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Density-dependent nest destruction and population fluctuations of Guianan leatherback turtles

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Abstract

Approximately 40% of the world's leatherback marine turtles (*Dermochelys coriacea*) nest in Suriname and French Guiana. Trends in nest numbers reconstructed for the last 34 years indicate several up and down events. We undertook computer simulations to determine whether a density-dependent phenomenon might be involved because the period of high-density nesting coincides with a high level of nest destruction by nesting females. The parameters of density-dependent nest destruction were calculated for the Ya:lima:po-Awa:la beach. We show that: (1) density-dependent nest destruction occurs, but (2) it promotes a density-dependent feminization of hatchling sex ratio, and consequently (3) the global production of juveniles continues to increase in relation with the increasing number of deposited nests even for the highest densities observed at that beach. Mean annual production of female hatchlings per adult female, although density dependent, is less than two juveniles even at the lowest densities of nesting females.

INTRODUCTION

Many major nesting beaches of the leatherback turtle (*Dermochelys coriacea* Vandelli 1761) have seen notable declines in the annual numbers of nesting females over the last decade (Spotila *et al*., 1996). Population declines may be linked to local harvesting of eggs as in Malaysia (Chan & Liew, 1996) or to heavy egg collection and adult mortality on the beach and at sea as in Mexico (Eckert & Sarti, 1997). On the other hand, small rookeries, mainly in the Atlantic, have experienced increasing nesting populations. French Guiana and Suriname beaches (Fig. 1(a)) host approximately 40% of the world's population of nesting leatherbacks (Spotila *et al*., 1996). A 34-year reconstruction of trends in annual nesting there demonstrated several up and down events (Fig. 1(b)) (Chevalier & Girondot, 1998 and unpublished data from Suriname and French Guiana). There is an urgent need to understand the current trends for Suriname and French Guiana because the decrease can be very rapid as observed in other nesting beaches (Malaysia, Mexico).

In French Guiana, local harvesting of eggs or nesting females does not occur. A seldom considered alternative is that the observed trends are natural fluctuations in population size (Pritchard, 1996). However, no one has tested, in a rigorous way, the hypothesis that density-dependent mechanisms are at work in a sea turtle population. To assess this possibility, the hatchling production of the population must be evaluated to determine whether density-dependent regulation could account for a recent population decline. Such a density-dependent regulation would explain why smaller rookeries (St Croix, Florida, Culebra) have experienced increasing nesting populations relative to larger rookeries (Spotila *et al*., 1996). An earlier analytic model on population regulation explored the effect of high density of nests for green turtles as the digging of females caused the destruction of earlier nests (Bustard & Tognetti, 1969). For marine turtles, the indirect influence of a dynamic beach environment is important for the success or failure of each nest. On beaches with nests at high density, biotic factors (i.e. intraspecific nest destruction) may be at least as important in determining nest success as are abiotic factors (e.g. erosion, flooding) (Bustard & Tognetti, 1969). Previous workers at a nesting beach within the same estuary (Pointe Kawana beach, no longer existent) proposed that nest destruction could be the main factor governing population dynamics (Fretey & Lescure, 1979).

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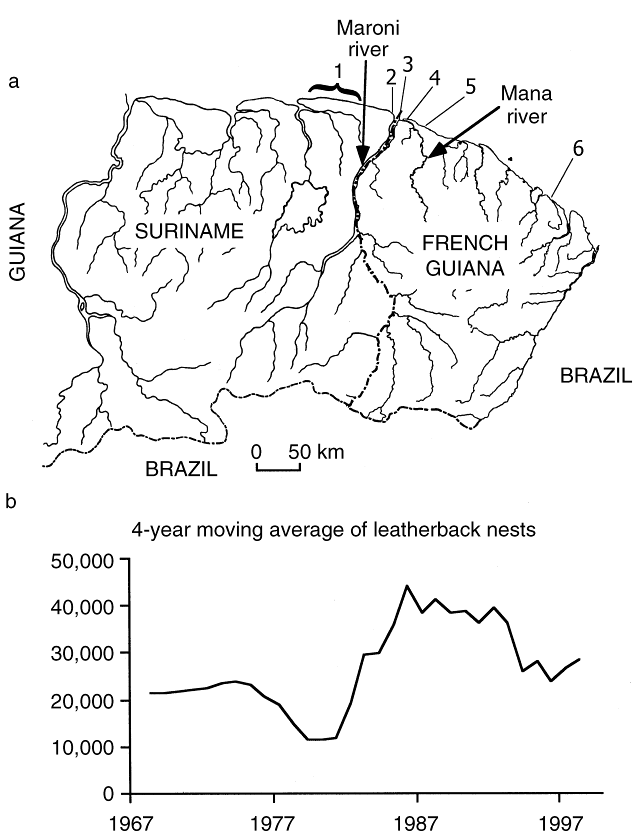

Fig. 1. (a) Location of the nesting beaches for *Dermochelys coriacea* in French Guiana and Suriname: (1) Matapica, (2) Galibi, (3) Ya:lima:po, (4) Apo:tïlï, (5) Organabo, (6) Remire-Monjoly. (b) Total number of leatherback nests in Suriname and French Guiana nesting beaches (4-year moving average).

