Evaluation of density-dependent processes and green turtle *Chelonia mydas* hatchling production at Tortuguero, Costa Rica

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ABSTRACT: The role of density-dependent processes in sea turtle populations remains largely unknown. This study quantified density-dependent and density-independent processes that underlie hatchling production in the green turtle nesting population at Tortuguero, Costa Rica, and estimated current mean hatchling output and potential carrying capacity of Tortuguero beach for hatchlings and nesting females. Density-dependent effects of nest destruction by nesting females and coatis were evaluated in the 2000 nesting season along the 28.8 km nesting beach. To quantify factors affecting hatchling production, the fates of nests were monitored in twelve 50 m long study plots. Density-dependent factors included nest destruction by nesting females and predation by coatis, whereas density-independent factors included beach erosion, beach flooding, and below-beach-surface destruction by crabs, ants, microbes, and plant roots. Calculations indicated that between 5 and 6 million hatchlings are currently produced, while a simulation model suggested that at carrying capacity, 6 to 10 times as many hatchlings could be produced by more than 600 000 nesting females. The current mean number of females nesting at Tortuguero is between 3 and 4 % of the population that is estimated to nest at carrying capacity. This estimate is consistent with previous estimates that modern day populations of Caribbean green turtles represent only 3 to 7 % of pre-exploitation levels. The hatchling production model is applicable to other beaches and sea turtle species, and provides a framework to evaluate recovery goals for sea turtles.

KEY WORDS: Green turtles · *Chelonia mydas* · Density-dependent effects · Density-independent effects · Hatchling production · Carrying capacity · Tortuguero · Costa Rica

INTRODUCTION

The role of density-dependent processes in population regulation has been controversial in ecology (Howard & Fiske 1911, Nicholson 1933, Andrewartha & Birch 1954, Lack 1954, Murray 1994, Sale & Tolimeiri 2000). As population density increases, density-dependent factors such as predation, disease, and competition for resources take effect to limit population size. While density-dependent factors have been quantified in numerous systems and organisms, the role of density dependence in the regulation of sea turtle populations has remained largely unstudied.

Sea turtles move among widely dispersed terrestrial, oceanic, and neritic habitats, making it difficult to collect demographic data at different life-history stages and habitats. Furthermore, current population densities in many sea turtle species are apparently far below levels at which density-dependent processes would play a significant role. Previous models simulating density-dependent effects at the nesting beach have either examined a single density-dependent factor (Bustard & Tognetti 1969) or have evaluated density-

dependent effects with a limited number of parameters derived statistically (Girondot et al. 2002). A recent study by Caut et al. (2006) improved on the density-dependence model developed by Girondot et al. (2002) and highlighted population regulation through density-dependent nest destruction at a high-density leatherback *Dermochelys coriacea* nesting beach in French Guiana. Away from the nesting beach, Bjorndal et al. (2000) reported evidence for density-dependent effects on somatic growth rates in immature green turtles in the southern Bahamas. In general, models of population dynamics developed for sea turtles have either explicitly omitted density-dependent processes or have used assumptions that need to be validated (Chaloupka & Limpus 1996, Chaloupka & Musick 1997, Chaloupka 2003, Heppell et al. 2003). Density-independent models are entirely appropriate for predicting population dynamics at low densities and evaluating the short-term effects of different conservation strategies (de Kroon et al. 2000). However, evaluating density-dependent effects at all stages will become essential for predicting population dynamics as populations recover and population densities increase (Bjorndal 2003), for establishing recovery goals, and for guiding management questions pertaining to exploitation of sea turtle populations. This study is an attempt to quantify density-dependent and density-independent processes that limit hatchling production in the green turtle nesting population at Tortuguero, Costa Rica.

Tortuguero supports the largest green turtle rookery in the Atlantic system, and the number of green turtles nesting annually has increased over the past 30 yr (Bjorndal et al. 1999, Troëng & Rankin 2005). The annual number of nesting females varies widely between successive years at Tortuguero, apparently in response to environmental factors that affect the length of the interbreeding intervals of individual turtles (Solow et al. 2002). Analyses of spatial variation in nest distribution in this increasing and naturally fluctuating nesting population over a 30 yr period have demonstrated a remarkably consistent pattern in nest distribution within and among years (Tiwari et al. 2005). Therefore, while the overall strength of density-dependent effects will vary proportionally between high and low nesting years, relative nest densities along the beach are consistent among years.

At Tortuguero, nests are destroyed by nesting sea turtles (Fowler 1979, Spotila et al. 1987, Horikoshi 1992) and by natural predators including coatis *Nasua narica*, crabs *Ocypode quadrata*, ants (unidentified species), termites (unidentified species), maggots *Megaselia scalaris*, and mites *Casloglyphus* sp. (Fowler 1979, Horikoshi 1992). Domestic and feral dogs *Canis familiaris* have also been observed depre-

dating turtle nests at Tortuguero (Fowler 1979, Horikoshi 1992). As egg and eggshell remains accumulate, increased microbial activity may result in higher egg mortality (Cornelius et al. 1991, Marcovaldi et al. 1999, Phillott & Parmenter 2001). Sand erosion and accretion as well as beach flooding during heavy rains at Tortuguero often result in nest loss (Horikoshi 1992). Finally, people still occasionally collect eggs for consumption on Tortuguero beach.

