

The Inverse Problem Applied to the Observed Clutch Frequency of Leatherback Turtles from Yalimapo Beach, French Guiana

JEAN-PAUL BRIANE¹, PHILIPPE RIVALAN¹, AND MARC GIRONDOT^{1,2}

¹Laboratoire d'Ecologie, Systématique et Evolution, UMR 8079 CNRS, ENGREF, INRA et Université Paris-Sud XI, 91405 Orsay Cedex, France [jean-paul.briane@u-psud.fr; philippe.rivalan@u-psud.fr; marc.girondot@u-psud.fr];

²Laboratoire des Reptiles et Amphibiens, Muséum National d'Histoire Naturelle de Paris, 25 rue Cuvier, 75005 Paris, France

ABSTRACT. – Observed clutch frequency is the observed number of clutches deposited by a female turtle in a single nesting season. This value is generally biased compared to the true nest number because some clutches could have been missed by beach patrols. We constructed an analytical model to search for the distribution of observed clutch frequency according to 1) the distribution of the clutch number per female, 2) the probability of female capture on the beach, and 3) the probability that a female was an intraseasonal one-time nester. We used data from 1987 to 2003 collected on leatherbacks nesting on Yalimapo beach in French Guiana to test the power of the model. Whereas for 13 of the 16 years, the model produced estimates concurrent with the field data; for the other 3 years, there was no concordance, indicating a lack of power of the model. We describe a required level of capture effort on the beach that will be sufficient for the model to adequately describe clutch frequency across the nesting season. This level is the product of the proportion of the season monitored times the instantaneous probability of the presence and the detection for a particular female during 1 nesting event.

KEY WORDS. – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; marine turtle; nesting; observed clutch frequency; methodology; analytical model; French Guiana

The quantification of nesting activity for marine turtles is a challenging statistical process. Most females nest several times during the nesting season (Miller 1997). Determining the number of times a turtle nests during a reproductive season is important, particularly if these data are averaged and used to estimate the number of female turtles in the population (Broderick et al. 2002). Several statistical measures have been employed to describe the nesting activity of a particular female during the nesting season. The observed clutch frequency (OCF) is simply the number of observations of nest depositions for a female during the nesting season (Frazer and Richardson 1985; Johnson and Ehrhart 1996; Broderick et al. 2002). However, not all nesting females are observed during a nesting season (e.g., Girondot and Fretey 1996), often resulting in OCF being underestimated. Physiological constraints induce regularity in the nesting process for a particular female (Miller 1997): nest depositions are separated by periods of 9–10 days on average for *Dermochelys coriacea* (Fretey and Girondot 1989a; Rivalan et al. 2006), 10–15 days for *Chelonia mydas* (Miller 1997; Sato et al. 1998) and solitary *Lepidochelys olivacea*, and longer and more variable periods for *L. olivacea* nesting in *arribadas* (Kalb 1999). This regularity of the number of days between 2 nesting attempts can be used to calculate the estimated clutch frequency (ECF) from the OCF value: $ECF = 1 + (d_2 - d_1)/N_d$ with day d_1 representing the first observation of the nesting female in the season, day d_2 the last observation of the nesting female that season, and N_d the average number of days

between 2 nests (Frazer and Richardson 1985; Johnson and Ehrhart 1996; Broderick et al. 2002). ECF is equal to or higher than OCF. However, ECF is a biased estimator of true clutch frequency (CF), which is defined as the true number of clutches deposited by a female. Indeed, before the first observation and after the last one, this female could have laid unobserved clutches. Therefore, CF is higher than or equal to ECF, although this bias often is not considered (Alvarado and Murphy 1999).

Another limitation in the use of the OCF and ECF estimates is the inability to deduce the shape of the distribution of CF. The shape of the distribution can deeply affect the average of CF or ECF. For example, the ECF for leatherbacks is highly variable according to the year, study site, and protocol (Steyermark et al. 1996), and at least part of this variation could be due to change in the distribution of CF. In French Guiana and Suriname, many females are encountered only once during the nesting season (the intraseasonal one-time nesters, OTN). OTN females simply could be visitors from other nesting beaches that nest occasionally on another beach or juvenile females that nest only once (Hilterman and Goverse 2007). When the number of these OTN females observed on a nesting beach is high, the mean value of CF can be driven to a low value. This factor could be of major importance for leatherbacks in French Guiana and Suriname where low nest sites fidelity is observed (Girondot et al. 2007).