We initially considered the effect of nest density on population regulation for hatchlings of both sexes just as an earlier model had developed for green turtles (Bustard & Tognetti, 1969). However, in terms of juvenile production, only the female juveniles are of primary importance for chelonian population dynamics as well as for many other reptiles because the number of offspring is directly related to the number of females (Girondot & Pieau, 1996). Marine turtles exhibit temperature-dependent sex determination, with the conditions of egg incubation directly influencing the primary sex ratio: lower incubation temperatures are masculinizing and higher ones are feminizing (Chevalier, Godfrey & Girondot, 1999). In French Guiana, the leatherback nesting season extends from early March in the (cooler) rainy season to mid-August in the (warmer) dry season (Girondot & Fretey, 1996). Sex determination is sensitive to incubation temperature during the thermosensitive period of development for sex determination (TSP) which occurs during approximately 15 days in the middle third of development (Desvages, Girondot & Pieau, 1993). In general, embryos are masculinized when the TSP occurs in the cooler wet season and they are feminized when TSP occurs during the warmer dry season (Rimblot-Baly *et al.*, 1986; Godfrey, Barreto & Mrosovsky, 1996). Moreover, incubation length is longer in the wet season than in the dry season, because the rate of embryonic development is inversely correlated with incubation temperature (Rimblot-Baly *et al.*, 1986; Godfrey *et al.*, 1996). Throughout the season, destruction of incubating nests will alter the percentage of nests which successfully produce a given sex, compared to the initial spatial and temporal distribution of deposited nests, and thus influence the hatchling sex ratio.

We incorporate these significant revisions in a model conceptually similar to that of Bustard & Tognetti (1969) for situations of high-density nesting. The revised model examines how density-dependent nest destruction affects the number of successful nests and the hatchling sex ratio as the mean temperature of a beach varies during the season. The model uses empirical data on intraspecific nest destruction, pivotal temperatures and temporal changes in the beach thermal profile collected at this major rookery in French Guiana. The results have implications not only in a theoretical framework, but also from a practical management viewpoint.

MATERIAL AND METHODS

Estimation of nest totals for the 1994 nesting season

During the 1994 nesting season, nests were counted on Ya:lima:po-Awa:la beach for 60 out of 170 nights between 1 March and 17 August. These data included counts for several consecutive nights and at least one count per week during the peak of the nesting season. The number of nests for the remaining 110 nights was estimated by Lagrange interpolation (Press *et al.*, 1992) (Fig. 2(a)). The interpolation method was validated independently with 1987 data, for which the number of nesting females was known for all nights. When only beach counts corresponding to the 1994 dates were taken from the 1987 time series, the error on total number of nests estimated by this method was less than 5%. The time series corresponding to the number of nests per night on this beach is called $N(t)$.

Rates of nest destruction

Female turtles were tagged by volunteers each night between 1 March and 17 August 1994. From 15 May to 2 August, when a female was encountered, we waited until it finished the nest excavation. Then, the number of viable nests (nests with living embryos) that were destroyed by these nesting females was recorded. Data were obtained for 2356 out of the 29,645 nesting events of the nesting season (7.9%). The number of females digging without destroying a viable nest was 1858, whereas 493 destroyed one viable nest (20.92%) and five destroyed two viable nests (0.03%). Owing to the small number of females that destroyed two viable nests and the difficulty of recognizing such events, data were grouped as ‘females destroying no viable nests’ and ‘females destroying at least one viable nest’. The proportion of the eggs destroyed for an excavated nest is impossible to estimate directly. Females that destroyed