Tortuguero provides an excellent opportunity to evaluate density-dependent and density-independent effects on hatchling production because of the large size of the colony and the consistent spatial distribution of nests within and among years. Jackson et al. (2001) estimated that the current populations of green turtles in the Caribbean represent only 3 to 7% of pre-exploitation level. Therefore, far greater numbers of turtles may well have nested at Tortuguero in the past. Quantifying density-dependent processes that affect hatchling production at Tortuguero will help identify what numbers could have nested in the past and what size populations could be supported in the future (see 'Discussion').

In this study, we used 3 approaches to examine density-dependent and density-independent effects on hatchling production at Tortuguero. First, we evaluated density-dependent effects of nest destruction by nesting females and predation by mammals on the entire nesting beach. Second, to quantify density-dependent and density-independent processes affecting hatchling production that could not be estimated at the level of the nesting beach, we monitored the fates of nests in twelve 50 m long study plots within the dense nesting section of the beach. Third, to estimate current mean hatchling output and potential carrying capacity, defined as the maximum number of hatchlings that can be produced in a season, we incorporated the density-dependent and density-independent parameters estimated from the study plots into a simulation model.

MATERIALS AND METHODS

The 28.8 km long Tortuguero nesting beach lies on the northern Caribbean coast of Costa Rica. Tortuguero village and a few tourist lodges lie within the northern 5.4 km, and Tortuguero National Park extends between kilometers 5.4 and 28.8. The beach is backed by low-lying tropical rainforest and is separated by Rio Tortuguero from the mainland.

Density-dependent effects along the entire beach. During the 2000 nesting season (mid-June to early December), the 28.8 km beach was surveyed at approximately weekly intervals by an observer walk-

ing the beach early in the morning and counting only the nests laid the previous night. Visible tracks and large depressions left in the sand by nesting females that emerged the previous night, which are easily distinguished from older tracks, were used to determine how many nests were laid. Locations of nests were not marked during these weekly surveys. In addition, the number of nests destroyed by nesting females and the number of nests depredated by mammals (primarily coatis) since the previous survey were counted. Once a month the width of the beach, from the vegetation to the most recent high tide line, was measured every 1.6 km to estimate changes in available nesting area.

To evaluate density-dependent effects of nest destruction by nesting females, nest density and the probability of a female destroying a nest were estimated from the data collected. Average nest density for the 28.8 km beach (= beach density) on a given day was calculated from the estimated number of nests in the beach on that day and mean beach area (= 28.8 km × mean monthly beach width). The number of nests incubating in the beach on a given day was estimated by determining the mean number of nests laid on each day from weekly nest counts during that month, assuming that all nests had an incubation period of 60 d, and summing all the nests laid in the 2 mo prior to the day for which beach density was being calculated.

The probability of a female destroying a nest was evaluated as an index of destroyed nests (= [no. of nests destroyed by nesting females since previous survey]/[no. of females that nested the previous night]). An index was used because the nest destruction count attempted to include nests destroyed since the previous survey, whereas the number of new nests laid could only be determined for the previous night. We also evaluated the relationship between beach density and the number of nests depredated by mammals (primarily coatis), as well as the relationship between estimated hatching density (= density of nests hatching on the 28.8 km beach) and the number of nests depredated by mammals.

Density-dependent and density-independent effects in study plots. To quantify density-dependent and density-independent parameters affecting hatchling production that could not be determined at the level of the nesting beach, 12 randomly selected 50 m long plots were set up between kilometers 9.6 and 13.6, which lie within the high-density nesting area of the beach (Tiwari et al. 2005). Each plot was further divided into 3 zones: the vegetation zone at the back of the beach had 100% shade, the border zone within 2 m of the vegetation had 5 to 100% shade, and the open zone between the border zone and the surf had less than 5% shade. Thermocouples were buried in the vegetation, border, and open zones of 6 plots at mean

mid-clutch depth of 70 cm (Horikoshi 1992). Sand temperatures were monitored to determine whether they remained within the thermal tolerance range for sea turtle embryos, estimated to lie between 25 and 35°C (Ackerman 1997) or between 24 and 32°C (Yntema & Mrosovsky 1982). Eighteen PVC pipes, 10 cm in diameter, were placed in the open and vegetation zones to a depth of 140 cm in 9 plots to determine when ground water level was high enough to drown nests. To calculate plot area and estimate changes in plot area over the nesting season, the width of each plot was averaged from measurements taken from the vegetation to the most recent high tide line and to the current tide line, approximately every 5 d at the north and south ends of each plot. Data in the plots were collected from mid-June to early December 2000.