The derivation of CF distribution from OCF is challenging. This problem is related to the inverse problem in the field of ecology. In a typical direct problem, one

prescribes model ingredients that describe mechanisms such as aging, growth, and survival at the individual level, then elevates the model to the population level, and finally studies the phenomenon at the population level. For the inverse problem, the situation is reversed: using information about the population, one seeks to deduce the underlying mechanisms at the individual level. An early attempt on the use of OCF distribution to estimate the total number of females has been performed by Barata (1998). Alternatively, Schaub et al. (2001) used capture–recapture methodology to estimate the stopover of birds during migration. When applied to marine turtles (Rivalan et al. 2006), this model estimated the length of the presence of an individual on a precise site. Here, we couple and expand these 2 statistical models to describe the peculiarities of the leatherback nesting process. We use this new statistical method to analyze intraseasonal capture–recapture survey on the leatherback turtle population nesting at Yalimapo beach in French Guiana from 1987 to 2003. Our objective is to estimate the distribution of clutch frequency and the total number of females nesting per year. We propose to call the clutch frequency obtained by this method the total clutch frequency (TCF).

METHODS

Study Site. — Fieldwork has been conducted annually on Yalimapo beach, French Guiana (5°44'35"N, 53°55'37"W) since 1985. In different years, night patrols tagged and recaptured marine turtles from March or April to July or August. For our analyses, we considered that the nesting season for leatherbacks on Yalimapo occurred between 1 March and 17 July (139 days). Titanium tags placed in the rear flippers were used in 1987 to identify females on the beach. From 1988 until 1997, Monel tags in the rear flippers were used, and PIT tags were used from 1994 onwards. No data are available for 1989. When patrols were on the beach, they tagged or read information for all the encountered females (basic statistics are presented in Table 1).

Statistical Modeling. — The description of nesting activity by a single female on different beaches during a single season suggests the occurrence of intraseasonal OTN (Girondot et al. 2007). Consequently, we introduce the parameter p_1 , which is the probability of being an OTN among the nesting females, and $q_1 = 1 - p_1$, the probability of not being an OTN (noted \neg OTN) (Fig. 1). The sum of OTN and \neg OTN is equal to the total number of females nesting on the beach for a given year.

We also define 2 stochastic variables:

1. Z = number of observed nests per turtle
2. Ω_p = real number of nests per \neg OTN turtle

Distribution of Ω_p (Real Number of Nests per Female). — This Ω_p variable follows a discrete law that takes its values in [1...25]. The value of $n_{max} = 25$ is set to

Table 1. Synthesis of data used to model true clutch frequency. OCF is observed clutch frequency, and ECF is estimated clutch frequency. The nesting season is defined 1 Mar–17 Jul, and α is the proportion at the middle of this period with data. The capture probability obtained by comparison of ECF and OCF is called p_{ECF} . The value p is the global capture probability during the entire season.

Years	1987	1988	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Days patrolled	112	130	65	71	93	94	85	77	79	67	71	52	86	122	113	109
α	0.806	0.935	0.468	0.510	0.669	0.676	0.612	0.554	0.568	0.482	0.511	0.374	0.619	0.878	0.813	0.784
OCF	1	701	1007	1223	2199	780	1118	272	331	726	656	832	1225	1145	463	744
	2	345	267	216	431	387	749	169	128	482	293	331	325	425	181	240
	3	152	1019	20	68	193	379	101	117	200	139	168	109	254	140	142
	4	70	841	2	9	89	134	57	56	97	36	61	36	199	109	113
	5	14	512	0	1	27	42	17	23	25	10	11	6	129	68	68
	6	4	223	0	0	11	6	2	11	5	1	1	1	85	53	32
	7	0	65	0	0	1	0	0	3	0	0	0	0	48	35	24
	8	0	17	0	0	0	1	0	0	0	0	0	0	14	10	9
	9	0	0	0	0	0	0	0	0	0	0	0	0	4	6	1
	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Mean OCF	1.727	2.717	1.275	1.179	1.220	1.812	1.870	2.003	2.038	1.845	1.637	1.640	1.399	2.258	2.552	2.099
Max ECF	11	14	12	11	10	10	9	10	8	9	7	7	11	13	11	10
Mean ECF	2.647	4.594	1.602	1.529	1.546	2.587	2.587	2.820	2.659	2.369	2.079	1.91	1.955	3.128	3.436	2.88
p_{ECF}	0.228	0.350	0.107	0.044	0.091	0.302	0.315	0.351	0.462	0.369	0.328	0.456	0.176	0.464	0.527	0.451
$p = \alpha p_{ECF}$	0.183	0.327	0.050	0.022	0.061	0.204	0.192	0.194	0.262	0.178	0.167	0.170	0.109	0.407	0.428	0.353