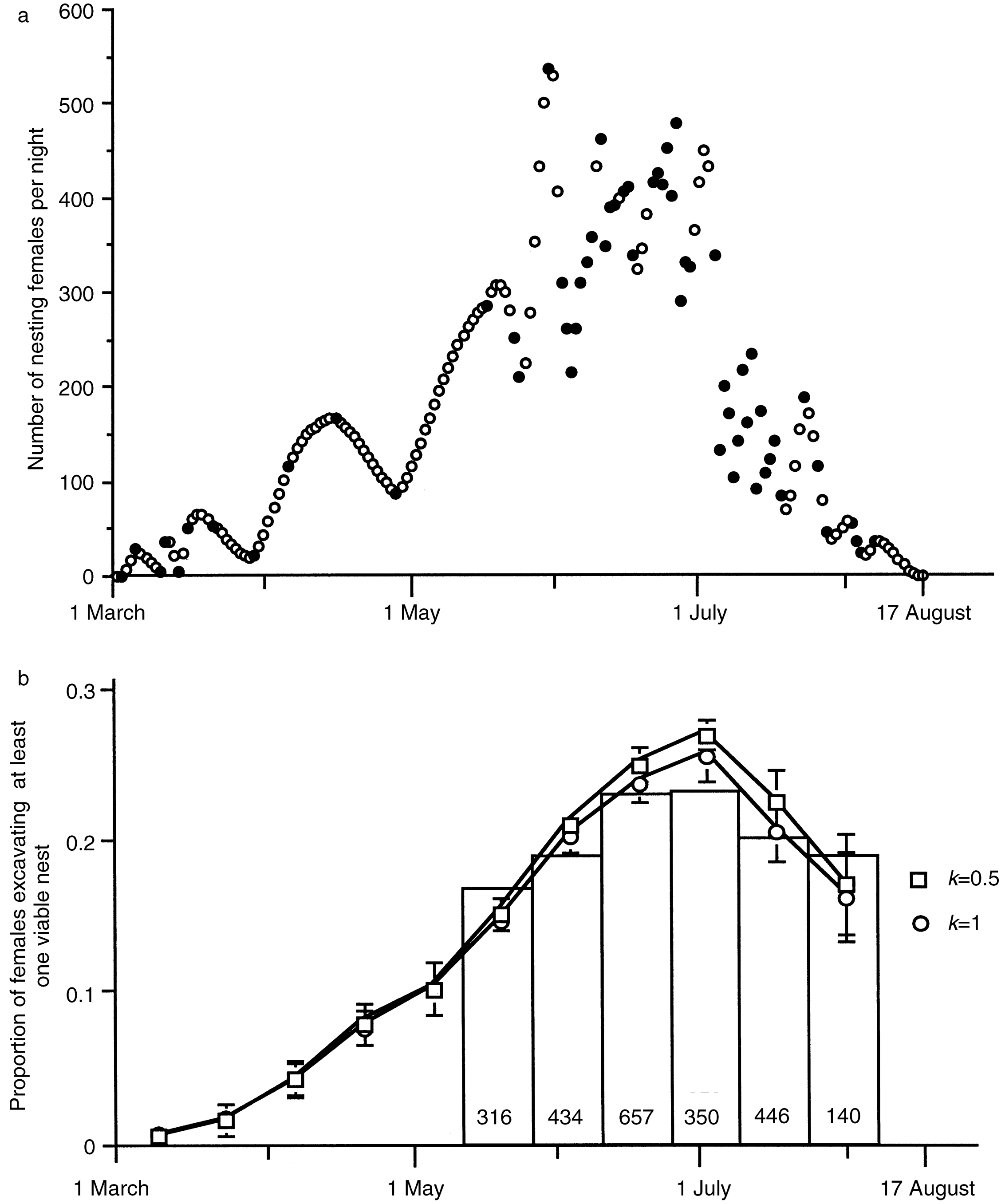

Fig. 2. (a) Number of nesting females per night from 1 March to 17 August 1994. Closed circles are observed values and open circles are calculated ones (see text). (b) Comparison between observed (histogram) and calculated (lines) distribution of probability for 2-week periods that females excavated a previously layed nest with living embryos, obtained from the best set of *xy* and *d* parameters (for $k = 0.5$ and $k = 1$). Error bars are two SD. Sample size in each period is indicated.

at least one viable nest were grouped in 15-day units which spanned to include both a full moon and last quarter or a new moon and first quarter. Each data group was therefore homogeneous relative to nesting frequency since it included a peak of nesting activity (full moon or new moon) and a period with fewer nesting females (first or last quarter) (Girondot & Fretey, 1996). This time series was called ε(t) and based on observed data is [ε_{obs}(t)] (Fig. 2(b)) or based on estimated data from the simulation [ε_{est}(t)] (see below).

Theoretical dynamics of nest destruction by nesting females

1. Time-series inputs and outputs

The 1994 nesting season gave empirical data for the time series $\varepsilon_{obs}(t)$ of the probability that a female excavated a previous nest and the nightly number of nests deposited on the beach, $N(t)$ (Fig. 2). We calculated a probability that a nest could produce hatchlings as a time-series defined by three parameters. First, d is the daily probability that a nest is completely destroyed (i.e. no more living embryos) by abiotic or biotic factors, but excludes destruction by other nesting females. This last factor is described separately as a time-series describing the probability that a nesting female excavates a nest with viable embryos (defined as viable nests). The parameter k is the probability that no embryo survives in an excavated nest. The probability that a viable nest is excavated is dependent on the density of viable nests on the beach. This density depends on the number of nests still viable and not yet emerged, and also on the size of nesting beach in m^2 called xy. In short, $N(t)$ and $\varepsilon_{obs}(t)$ are the observed distributions. We searched for d, k and xy values that produced an estimated distribution $\varepsilon_{est}(t)$ comparable to the observed one, $\varepsilon_{obs}(t)$.

2. *The effective size of nesting beach*

The actual spatial distribution of nests along the beach was not uniform, in neither length nor width. The 1991–93 pilot studies indicated that nest distribution can even be locally influenced by the presence of dead trees or other large objects on the beach, such as beached boats (unpubl. data). Therefore, for simulation purposes we used a simpler model structure than the unknown distribution of real nests on the beach. We defined the concept of 'effective size of the nesting beach' as the equivalent size, xy, of a hypothetical beach with properties similar to the actual beach for the probability that a female excavates a previously deposited nest ($\varepsilon(t)$ distribution) but with a uniform spatial distribution of nests.

3. *Modelization of the nesting process*

We considered the period of 1 March–17 August 1994 as the nesting season (Fig. 2) since the number of nesting females outside the period was negligible (< three nests per night). The beach was defined by x_m and y_m as the length and width of the beach so that the product xy represents the area of available nesting substrate ($x_m \times y_m$). Each nest i was characterized by its location on the beach (x_i, y_i) and the date of nesting t_i (1 March was defined as day 0). Females deposit nests randomly during the nesting season in a uniform spatial pattern on the beach of size xy. The number of nests deposited per night was obtained directly from the observed distribution for 1994 (Fig. 2(a)). When a new nest is added in simulation, all previous nest locations on the beach are checked to determine if the new excavation occurs at the same location as a previous nest (i.e. centres located less than 30 cm from each other). In such case, two possibilities were encountered: (1) the previous nest had hatched or all embryos were already dead or (2) the previous nest still contained living embryos that were killed with a k probability. In both cases the new nest begins its incubation. To discriminate between these two possibilities, incubation length and daily probability of nest destruction of the previously laid nest must be taken into account. As the sand temperature increases during the season, incubation time decreases from 75 to 60 days (Rimblot *et al.*, 1985). Incubation length l_i for a nest i oviposited on day t_i is the number of days for incubation to complete with $l_i = 75 - 0.1(t_i)$. The number of days m_i an individual nest i remained undestroyed was calculated using random numbers based on daily d probability that the nest contains no more living embryos.

If $l_i < m_i$, the nest i could complete its entire incubation without being destroyed by the effect of the d parameter. But, if a female excavated this nest site, the nest i was completely destroyed with a k probability.