Each morning, the locations of all new nests, depredated nests, and nests destroyed by nesting females from the previous night, as well as the locations of nests lost to erosion and poaching (i.e. nests illegally collected by humans for consumption), were recorded in the 12 plots. Nest destruction occurring below the beach surface by invading plant roots or by predators such as crabs, ants, and microbes could not be monitored on a daily basis. Therefore, a subset of randomly selected nests was marked for nest inventories to quantify these sources of nest destruction after the main hatchling emergence event or after the estimated incubation period. During a nest inventory, clutch size (defined as the number of eggs in a nest) was estimated by counting eggshells that were ≥50% intact and the unhatched eggs. Eggs that were still turgid and white in color and showed no evidence of decomposition were classified as infertile (Blanck & Sawyer 1981, G. Webb pers. comm.). Mortality caused by beach flooding in the excavated nests was also recorded. The average incubation time (the time between clutch deposition and hatchling emergence) was determined from nests for which the date of hatchling emergence was recorded.

From data collected in the study plots, we quantified the relationships between nest density and (1) nest destruction by nesting females, (2) predation by mammals (primarily coatis), and (3) below-beach-surface nest destruction, which included destruction by crabs, ants, microbes, maggots, and root invasions. Root invasion was included because developing eggs may provide an additional source of nutrients for these plants, leading to the proliferation of roots as nest density increases. Different measures of nest density were deemed appropriate to quantify each of these relationships and are described below.

Individual nesting females or coatis could destroy nests anywhere in the plot. Therefore, the measure of nest density used to evaluate nest destruction by

females and coatis was defined as the number of incubating nests per plot area (= plot density). The relationship between plot density and the probability that a nesting female destroys another nest was quantified by determining the outcome of female nesting activity (no. of females that destroyed/did not destroy a nest) for all observed plot densities in the 12 plots. Data were analyzed using binomial generalized linear models (GLM). In order to fit the expected relationship p(destroyed) = $1 - e^{-AD}$, where A is the area disturbed by a nesting female and D is density, a quasibinomial GLM using a log link and an intercept forced to 0 was fit to the number of nests surviving (rather than number of nests destroyed) (Strong et al. 1999). The model predicts the probability of nest survival p_S; $1 - (p_S)$ gives the estimated probability of nest destruction at each density. To account for overdispersion (variance greater than expected from a binomial model, estimated as residual deviance/residual df), the quasibinomial model was used for model evaluation (McCullagh & Nelder 1989). Data were also analyzed with plot as a fixed effect (Agresti 1996); analyzing binomial data with random effects is challenging, and a fixed-effect model should be sufficient to detect major variation in nest destruction among plots.

The relationship between plot density and the probability of a nest being depredated by coatis was quantified by determining the number of incubating nests that were depredated and the number of incubating nests that were not depredated in the study plots on a per night basis, with plot density averaged over the 12 plots because a minor percentage of nests were depredated. This relationship was analyzed using a binomial GLM with a logit link and a quasibinomial model. The r^2 values were calculated as ([null deviance – residual deviance]/[null deviance]).

To evaluate potential density-dependent effects of below-beach-surface nest predation (= destruction by crabs, ants, microbes, maggots, and root invasions) on hatching success, the appropriate measures of density are the number of neighbors and distance to nearest neighbor. We used both the average number of nests within a 1.5 m radius over the incubation period of a nest and the minimum distance to nearest neighbor as independent variables in the same analysis to quantify nest density (= neighbor density); co-linearity between these 2 measures of neighborhood density was not a problem because of a non-linear relationship between minimum distance to nearest neighbor and average number of neighbors within a 1.5 m radius. Given that green turtles have a track width between 100 and 130 cm (Pritchard & Mortimer 1999) without complete extension of the front flippers, and an average straight carapace length of 100 cm at Tortuguero (Bjorndal & Carr 1989), we assumed that the area of disturbance by

a turtle excavating a body pit and then later vigorously camouflaging the area would have a radius of 1.5 m. This represents a disturbed area of 7 m^2 and is close to Hendrickson's (1958) estimate of an area between 5 and 6 m^2 for green turtles nesting in Malaya and Sarawak, which have radii of 1.3 and 1.4 m, respectively. This larger area of disturbance in our analysis assumes that indirect effects could act over a greater distance than direct destruction.

Neighbor counts included incubating nests as well as hatched, destroyed, and depredated nests because the presence of decomposing eggs and eggshells may escalate microbial activity and attract predators. Nests that were eroded or collected by humans were removed from the analysis on that day.

To evaluate the relationship between neighbor density and the proportion of eggs lost to below-beach-surface predation, the number of eggs that hatched and the number of eggs that did not hatch were determined for each nest. Eggs classified as infertile were not included. Nests that were located less than 1.5 m from either end of the plot were not included in this analysis because location or number of neighbors outside the plot were not known. The binomial GLM with a quasibinomial model and a logit link function was used to analyze the relationship. Data were also analyzed with plot and beach zone as fixed effects.

R software (R Development Core Team 2004) was used for GLM analyses.