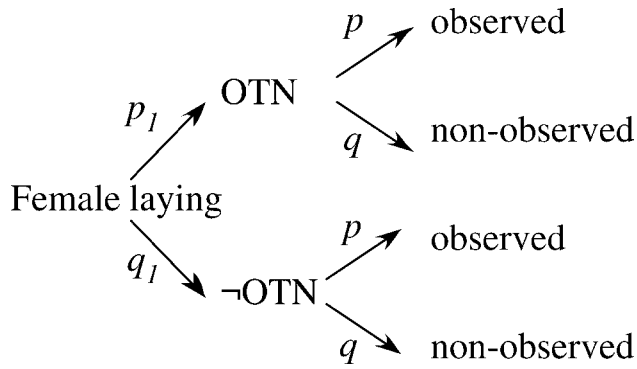


Figure 1. State of a female during a particular nesting occasion. One-time nesters (OTN) and \neg OTN are, respectively, intra-seasonal OTN and non-OTN, with probability p_1 and $q_1 = 1 - p_1$. The capture probability is p .

ensure it does not limit the fit because no marine turtles will exhibit such a high CF. Barata (1998) tried to directly fit this distribution from OCF data. However, this method induces an overly high number of parameters to be estimated, and the degrees of freedom become null or negative. Alternatively, Ω_p can be derived from any function Λ_p by grouping the values by class. Here, we use Λ_p as a lognormal, but many other functions could be used. The lognormal is positive and asymmetrical, with the right tail longer than the left one. It exhibits a large range of shapes depending on 2 parameters, μ_p and σ_p (Fig. 2). The sum of the probabilities among the n_{max} classes is standardized to 1.

Distribution of Z (Number of Observed Nests per Female). 1. *Conditional distribution of Z given Ω_p .* — For a fixed value of Ω_p , the number of observed nests per turtle, Z , follows a binomial law $\mathcal{B}(p, n)$:

$$\text{Prob}(Z = k | \Omega_p = n) = C_k^n p^k (1 - p)^{n-k} \quad [1]$$

Where p is the instantaneous probability of capture and $q = 1 - p$.

2. *Conditional distribution of Z given \neg OTN.* — We can directly express the probability that $Z = k$ for \neg OTN:

$$\begin{aligned} \text{Prob}(Z = k | \neg\text{OTN}) \\ = \sum_{k \leq n \leq n_{max}} C_k^n p^k (1 - p)^{n-k} \text{Prob}(\Omega_p = n) \end{aligned} \quad [2]$$

3. *General distribution of Z.* — General expressions of $\text{Prob}(Z = k)$ for OTN and \neg OTN are:

$$\begin{aligned} \text{Prob}(Z = 0) &= p_1 q + q_1 \sum_{1 \leq n \leq n_{max}} q^n \text{Prob}(\Omega_p = n) \\ \text{Prob}(Z = 1) &= p_1 p + q_1 \sum_{1 \leq n \leq n_{max}} n p q^{n-1} \text{Prob}(\Omega_p = n) \\ &\vdots \\ \text{Prob}(Z = k) &= q_1 \sum_{k \leq n \leq n_{max}} C_k^n p^k (1 - p)^{n-k} \text{Prob}(\Omega_p = n) \\ &\vdots \\ \text{Prob}(Z = n_{max}) &= q_1 p^{n_{max}} \text{Prob}(\Omega_p = n_{max}) \end{aligned} \quad [3]$$