If $l_i > m_i$, the nest i contained living embryos only from day t_i to day $t_i + l_i$ but not after this period. Thus, if a female excavated a nest site during this incubation period (days t_i to $i_i + l_i$), it was counted as 'female destroying at least one viable nest' and the nest i was immediately destroyed with a k probability. When a female excavated a site of nest i after the day $t_i + l_i$, the original nest i contained no more living embryos and the event was counted as 'female destroying no viable nest'.

Parameters adjustment to the observed distribution

Owing to the complexity of the nesting process and the interrelation between all the parameters, it is not possible to describe the model analytically, and computer simulations are used instead. We used linear optimization to solve for the unknown parameters xy, d and k. We compared the observed $\varepsilon_{obs}(t)$ and estimated $\varepsilon_{est}(t)$ distributions of females excavating previously laid nests with still living embryos using a maximum likelihood approach. For each group of 15 days ($t_1 \ldots t_6$), the number of females that excavated, $E(t_i)$, or did not excavate, $NE(t_i)$, a viable nest is known, with $\varepsilon_{obs}(t_i) = E(t_i)/(E(t_i) + NE(t_i))$ (Fig. 2(b)). For a set of xy, d and k values, the corresponding $\varepsilon_{est}(t_i)$ were calculated. The probability p of obtaining $E(t_i)$ and $NE(t_i)$ females is the application of the output of one simulation with a particular set of parameters (xy, d and k) to a binomial distribution:

$$p\big(\varepsilon_{obs}(t_i) = \varepsilon_{est}(t_i)\big) = C_{E(t_i)+NE(t_i)}^{E(t_i)}\big(\varepsilon_{est}(t_i)\big)^{E(t_i)}\big(1-\varepsilon_{est}(t_i)\big)^{NE(t_i)} \tag{1}$$

The log likelihood of the observations is the combination of the six probabilities obtained from equation 1:

$$\begin{aligned}&\ln L\big(\varepsilon_{obs}(t_1)\ldots\varepsilon_{obs}(t_6)\big)\\&= T + \sum_{i=1}^{6}\Big(E(t_i)\ln\big(\varepsilon_{est}(t_i)\big) + NE(t_i)\ln\big(1-\varepsilon_{est}(t_i)\big)\Big)\end{aligned} \tag{2}$$

where T is a constant term:

$$T = \sum_{i=1}^{6}\Big(\ln C_{E(t_i)+NE(t_i)}^{E(t_i)}\Big) = 1180.05 \tag{3}$$

We fitted the likelihood function iteratively to find its maximal value. Variances were obtained by numerical approximations from the inverse of the second-order partial derivative function for each of the three parameters at the maximum likelihood.

Sex ratio calculation

The hatchling production and sex ratio (male frequency) at hatching were calculated from the *xy*, *k* and *d* values maximizing the likelihood. We used the mean monthly data determined for 14 seasons at a nearby rookery for *D. coriacea* in Suriname (Godfrey *et al.*, 1996), since the data were concordant with the ratios recorded for 2 years at the Ya:lima:po beach in French Guiana (Rimblot *et al.*, 1985; Rimblot-Baly *et al.*, 1986). The annual female frequency was then estimated by:

$$0.48\ \mathrm{p_{March}} + 0.15\ \mathrm{p_{April}} + 0.46\ \mathrm{p_{May}} + 0.73\ \mathrm{p_{June}} + 0.91\ \mathrm{p_{July}} + 1.00\ \mathrm{p_{August}} \qquad (4)$$

where $\mathrm{p_{Month}}$ is the relative proportion of successful nests for the corresponding month.

Measures of density-dependence of the outputs of the model

The influence of density-dependence on hatchling production was related to variation in the yearly total number of nests deposited on the beach. The distribution of nest numbers per night during the nesting season was unchanged from the 1994 nesting season data, but the actual values were multiplied by a constant to vary the total number of nests. Density-dependence was thereby calculated from (a) the total proportion of viable nests, (b) the total number of viable nests, (c) the male-frequency of viable nests, (d) the equivalent number of viable feminized nests.

RESULTS

Parameter estimations

The nightly distribution of nesting females (observed and calculated numbers) and the proportion of females that excavated at least one nest with living embryos (defined as viable nest) are shown in Fig. 2. The proportion of nesting females excavating previous nests had a maximum at 23% during late June and early July and decreased thereafter.

Parameters that maximized the likelihood (Ln L = –18.42) between the observed and calculated distributions of nest destruction by nesting females were an effective beach size xy = 7,340 m^2 (SD 288), daily probability of nest failure d = 0.034 (SD 0.002) and probability that an excavated nest was completely destroyed k = 1 (SD 0.30) (Fig. 2(b)). The surface fitting for *xy* and *d* parameters shows that only one maximum is observed (Fig. 3). The observed distribution $\varepsilon_{obs}(t)$ and the estimated distribution for values maximizing likelihood $\varepsilon_{estML}(t)$ were not significantly different (χ^2 = 1.55, 3 d.f., P > 0.9). The outcomes established that simulations were accurate representations of processes that occurred on the beach.

To demonstrate that a uniform nesting probability (essential to the concept of effective size of nesting beach) produced unbiased results, we determined the time-series $\varepsilon_{estML}(t)$ obtained for d = 0.034, k = 1, for a beach length x = 734 m and a Gaussian probability of nesting on the beach width (y axis). A $\varepsilon_{est}(t)$ distribution similar to $\varepsilon_{estML}(t)$ was obtained (χ^2 = 10.59, 10 d.f., P = 0.4) with a standard deviation of 2.7 m for the dispersion of nests around the centre of the beach. The density of nests for the beach with a uniform probability of nesting is shown in Fig. 4(a) whereas an equivalent beach with Gaussian distribution of nests is shown in Fig. 4(b). In Fig. 4(b), more nests are concentrated in the centre of the beach (higher destruction rate), and even though the effective beach width is larger than in Fig. 4(a), the overall outputs are the same.