RESULTS

Density-dependent effects along the entire beach

The index of nests destroyed by nesting females closely tracked estimated beach density (= nest density for the 28.8 km beach) (Fig. 1a). Coati predation increased at the end of the season when beach density was low, but when hatching density increased (Fig. 1b). Mean beach width for the season was 26 m (range of mean monthly beach width = 13.5 to 34.5 m, n = 6).

Density-dependent and density-independent effects in study plots

Clutch and environmental parameters

A total of 3081 nests was laid in the 12 study plots with an average of 257 nests per plot (range = 159 to 328, SD = 59.8; n = 12). Mean clutch size was 108 eggs (range = 31 to 206, SD = 24.6, n = 316). Mean incubation period, estimated for every half-month
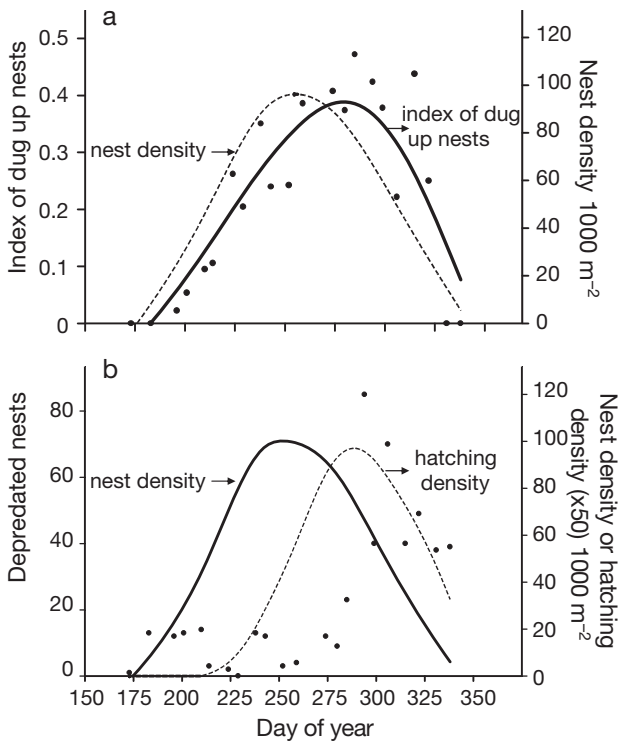
Fig. 1. (a) Relationship between index of dug up nests (• and — = [no. of nests destroyed by nesting females since previous survey]/[no. of females that nested the previous night]) and density of nests on the 28.8 km beach (----). (b) Relationship of no. of nests depredated by mammals (primarily coatis) (•) with nest density (—) and hatching density (= density of nests hatching on the 28.8 km beach, multiplied by 50 to share same axis as nest density; ----) on the 28.8 km beach during the 2000 nesting season. Solid and dashed lines are fitted smooth (cubic smoothing splines). Day of Year 150 = 29 May 2000

period in each of the 12 plots, was 60 d (range = 54 to 68, n = 90). Only 1.2% (n = 37) of nests laid in the plots were lost to beach erosion, and the average daily probability of nest erosion was estimated to be 0.00018 by determining the probability of viable nests being eroded daily. Only 12 nests (0.4%) were collected by humans.

Average sand temperature at 70 cm (mean midclutch depth) was 28.3°C (range = 25.4 to 30.7°C) in the open zone, 26.2°C (range = 24.9 to 27.8°C) in the border zone, and 25.6°C (range = 24.5 to 30.1°C) in the vegetation zone. Sand temperature during the nesting season stayed within acceptable incubation range in all zones and is unlikely to have contributed to embryo mortality. The water table rose to a minimum depth of 66.5 cm (mean = 89.3 cm; range = 66.5 to 132 cm) in the open zone and to 45.4 cm (mean = 90.9 cm; range = 45.4 to 132 cm) in the vegetation zone, causing flooding of nests that were at a mean nest depth of 75.5 cm (nest depth range = 29.5 to 113.3 cm). In the excavated

nests in which flooding was a major source of mortality (n = 17), the proportion of eggs surviving ranged from 0 to 75%.

Nest destruction by nesting females and coatis

Nest destruction by females closely tracked the pattern of female emergence as observed at the level of the nesting beach (Fig. 1a). Of the 3081 nests laid in the 12 plots, 11% (n = 340) of incubating nests were destroyed by nesting turtles. In the 32 affected nests that were inventoried, the number of eggs remaining ranged from 1 to 132. The proportion of these remaining eggs that hatched ranged from 0 to 100%. Increasing plot density significantly increased the probability that a female would destroy a nest (Wald test, p < 0.0001; Fig. 2); the estimated coefficient of the log slope was −1.66, corresponding to a destruction area of 1.66 m^2 or a destruction radius of 0.73 m. The plot-by-density interaction (i.e. the variation in slope from plot to plot) was significant ($F = 2.35$, p = 0.01), with estimated destruction radii ranging from 0.47 to 0.99 m in different plots.