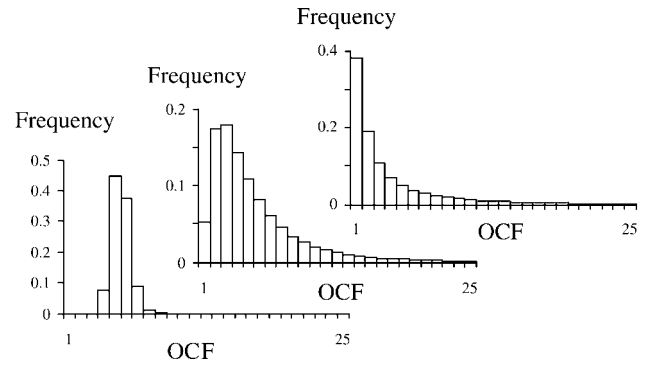


Figure 2. Examples of shape of clutch frequency using a lognormal function. Note that the mean of these 3 distributions is always 5 despite their different shapes.

Parameter Adjustment. — Assume N the total number of females (during the season) and N_i the number of i -times observed turtles. A vector represents the sample: $N = (N_0, N_1, N_2, \dots, N_k, \dots, N_{n_{max}})$

N_0 is unknown but the relation (4) defines the constraint (Sanathanian 1972):

$$N_0 = N - \sum_{1 \leq k \leq n_{max}} N_k \quad [4]$$

For fixed p_1 , p , μ_p , σ_p , and N , we can calculate the theoretical values of OCF:

$$N_k^{theo} = N \text{Prob}(Z = k) \cdot \forall k \in \{0, \dots, k, \dots, n_{max}\} \quad [5]$$

Maximum likelihood estimation is used to estimate the vector of parameters $\theta = (N, p, p_1, \mu_p, \sigma_p)$

$N = (N_0, N_1, N_2, \dots, N_k, \dots)$ follows a multinomial law whose likelihood is given by

$$\begin{aligned} L(N | \theta) &= \frac{N!}{\left(N - \sum_{1 \leq i \leq n_{max}} N_i \right)! N_1! \dots N_m! \dots N_{n_{max}}!} \\ &\prod_{0 \leq k \leq n_{max}} \text{Prob}(Z = k)^{N_k} \end{aligned} \quad [6]$$

The Delphi source of this software is available on request.

Estimation of p Value. — When the range of OCF is low, the model sometimes converges to boundaries of parameters. To alleviate this problem, we used the comparison of ECF and OCF to derive an estimate of p to gain 1 degree of freedom. When ECF is ≥ 3 , a period exists between the first (day d_1) and last observation (day d_2) during which the female is potentially present on the nesting beach but could have been overlooked. Between these boundaries, nesting females have not been observed ECF – OCF times over the ECF – 2 possible times. The value $p_{ECF} = 1 - ((ECF - OCF)/(ECF - 2))$ is the capture probability for this female during the period $d_2 - d_1$. The weighted average of capture probabilities for all females for the season has been estimated. The weighting coefficient is the number of intervals used for estimation, ECF – 2. In some seasons, the beginning or end of patrols

did not coincide with the beginning or end of the nesting season. If we let α be the fraction of the nesting season covered by patrols, then the capture probability corrected for incompleteness of coverage over the nesting season is $p = \alpha p_{ECF}$.

Application to Leatherback Data. — The procedure has been applied to the OCF data obtained from 1987 until 2003 (Table 1). For each year, an estimation of $\theta^* = (N^*, p_1^*, \mu_p^*, \sigma_p^*)$ has been obtained.

The estimation of parameters was completed by bootstrap method. For each year, we generated 500 bootstrapped-samples (b-samples) randomly chosen from the observations. The model was adjusted for each b-sample to produce a set of optimal parameter estimations. On the basis of 500 b-samples, a nonsymmetrical unbiased accelerated confidence interval (at 5%-level) was calculated for each estimated parameter (Efron 1993; Rappachi 1994).