After explaining the spatial dimensions of nest deposition and destruction, we accounted for temporal shifts of sex ratios in the viable nests that went full-term. Because the standard deviation of the *k* parameter was

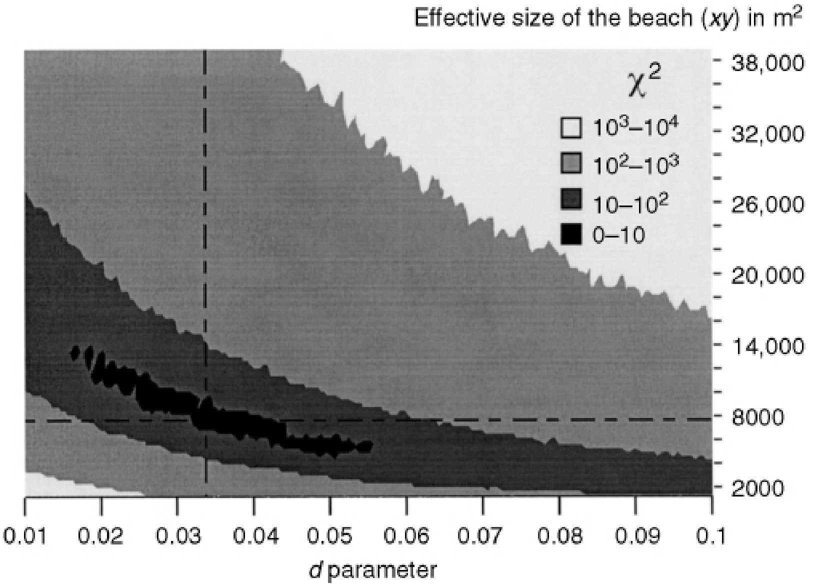

Fig. 3. Fitting surface measured as the χ^2 between model and data for *xy* and *d* parameters.

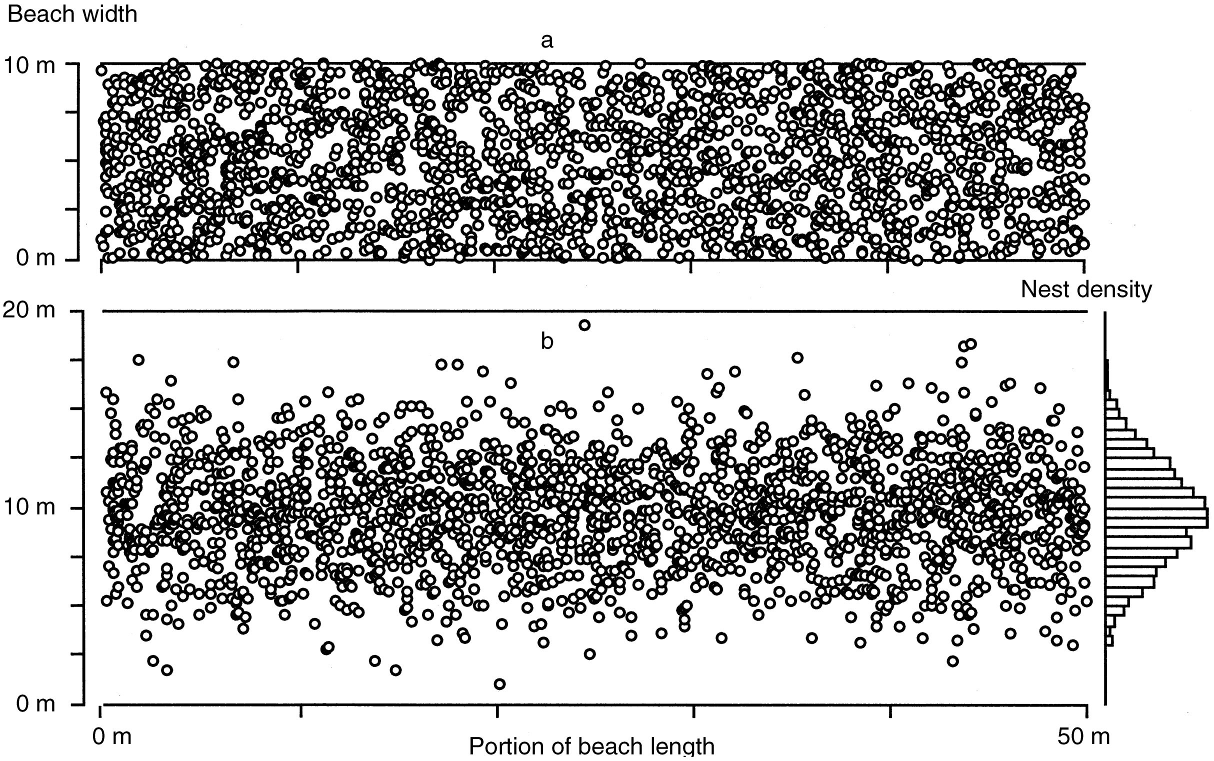

Fig. 4. Nest distribution on a representative 50 m length beach with uniform (a) or Gaussian (b) probability of nesting along the width of the beach. Both situations exhibit the same output.

high, in all further simulations this parameter was varied from 0.5 to 1 (step 0.1), though only the two extremes are illustrated (Figs 2–7). From the estimated *d* and *xy* values, the calculated distribution of nests not destroyed at the end of the incubation period was established for 20 trials (Fig. 5(a)). The highest probability of destruction was observed for nests laid in late April and early May during the male-producing period. The proportion of viable nests at the end of incubation compared to the total nest number for the 1994 nesting season was between 8.9% (SD 0. 005) for $k = 0.5$ and 7.2% (SD 0.06) for $k = 1$ (Fig. 5(b)).