Predation by coatis was extremely low in the study plots. Of the 3081 nests laid in the 12 plots, coatis depredated 0.8% (n = 24) of the incubating nests and excavated 0.3% (n = 10) of the nests after hatchling emergence. Between July and September 2000, the mean daily probability of a nest being depredated was 0.0001; between October and December 2000, mean daily probability of predation was 0.0003. In 3 depredated nests that were inventoried, the number of
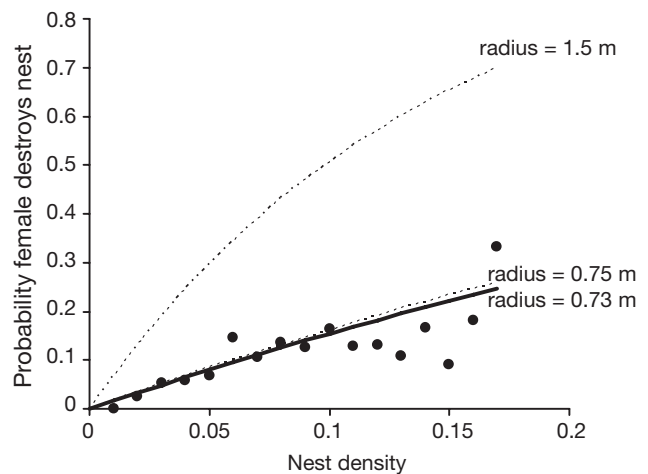

Fig. 2. Relationship between nest density (no. of incubating nests per plot area) and probability that a female destroys another nest (•). Solid line shows fit of a binomial GLM to the relationship $p = 1 − e^{−AD}$, where A is the area disturbed by a nesting female and D is density; dashed lines show relationships for other radii

remaining eggs ranged from 33 to 84. The proportion of these remaining eggs that hatched ranged from 73 to 90%. There was a very small but significant negative relationship between plot density and predation by coatis (GLM; $r^2 = 0.07$, $F = 4.55$, p = 0.03), which was probably caused by an increase in coati predation towards the end of the season when hatching increased, rather than by any causal relationship between density and coati predation (Fig. 1b).

Below-beach-surface predation

The mean proportion of eggs in a nest that survived below-beach-surface sources of mortality was 88.7% (range = 14.3 to 100%; n = 290 nests). There was no significant relationship between proportion of the nest destroyed by below-beach-surface predation and the average number of neighbors (GLM; $F = 0.10$, p = 0.76), minimum distance to nearest neighbor (GLM; $F = 1.68$, p = 0.2), or the interaction between average number of neighbors and minimum distance to nearest neighbor (GLM; $F = 0.16$, p = 0.69). When plot and zone were included in the model with average number of neighbors and minimum distance to nearest neighbor, there was no significant effect of plot, zone, or their interaction (p > 0.05).

SIMULATION MODEL

Model description

We developed a model to simulate processes that affected hatching in the 12 study plots to estimate current mean hatchling output, the carrying capacity of the 28.8 km beach (the maximum number of hatchlings that can be produced at Tortuguero), and the time to reach carrying capacity. For the simulation, the 28.8 km beach was divided into 36 segments that were each 800 m in length. In addition, mean beach width from the vegetation to the high tide line for the 28.8 km beach (26 m) was divided into 13 segments of 2 m each. The number of nests present on the beach on each day (*t*), summed over the 36 segments along the length of the beach (*x*) and the 13 segments across the width of the beach (*y*), can be summarized by:

$$\text{Nests}_t = \sum_{x=1}^{36} \sum_{y=1}^{13} (\text{Nests}_{(t-1)xy} - F_{txy} + N_{txy} - C_{txy} - E_{txy} - H_{txy})$$

On each day (*t*) for 185 d, the model simulated a random value (according to the rules given below) for each of the 2 by 800 m segments (36 along the beach and 13 across the beach: n = 468 segments) for the

number of nests destroyed by nesting females (*F*), the number of nests deposited each day (*N*), and the number of nests depredated by coatis (*C*), eroded (*E*), and hatched (*H*).

Only nesting in the main months (1 July to 31 October) on the 28.8 km beach was considered in the model, but the model was run until the end of December (*t* = 185 d) to allow all nests laid in October to complete their incubation period of 60 d, estimated from the study plots. The number of nests laid each day (*N*) was drawn from a Poisson distribution whose mean was the product of the total number of nests laid in the season and the mean proportion of nests laid on that day identified from general additive models in Tiwari et al. (2005); a clutch size of 108 eggs, estimated from the study plots, was assigned to each nest. To mimic the observed spatial distribution of nests along the beach, with a central peak skewed towards the northern end of the beach (Tiwari et al. 2005), the expected distribution of nests along the length of the beach was parameterized by a Beta-distribution (scaled from its usual domain of [0, 1] to [0, 28.8] to match the length of the beach) with shape parameters 2.11 and 1.87 estimated by the method of moments from the mean and variance of spatial nesting data along the beach. Similarly, the nest distribution across the beach — clustered close to the vegetation and in the open sections of the beach with nest numbers decreasing towards the tide line — was simulated by a Beta-distribution with shape parameters 1.72 and 2.69, estimated from the mean and variance of nest location data collected in the study plots.