To test for the necessity of introducing a parameter to account for OTN, the likelihood of the data was also estimated both with p_1 fixed to 0 (i.e., no OTN) or with p_1 free to vary. We used the Akaike Information Criterion (AIC, Akaike 1974) and Akaike Weight (also called Evidence Ratio) (Burnham and Anderson 1998) to test whether the presence of the OTN in the model was necessary to describe the data. AIC is a measure that selects the best model, incorporating the value for likelihood while penalizing for a higher number of parameters. The Evidence Ratio measures the probability for each model to be the correct one among several models tested on the same dataset. The global probability associated with model with or without OTN parameters has been calculated by combining probabilities (Sokal and Rohlf 1981). The actual computation is based on the fact that the $-2 \ln P$ is distributed as a χ^2 with 2 DF. Finally, the probabilities of the 16 years were summed into a single χ^2 statistic with 32 DF.

RESULTS

OCF and ECF Distributions. — OCF ranged from 1 to 11, and ECF ranged from 1 to 14 with important annual variation (Table 1). Capture probabilities measured from the difference between ECF and OCF ranged from 0.044 in 1987 to 0.527 in 2002. This could be explained by 2 phenomena: 1) turtles were present on Yalimapo beach but were overlooked by patrols, and 2) turtles nested on other nesting beaches. Both explanations probably are correct. The fraction of the season patrolled during the nesting season ranged from $\alpha = 0.374$ to 0.935. The corrected capture probability αp ranged from 0.022 in 1991 to 0.428 in 2002. As expected, both mean OCF and ECF were significantly positively correlated with angular transformation of $p = \alpha p_{ECF}$ ($r = 0.92$, $p < 0.0001$ and $r = 0.83$, $p < 0.0001$, respectively). This result emphasizes the need to correct for capture probability to obtain an unbiased estimation of nesting activity.

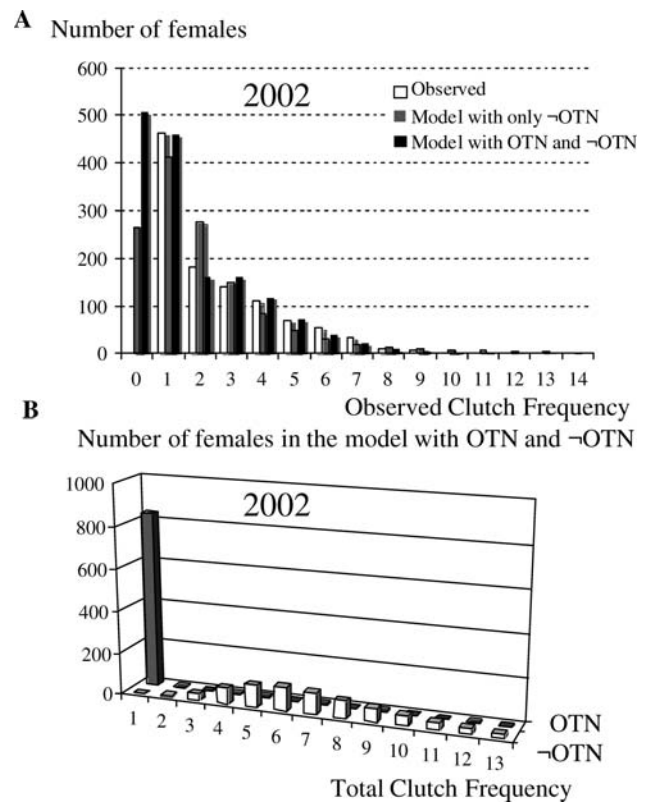


Figure 3. (A) Observed clutch frequency (OCF) of females nesting on Yalimapo beach, French Guiana, within the 2 models compared to the observed data. (B) Distribution of total clutch frequency for the 2 categories, \neg OTN and OTN females, for the selected model.