Density-dependent outputs of the model

A. Proportion of viable nests (Fig. 6(a))

When the proportion of viable nests was obtained with a yearly number of nests from 10,000 to 200,000 (step 10,000), a density-dependent nest destruction was observed: a higher rate of destruction associated with larger numbers of nests. To check the relative contribution of destruction by nesting females (*k* parameter) compared to destruction by other factors (*d* parameter), the value of *k* is set to 0 (nests are not destroyed even if excavated): the percentage of viable nests remaining at the end of the incubation season was only 0.116. Therefore, our model predicts that the main destruction on the beach is produced by biotic or abiotic factors (*d* parameter) during incubation but not by nest excavation.

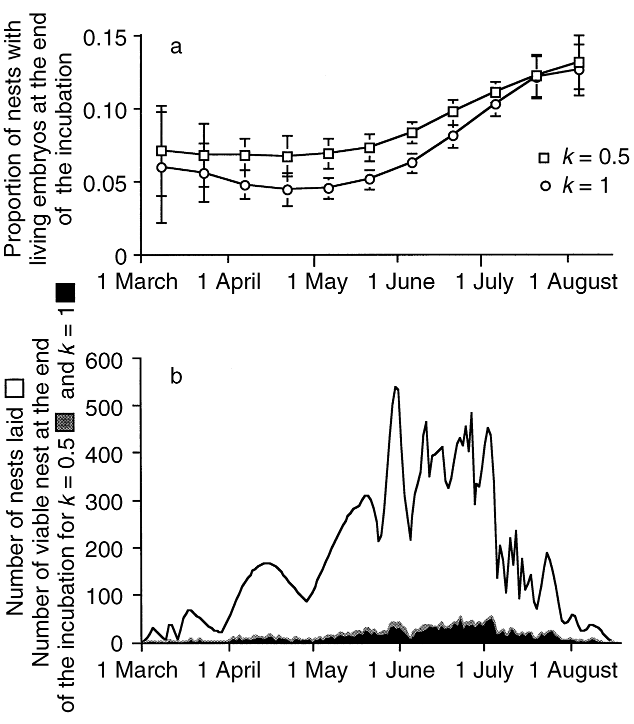

Fig. 5. (a) Proportion of nests with living embryos at the end of the incubation relative to the number of deposited nests according to the date of laying (for $k = 0.5$ and $k = 1$). (b) Number of nesting females each night (upper line) and number of nests with living embryos at the end of the incubation for $k = 0.5$ and $k = 1$. Error bars are two SD.

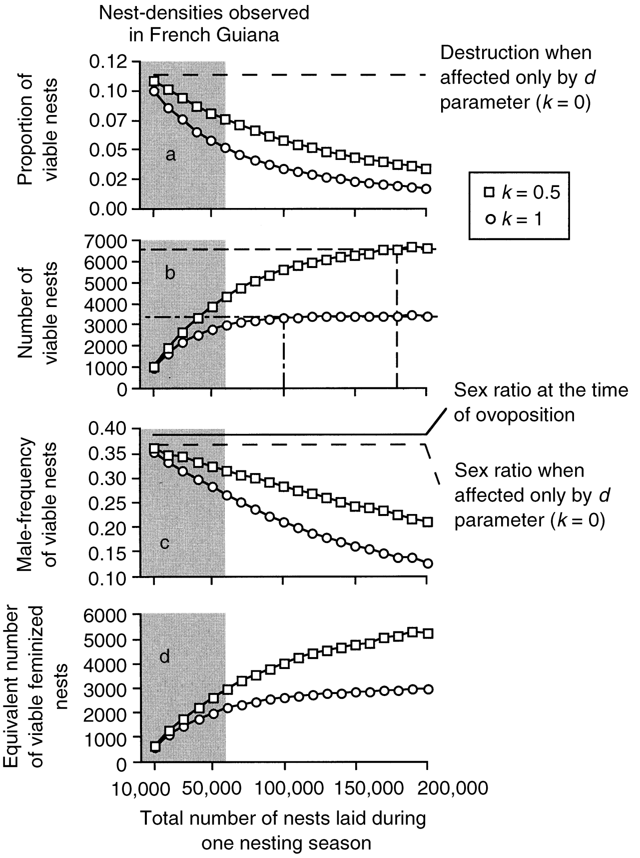

Fig. 6. Proportion (a) and number (b) of nests containing living embryos at the end of the incubation versus the total number of nests on the beach for $k = 0.5$ and $k = 1.0$; (c) sex ratio (male frequency) and equivalent number of feminized nests (d) for the nests containing living embryos at the end of the incubation relative to the total number of nests laid on the beach for $k = 0.5$ and $k = 1$. Values of k between 0.5 and 1 produce an intermediate effect and are not shown. Error bars for 20 trials are too small to illustrate.

B. Number of viable nests (Fig. 6(b))

The total number of viable nests at the end of their incubation was estimated based on the same method (see A). It reached a maximum value between 3400 ($k = 1$) and 6600 nests ($k = 0.5$) that represented the highest possible production of the beach. These values were attained at 100,000 ($k = 1$) and 180,000 ($k = 0.5$) nests deposited on the beach during a nesting season. The values define a 'maximum carrying capacity of the beach', i.e., the maximum number of nests deposited on the beach for which an increasing hatchling production is still observed. Whatever the k value, the highest density observed in French Guiana (60,000 nests per nesting season) was far below the maximum carrying capacity of the beach.