The expected probability of a nest being destroyed by a nesting female is given by the equation $1 - e^{-AD}$, where *A* is the area of destruction and *D* is nest density at time of nest destruction. The radius of the area (assumed to be circular) within which a female is likely to destroy another nest during her nesting process was determined from the GLM fit discussed above; a radius of 0.75 m, equivalent to an area of 1.77 m^2, was used as an approximation to the precise estimate of 0.73 m/1.66 m^2 (a reasonable approximation given the wide range of variation among plots). Bustard & Tognetti (1969), in their model simulating density-dependent nest destruction by females in green turtles nesting in Australia, estimated that the body pit excavated by the turtle during her nesting process was 1.5 by 1.2 m, which corresponds to a radius of about 0.75 m. The number of nests destroyed by each female on each day in every segment was drawn from a Poisson distribution with a mean equal to 1.77 times the current density in the sub-plot. This assumes that nests are randomly distributed within sub-plots even though they are non-randomly distributed across sub-plots. A female was allowed to destroy more than 1 nest, but

the total number of nests destroyed in a segment could not exceed the total number of nests in that segment. In a conservative model, the fraction of the nest destroyed was set to 100%. In a less conservative model, the fraction of the nest destroyed by a nesting female varied from a few eggs to most of the eggs; a random fraction of eggs selected from a uniform distribution was subtracted from the clutch.

All incubating nests were subjected to a daily probability of predation by coatis and erosion until they had completed their incubation period. The mean daily probability of a nest being depredated in the model was 0.0001 during the nesting months (July to September) and 0.0003 from October to December when hatching increased, as estimated from the study plots. The mean daily probability of a nest being eroded in the model was 0.00018, also estimated from the study plots. All the eggs were destroyed in an erosion event. Each day in each segment, the number of nests depredated (C) or eroded (E) was selected from a binomial distribution with the appropriate probability of predation and erosion. In a conservative model, egg destruction by coatis was set to 100% in depredated nests. In a less conservative model, the fraction of the nest depredated varied; a random fraction of eggs selected from a [0, 1] uniform distribution was subtracted from the clutch. Nests containing eggs that successfully completed 60 d of incubation (H) were subtracted from the model each day.

Hatchling output on each day (t) is summarized by:

$$\text{Hatchlings}_t = \sum_{x=1}^{36} \sum_{y=1}^{13} \sum_{i=1}^{H_{txy}} (CS \times P_{txy})$$

where hatchling output from nests successfully completing incubation (H) is determined by multiplying the number of eggs or clutch size (CS) in each nest ready to hatch (i) by a proportion (P) randomly selected from a Beta-distribution with shape parameters 1.32 and 0.23. These parameters were estimated by the method of moments from the proportion of eggs surviving in the nests affected by below-beach-surface predation and flooding in the study plots. Nests partially destroyed by nesting females and coatis were subjected to a similar random reduction of eggs due to ant and crab predation and microbial infestation observed in the remaining incubating eggs. The total number of hatchlings produced each day was determined by summing across all 36 segments (x) along and 13 segments (y) across the beach. The simulation model was run from the mean estimate of 72 000 nests for Tortuguero (modified from Bjorndal et al. 1999) for the years 1992–1996) up to 10 million nests.

Finally, to determine how sensitive the model was to moderate changes in model parameters, the following

changes were made to some of the parameters: 20% increase in the daily probability of coati predation (nesting months = 0.00012, hatching months = 0.00036), 20% increase in the daily probability of erosion (0.000216), 20% increase in below-beach-surface predation, and an increase of 100% in a female's radius of destruction to 1.5 m. A 20% increase was assumed to be a suitably moderate value to detect sensitivity in the model. The 1.5 m radius of destruction is similar to the value estimated by Hendrickson (1958) for green turtles nesting in Malaya and Sarawak. These changes were incorporated individually in the model in which destruction by nesting females and coatis was complete, and in the model in which destruction by nesting females and coatis was partial. These simulations were run for 100 000 to 10 million nests. The R software (R Development Core Team 2004) was used to run the models.

Model results

When nesting females and coatis completely destroyed nests in the model, 72 781 nests produced 5.76 million hatchlings. In this model 10.7% of the nests were destroyed by nesting females, 1% were depredated by coatis, and 1% were lost to beach erosion; as expected, these values are consistent with similar values in the study plots. Carrying capacity was reached between approximately 30 million and 35 million hatchlings, which is approximately 6 times the current hatchling output (Fig. 3a). This carrying capacity was reached between 2 million and 6 million nests, which represent 2.6 and 8 nests m^{-2}, respectively, for the 748 800 m^2 (28 800 m × 26 m) nesting beach if nests were uniformly distributed. However, nest density in some sections of the beach will be much higher because of the consistent unimodal spatial nesting pattern at Tortuguero (Tiwari et al. 2005). Using a mean annual population growth rate of 4.8% for Tortuguero (Bjorndal et al. 2005), the lower estimate of 2 million nests would be reached in approximately 72 yr in an exponential growth model. However, as this rate of increase would decrease as the beach approaches carrying capacity, 72 yr underestimates the time to reach carrying capacity.

