destruction.

Figure 4 clearly shows the effect of nest density on the number of viable nests at the end of the nesting season using the parameters previously established from artificial incubation. The number of nests to be deposited on the beach to obtain this effect is around 60 000. The number of viable nests decreases dramatically above this threshold. A higher number of nests have already been observed on the Awa:la-Ya:lima:po beach (Fig. 5). This result is at odds from the one obtained by Girondot *et al.* (2002) in which no decrease was observed. The 'maximum carrying capacity of the beach' (Girondot *et al.*, 2002), i.e. the maximum number of nests deposited on the beach for which an increasing hatchling production is still observed, was 95 000 nests, far beyond the highest density observed in French Guiana (60 000 nests per nesting season; Fig. 6). With the new parameterization of this model, we show that the 'maximum carrying capacity of the beach' has already been attained in Awa:la-Ya:lima:po beach. Evidently, this density-dependence mechanism is one of the numerous mechanisms that can regulate populations.

Given the hypothesis of density-dependent regulation on the beach of Awa:la-Ya:lima:po, it is extremely difficult to

come to any definitive conclusion about conservation guidelines concerning leatherback clutches on this beach. Considering that the transplanted nests were laid below the high tide line, the hatchery yields higher hatching success than these nests would have experienced if left on the beach. But the results of the fieldwork show that the open-air hatchery had a significantly lower hatching success rate than the beach itself. This confirms the idea shared by many scientists that the use of hatcheries for leatherback turtles is not a viable alternative. The only way to protect nests and to increase hatching success is to focus on natural nests. One idea could be to decrease the number of nests at the beginning of the nesting season to decrease the probability of covering for the rest of the season. But this method is problematic in that it could lead to an increase in the number of nesting females over subsequent years because nests deposited late in the season are feminized (Girondot *et al.*, 2002). The density-dependent regulation would just occur later and could be even greater as a result of the increase in the number of nests.

The experimental results of our study have permitted us to greatly improve the model of Girondot *et al.* (2002) concerning the modelling of the nests' recovering process. By comparing the outputs of the two versions of the model, we can then understand the influence of nests recovering in the density-dependent regulation occurring on the nesting beach. This method of improvement of the model using experimental results is very useful in assessing the relative importance of a precise phenomenon. From a more general point of view, it shows well the essential synergy between modelling and experimentation. The model used here must obviously be improved in order to increase our understanding of the nesting process and the way in which the beach functions. At this time, the results of the simulations only allow us to obtain the number of nests completely destroyed or not. It would be interesting to obtain the number of hatchlings produced by each nest, by working with a number of eggs destroyed or still containing living embryos. Another major improvement to this model would be to consider the impact of density on the sex ratio of the juveniles produced. Girondot *et al.* (2002) took this effect into consideration, but
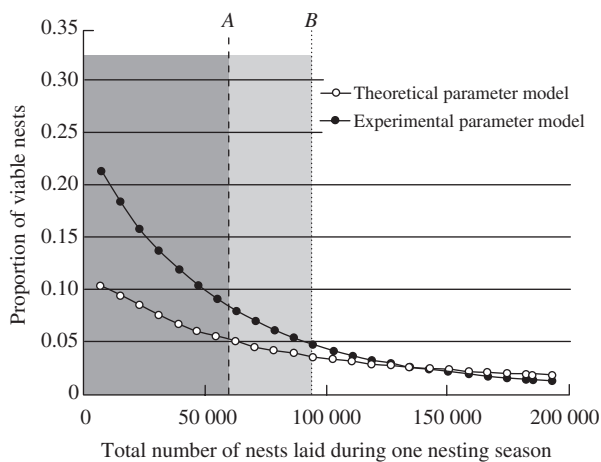

Figure 5 Proportion of viable nests versus total number of nests on the beach for the theoretical parameter model (Girondot *et al.*, 2002) and the experimental parameter model. *A* and *B* represent the 'maximum carrying capacity of the beach' for the experimental parameter model and the theoretical parameter model, respectively.
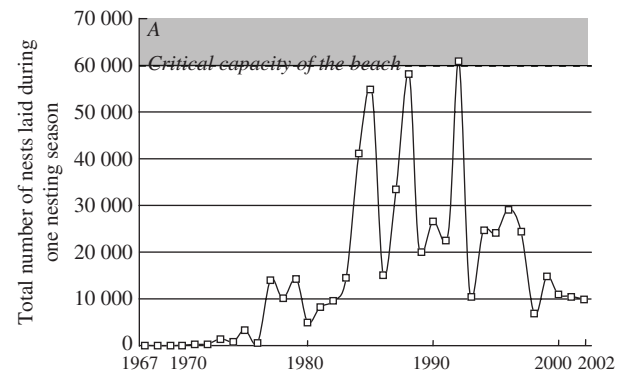

Figure 6 Total number of leatherback turtle *Dermochelys coriacea* nests on Awa:la-Ya:lima:po beach (French Guiana). *A* (grey area) represents a critical zone.

in a very imprecise way. Studies are presently being carried out on this phenomenon and could lead to results that could be used in our model. This model has been built in such a way that it can be improved with additional information collected about phenomena that occur on the beach or about the biology of leatherback turtles. For example, the impact of the variation in beach length and width, the aggregation of nests in time or space, etc., would be very interesting to improve our understanding of how this beach functions.

Another considerable improvement would be to generalize this model and its conclusions to other beaches where leatherback turtles nest. However, this is not that simple as the nesting beaches of French Guiana and Suriname are very unique in the way that they vary over time (erosion, accretion of sand).

Acknowledgements

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