C. Sex ratio of viable nests (Fig. 6(c))

The expected sex ratio M/(M+F) at the time of oviposition for an equal probability of hatching of all the nests was defined as the 'sex ratio at oviposition'. In 1994, the estimated sex ratio at oviposition based on equation 4 was 0.387. The hatchling sex ratio was defined as the sex ratio at the end of incubation. Two factors affected hatchling sex ratio compared to sex ratio at oviposition. First, incubation length was longer for nests at lower temperature. Hence, male-producing nests were subject to nest destruction for a longer period, i.e. influenced by the d parameter. The outcome was a density-independent feminization of hatchling sex ratio compared to sex ratio at the time of oviposition. The estimated hatchling sex ratio taking into account only this effect was 0.365 (SD 0.006). Second, early nests were subject to higher probability of destruction by other nesting females (Fig. 5) and these first-laid nests were mostly masculinized. The effect produced a density-dependent feminization of hatchling sex ratio compared to sex ratio at oviposition. The feminization effect was higher as the annual nest production was enhanced and also higher when k tended to 1. The estimated hatchling sex ratio can reach a value near 0.25 for the highest nest density observed in French Guiana.

D. Equivalent number of viable feminized nests (Fig. 6(d))

Based on the number (Fig. 6(b)) and the male-frequency (Fig. 6(c)) of viable nests, the equivalent number of feminized viable nests was estimated. The shape of the curves is roughly the same as for the number of viable nests (Fig. 6(b)) but with one important difference. As female-frequency is enhanced for larger total numbers of nests (Fig. 6(c)), asymptotic values observed in Fig. 6(b) are no longer observed and the equivalent number of feminized viable nests continues to increase even for the largest number of nests deposited on the beach for both $k = 0.5$ and $k = 1$.

Per capita reproductive output

In the estuary of the Maroni and Mana rivers, leatherback females oviposit with a frequency of $C = 7.52$ clutches per year (SD 1.81) (Fretey & Girondot, 1989), the mean clutch size being $E = 85$ eggs (Fretey, 1980). The average hatching success for successful nests (S) was estimated at 10% for Galibi beaches in the same estuary (Hoekert *et al.*, 1998). The production of hatchlings per nesting female during one nesting season is $C \times E \times S$. Remigration intervals for females averaged $R = 2.5$ years between reproductive seasons (Girondot & Fretey, 1996) and the mean yearly production of hatchlings per female is then $(C \times E \times S)/R$. Defining T as the total number of nests deposited on the beach and F as the equivalent number of feminized viable nests (see Fig. 6(d)), the mean annual reproductive output per female (O) is:

$$O = (F/T) \times ((C \times E \times S)/R) = (C \times E \times S \times F)/(R \times T)$$

This value is also density-dependent and appears to be very low (Fig. 7(a)), and between one to two female

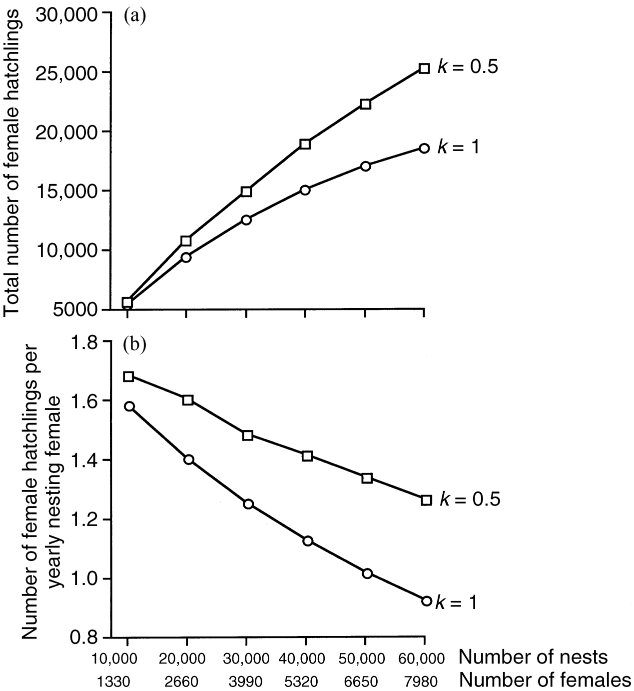

Fig. 7. Annual reproductive output expressed as (a) the total number of viable female hatchlings, and (b) the number of viable female hatchlings per nesting female for k = 0.5 and k = 1.

hatchlings produced per year per female in the population (Fig. 7(b)).

DISCUSSION

Leatherback turtles that nest in French Guiana represent about 40% of the world's breeding population. The serious decline in female populations at many of the world's leatherback rookeries (Spotila *et al.*, 2000) brings particular urgency to the need to understand better the status of the species at Ya:lima:po-Awa:la beach. Only three stages of leatherback life-history are observed in French Guiana: adult reproductive females, embryos, and hatchlings of both sexes. A single observation of copulation in front of the beach indicates that sometimes males are present but no quantification is available (Godfrey & Barreto, 1998). Previous workers at the site have proposed that the nest success was a significant factor governing the population dynamics (Fretey & Lescure, 1979). Moreover, density-dependent regulation of population size has been proposed to be of major importance in some populations of other marine turtles, *Chelonia mydas* (Bustard & Tognetti, 1969, but see Limpus *et al.*, 1991) or *Lepidochelys olivacea* (Eckrich & Owens, 1995).