When the model was run for approximately 72 000 nests with partial destruction by nesting females and coatis, 12% of the nests were destroyed by nesting females, 1.1% of the nests were depredated, and 1% of the nests were eroded. These values are consistent with similar estimates in the study plots; at current nesting levels there is not much difference between the complete and partial-destruction models. The current mean hatchling output for approximately 72 300
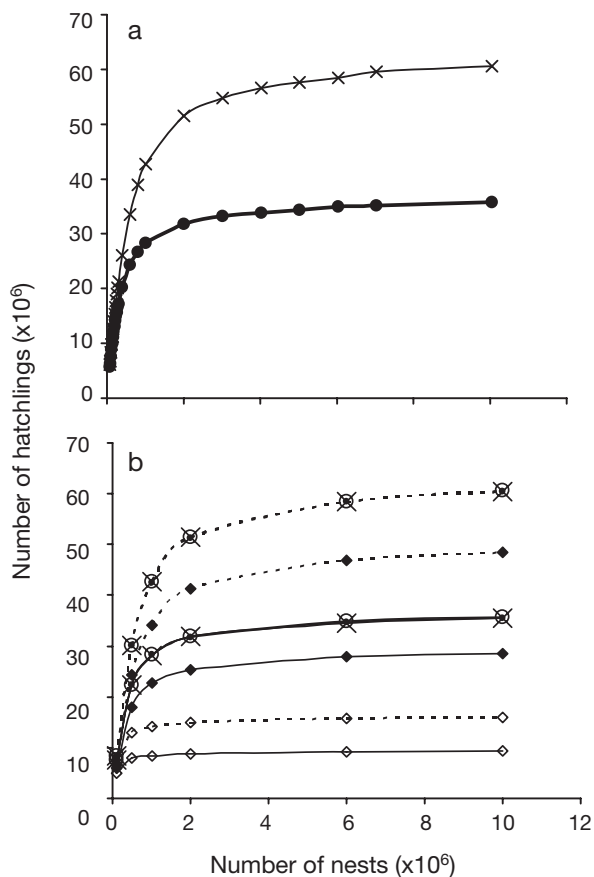
Fig. 3. (a) Simulation model outputs of no. of hatchlings produced at Tortuguero beach with increasing nest density when nests are completely (—, ●) and partially (—, ×) destroyed by coatis and nesting females. (b) No. of hatchlings produced when changes in model parameters are incorporated into initial models (○). Dashed lines represent models with partial destruction of nests by females and coatis; solid lines represent complete destruction of nests by females and coatis. Parameter changes include a 100% increase in a nesting female's radius of destruction (◇), and a 20% increase in below-beach-surface mortality (◆), coati predation (×), and erosion (●). The first data points in the figure represent no. of hatchlings produced from approximately 72 000 nests in both models

nests entered into this model is 6.14 million hatchlings. With partial destruction of nests by coatis and nesting females allowed in the model, the rate of increase in hatchling production decreased after 2 million nests were placed in the beach and carrying capacity was approached between 50 million and 60 million hatchlings, which is approximately 8 to 10 times the current hatchling output (Fig. 3a).

When a 20% increase in the daily probability of erosion and predation by coatis were individually incorporated into the above models, there was no change in hatchling output at carrying capacity (Fig. 3b). However, a 20% increase in below-beach-surface predation decreased hatchling output to between 25 million

and 28 million hatchlings in the model with complete destruction by nesting females and coatis, and to between 41 million and 48 million hatchlings in the model with partial destruction by nesting females and coatis (Fig. 3b). When the radius of destruction of a nesting female was increased to 1.5 m, carrying capacity dropped significantly to between 8 million and 9 million hatchlings in the model with complete destruction by nesting females and coatis, and to between 14 million and 16 million hatchlings in the model with partial destruction by nesting females and coatis (Fig. 3b). In all models, except the models in which a female's radius of destruction was increased, carrying capacity was approached when 2 million nests were laid on the beach. In models with increased radius of destruction by nesting females, carrying capacity was approached between 500 000 and 1 million nests.

DISCUSSION

At Tortuguero, nest destruction by nesting females and predation by coatis both affect egg production in a density-dependent way. The strength of density-dependent nest destruction by females will vary among years with differential density-dependent effects on hatchling production because of the consistent spatial pattern in nest distribution and natural fluctuations in nesting numbers among years (Tiwari et al. 2005). In the simulation model, a nesting female's radius of destruction was found to significantly affect hatchling output; more empirical data are necessary to determine the direct and indirect effects of a nesting female on surrounding incubating nests.