Parameter Estimation. — The model converged for all years with all various combinations. An example of the model fit with observed data for 2002 is shown in Fig. 3. For 3 years (1990, 1991, 1992), the AIC was lower with only 1 category of resident females and was nearly equal for both models in 1997 (Table 2). However, these 4 years showed a significant lower value of αp compared to the others, indicating that these years were poorly covered (the correlation between angular transformation of αp and the probability that OTN model is significant, $r = 0.755$, DF 14, $p = 0.0004$). Therefore, the lack of OTN detection for these 3 years likely was due to a lack of power of the test. When the 16 years were analyzed together, the probability that the model with resident and OTN was the best-fit model was close to 1 (Table 2). Figure 3 shows 1) the annual variations of an estimated number of females, 2) the mean number of nests per resident female, and 3) the proportion of OTN. Note that data for 1990, 1991, and 1992 were likely biased and will not be used for further tests and discussions.

The mean number of nests per \neg OTN female ranged from 4.90 to 9.92, concordant with previous estimates obtained with completely different methods (Freytey and Girondot 1988; Rivalan et al. 2006). The mean number of nests per female (OTN and \neg OTN) can be estimated using $p_1 + (1 - p_1) \mu_p$. It ranged from 3.12 to 5.82, similar to

Table 2. Model selection for the 16 years of available data collected on leatherback turtles nesting on Yalimapo beach in French Guiana. AIC is the Akaike Information Criterion, and the evidence ratio is the probability that the corresponding model is the correct one among the 2 tested (Burnham and Anderson 2002). The best AIC for each year is shown in bold.

Year	AIC		Δ AIC	Evidence ratio per year	
	Resident	+OTN		Resident	+OTN
1987	59.955	49.659	10.296	0.006	0.994
1988	409.646	119.891	289.755	0.000	1.000
1990	33.657	35.657	2.000	0.732	0.268
1991	29.948	31.948	2.000	0.732	0.268
1992	38.446	40.446	2.000	0.732	0.268
1993	71.292	53.245	18.047	0.000	0.999
1994	58.555	55.712	2.843	0.195	0.805
1995	56.086	47.249	8.837	0.012	0.988
1996	95.453	50.119	45.334	0.000	0.999
1997	55.792	55.787	0.005	0.499	0.501
1998	51.497	42.881	8.616	0.013	0.987
1999	73.588	44.580	29.008	0.001	0.999
2000	71.159	43.800	27.359	0.001	0.999
2001	278.173	121.787	156.386	0.000	1.000
2002	194.223	89.143	105.080	0.000	1.000
2003	177.368	82.892	94.476	0.000	1.000
		χ^2		799.8	9.75
		DF		32	32
		Combined evidence ratio		< 0.0001	> 0.99

values obtained in Suriname for this species (Hilterman and Goverse 2007).

A temporal decline was observed for resident females (\neg OTN), but this trend was only marginally significant (test of the slope, $t = -2.032$, $p = 0.0671$). An increase of p_1 according to the year was observed (Fig. 4C), but this tendency was also not significant ($p = 0.15$). The total number of females (\neg OTN and OTN) (Fig. 4A) and the mean number of nests for resident females (Fig. 4B) did not exhibit a significant trend ($p > 0.6$).

DISCUSSION

We developed a model that simply uses the distribution of OCF to model the distribution of clutch frequency. Surprisingly, the OCF distribution can provide much information on the nesting behavior of females. For most years, we demonstrate the presence of 2 groups of females that differed by the mean number of nests per female. The group with a large mean number of nests per female (from 4.90 to 9.92) is interpreted as resident females, and the turtles defined here as OTN could be interpreted as transient visitors from other nesting beaches (Girondot et al. 2007) or juveniles (Hilterman and Goverse 2007). The presence of these 2 groups of females was only detected when the capture effort was sufficient. We describe a threshold of capture effort on the beach that will predict whether the monitoring effort will be sufficient to adequately describe ECF during the nesting season. This is the product of the proportion of the season monitored by the instantaneous probability of presence and detection for a particular female during 1 nesting event. If this value is below 0.10, the monitoring effort is not sufficient. Between the 2 components used to estimate