We found that three parameters are sufficient to explain the actual distribution of females excavating previously laid nests: the daily probability of nest destruction (d), the effective size of the beach (xy) and the probability that an excavated nest does not contain any living embryos (k). The d parameter was relatively high: more that 3% of the nests are destroyed per day. The effective size of the beach ($xy = 7340$ m^2) was one tenth of the real size (near 80,000 m^2). This result was consistent with the observation that nests were grouped in the upper part of the beach. The value of k parameter was high, even taking into account the large standard deviation, but appears qualitatively correct since destruction of a previous nest yields broken eggs that are obvious when a female excavates it. Moreover, even if not all eggs are directly destroyed by the excavation of the second female, indirect destruction due to bacterial or fungal contamination from broken eggs continues to threaten viable eggs in the nest (Eckrich & Owens, 1995). We should also note that the bacterial or fungal contamination from broken eggs can conceivably affect the newly deposited eggs as well, a phenomenon that will amplify the density-dependent effects of nest destruction by nesting females.

The most simple model described here is sufficient to explain the pattern of nest destruction observed in 1994. However, a more complex (i.e. parameter rich) model could also have been used that may change some of the conclusions. For example, the d parameter which is one of the main determinants for nest output could be itself density-dependently correlated, either positively (e.g. more nests lead to more predator attraction) or negatively (e.g. saturation of a constant number of predators). In the absence of real data, we prefer to remain conservative and choose the simplest model that is not rejected statistically.

The simulations we report here lend support for density-dependence effects in nest survivorship, i.e., an increasing female density results in increased intraspecific nest destruction. Even so, the available space for nesting was far from saturated because the number of intact nests continued to increase even for the maximum nest density (60,000 nests in 1992) observed in French Guiana. The maximum number of nests observed on the Ya:lima:po-Awa:la beach is two to three times lower than the predicted maximum carrying capacity of the beach (Fig. 6(b)). Moreover, we did find a density-dependent bias towards feminization of primary sex ratio compared to sex ratio at the time of oviposition (Fig. 6(c,d)). The higher the number of nesting females, the stronger the female bias in juveniles, because of temporal changes to primary sex ratio. Consequently, the density-dependent nest destruction for feminized nests is reduced by this effect compared to the density-dependent nest destruction for total nests.

If density-dependent inversion in the nest output had been found, it would have been sufficient to explain the current decrease in the number of nesting females on French Guiana beaches. With the results found here, we need to incorporate the nest output of the model within a population dynamics model to check if it produces a population growth rate lower than 1. Unfortunately too many data are lacking (survival rates of all the stages are unknown) to produce such a model accurately. However, we find that the proportion of successful nests on this beach is very low (5 to 10.5% according to k parameter, Fig. 5(b)) compared to the values observed for this species on the Tortugero beach (57%) (Leslie *et* *al.*, 1996). Hatching success can be used as an upper estimation of the percentage of the proportion of successful nests. Hatching success is 75% at Culebra (Tucker, 1989) and 67% at St Croix (Boulon, Dutton & McDonald, 1996) which are both low-density leatherback rookeries. Thus, hatchling production per nest in French Guiana is the lowest reported so far for this species. It may not be sufficient to ensure the replacement of adults in the population because of the near-shore marine predation (e.g., by catfish and sharks) on neonates that enter the water and an estimated average age of sexual maturity at 13–14 years (Zug & Parham, 1996; but see Pritchard (1996) who proposed rather 3–5 years). However, we do not have any data to justify this hypothesis because annual survival rates for juveniles, subadults and even adults are not known.

Other alternative hypotheses may explain why the proportion of successful nests is very low in French Guiana. It is possible that the model produced a biased estimate of the nest destruction. However, this seems unlikely since the model's estimate of the proportion of viable nests at the end of the incubation (5 to 10.5% according to k parameter, Fig. 5(a)) was of the same order as the estimate derived from empirical studies: 2.78%, 17.97% and 5.53% for Fretey & Lescure (1979). Moreover, the sex ratio at the time of ovoposition in our study (0.387) falls within the range of values estimated for 14 years at the nearby Matapica beach (0.30 to 0.65 with a mean at 0.466) (Godfrey *et al.*, 1996). Several life history parameters of leatherback turtles are also debatable. For example, females of Pacific leatherback populations have been estimated to have a lower annual clutch frequency, i.e. 5 nests (Steyermark *et al.*, 1996) instead of 7.52 for French Guiana (Fretey & Girondot, 1989). However, this fecundity difference would not alter the conclusions concerning spatial patterns of nesting nor would it affect the probability of individual nest destruction (i.e. d, k and results presented in Figs 6–7 are unchanged). The mean yearly reproductive output per female (O) will be even lower than the value estimated with $C = 7.52$.

In summary, only 10% of viable nests incubate successfully at Ya:lima:po-Awa:la and the absolute number depends on nest density which can be very high at the rookery. However, nest destruction by nesting females is a minor phenomenon compared to destruction from other abiotic or biotic factors measured by the d parameter. Several such factors affecting incubation success are known for Surinamese and French Guianan beaches. Preliminary results indicate that 40% of leatherback eggs in Galibi beaches are predated by mole crickets (Hoekert *et al.*, 1998). Excessive soil moisture may be an additional relevant factor in the Guianese region as the nests incubated close to the saltwater on Galibi beaches often fail to hatch (Hoekert *et al.*, 1998). Furthermore, very large marshes behind the Ya:lima:po-Awa:la beach may affect incubation success because of sand saturated by freshwater drainage through the beach.

Here, we investigate only incubation effect. However, other factors involving adult mortality are also perhaps at work. Unfortunately, there are limited data on the fisheries of the Atlantic and Caribbean to support or refute this hypothesis. Illegal drift net fishing in this region is a suspected agent of adult mortality (Chevalier, Cazelles & Girondot, 1998). For example, three female leatherbacks tracked by satellite telemetry swam back and forth into fishing zones during the nesting season (Ferraroli *et al.*, 1999).

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