An observed increase in coati predation with hatching density is supported by Fowler (1979), who reported greater predation by dogs and coatis on nests containing hatchlings than unhatched nests during a 1-season study at Tortuguero. However, Horikoshi (1992) found seasonal variation in both the intensity and timing of mammal predation, primarily coatis, in a 3 yr study at Tortuguero. Coati predation peaked during the early part of the nesting season and then decreased in 1 yr, whereas in the other 2 years, coati predation either peaked at the end of the nesting season or continued to increase as the season progressed to an end (Horikoshi 1992). Coatis depredated a higher proportion of nests in the low nesting year of his study (Horikoshi 1992). During the 2000 season, coatis were observed to excavate both nests that had already emerged as well as nests that had not yet emerged. Therefore, temporal variation in coati predation among years would have varying results on hatchling production.

Below-beach-surface predation, erosion, and beach flooding were found to affect hatchling production at Tortuguero in a density-independent manner. Although one might expect a density-dependent effect of below-beach-surface nest destruction by crabs, ants, microbes, and plant roots combined, particularly mortality from microbial activity, current nest densities may be below the density threshold at which this effect might occur. Density-dependent effects should be re-evaluated when (if) higher nest densities are reached. Beach erosion was not severe in the study plots during the 2000 season, but nest loss from erosion varies considerably among years (Horikoshi 1992). The effects of beach flooding in November 2000 could not be extensively evaluated in this study, but nest loss due to flooding appeared to vary with section of beach, beach zone, and depth of nest.

The beach at Tortuguero appears to be well below its carrying capacity. If the mean number of clutches laid by an individual female in a nesting season at Tortuguero is 3 (Carr et al. 1978), the current mean number of females nesting at Tortuguero is about 24 000, representing 3.6 % of the approximately 600 000 females that would deposit 2 million nests at carrying capacity. More than 600 000 females nesting at Tortuguero is not unrealistic and is supported by the estimate that present day populations of green turtles in the Caribbean represent only 3 to 7 % of pre-exploitation levels (Jackson et al. 2001). Furthermore, as green turtles feed primarily on the seagrass *Thalassia testudinum* in the Caribbean (Bjorndal 1997), these numbers would be well supported by the existing seagrass pastures in the Caribbean whose most recent carrying capacity estimates range from 16 million to 586 million 50 kg green turtles (Moran & Bjorndal 2005). However, whether such high nest densities can be sustained, and whether 6 to 10 times the current estimate of hatchlings can be produced at Tortuguero, remains to be determined. Increased microbial activity in the sand resulting from greater nutrient load may severely lower hatching success after a certain nest density threshold is reached (Cornelius et al. 1991).

The time (72 yr or longer) estimated to reach carrying capacity is based on a steady 4.8 % increase in the number of females nesting at Tortuguero (Bjorndal et al. 2005) and would be greatly influenced by catastrophic density-independent processes and direct mortality. Sea turtle population growth is most sensitive to survival at the large juvenile and subadult stages (Crouse et al. 1987, Crouse 1999, Heppell et al. 2003). Therefore, the annual harvest of more than 11 000 adult and sub-adult green turtles in the waters of Nicaragua (Lagueux 1998), the main foraging ground for the Tortuguero green turtle population, may be of immediate concern to the future of the nesting population in Tortuguero. A recent model based on the catch of large juveniles and adult turtles on the foraging ground by the fisheries in Nicaragua suggests that the Tortuguero population is either in decline or will decline (Campbell 2003), and the effects of the harvest will be reflected in the number of turtles nesting at Tortuguero in subsequent years. However, as Campbell (2003) points out, her model was unable to account for density-dependent effects on the foraging ground and accurate estimates for some demographic parameters were not available. Modeling efforts incorporating more accurate demographic parameters both at and away from the nesting beach are needed to predict a more accurate trajectory for the Tortuguero population.

Our model is currently limited by lack of data on variation in strength and timing of processes among seasons. Over the 3 years that Horikoshi (1992) conducted his study at Tortuguero, the major factors affecting nests varied from beach erosion, flooding or hurricane, to predation by mammals. Nonetheless, the use of empirical data and the simple and flexible framework of this model represent major steps forward in our evaluation of density-dependent effects on hatchling production at the nesting beach, and provides a foundation for more accurate and sophisticated models to be built as more data become available. This model can be applied, with modifications to the intensity and suitability of parameters, to other sea turtle species and nesting beaches to establish recovery goals and develop appropriate management strategies.

In conclusion, this study further reinforces the assessment by Jackson et al. (2001) of modern day green turtle populations in the Caribbean and the evaluation by Moran & Bjorndal (2005) of the carrying capacity of existing seagrass pastures in the Caribbean for green turtles. With increasing efforts to reconstruct past ecosystems and identify the ecological roles of sea turtles (Bjorndal 2003, Bjorndal & Jackson 2003), and simultaneous discussions of consumptive and non-consumptive use of sea turtles (Godfrey et al. 2003), quantifying density-dependent and density-independent processes will be vital for devising meaningful conservation and management strategies.

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