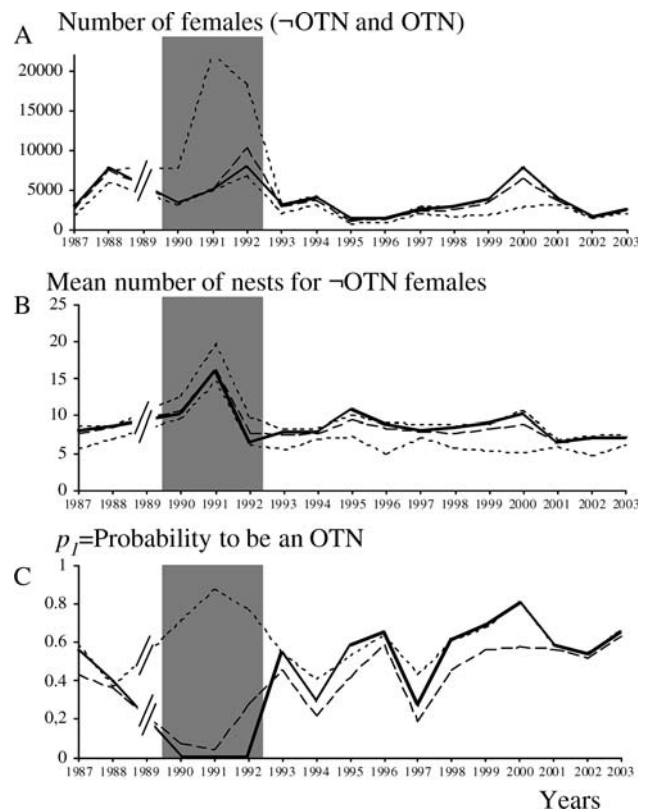


Figure 4. Output of the OCF-based model on leatherback data. (A) Total number of females, (B) mean number of nests per resident female, and (C) proportion of OTN among the females. Solid lines are the fitted values, dotted lines are the upper and lower bounds of 5% confidence intervals, and dashed lines are the average of bootstrap samples. The lack of OTN ($p_1 = 0$) for the 3 years shaded in gray is due to lack of power of the model (see text).

p , it appears that the capture intensity within the covered period (p_{ECF}) is the most important (see Table 1).

Nests counted on Yalimapo beach have strongly declined during recent years (Rivalan 2003). This observation can tentatively be explained by a changing of nesting beaches by females (Girondot et al. 2007). The outputs of the model described here show a higher proportion of OTN in recent years as well as a decline of the number of resident (\neg OTN) females. When tested, both tendencies could be explained by chance alone ($p > 0.05$), but these tendencies are still present in the sense that slopes of regression are negative. Because the OTN nest less often on the monitored site, it is normal to observe a decline in nest counts.

The model presented here can be enhanced in several ways. First, temporal variation in the parameters will be an elegant solution, but it will require implementing a stochastic rather than an analytic model to define the fit criterion. In conjunction, a model for the arrival date of females will be required. Second, many events were aggregated within this p value in the current version of the model. This parameter highlighted when patrols were not on the beach: at the beginning and end of the nesting season (modeled here by the α parameter) as well as during the period of normal work on the beach. When on the beach, patrols missed some females that came to nest. Indeed, whereas females nest mainly around high tide at Yalimapo beach (Fretey and Girondot 1989b), when the beach is patrolled during 6 hours a night, up to 20% of nesting females can be overlooked (Rivalan 2003). The p parameter value also integrated those females not completely faithful to 1 nesting beach. Also, resident females on the monitored beach sometimes nest on other beaches (Girondot et al. 2007) and thus are OTN on other beaches. Further improvements will use intraseasonal tag loss (Rivalan et al. 2005) or possible intraseasonal mortality. Another enhancement will be to define the behavior of the OTN using another \prod_p variable. However, we will be confronted with a lack of degree of freedom to fully fit the parameters because too few data are available using the sole Z variable. This could be resolved by implementing a multisite model where the residents of one site are the visitors of the others. Such a model requires the collaboration of all teams working in French Guiana and Suriname. Therefore, we urge all local associations and organizations working on sea turtles in the region to share collected data for comprehensive analysis because, as seen in this review, it is a necessary and essential step towards generating a realistic and representative view of the trend for this species in the region of Suriname and French Guiana.

ACKNOWLEDGMENTS

We are grateful to all groups working on the different nesting beaches in French Guiana and Suriname for their continuing efforts to collect important data. The tag

database used for this study is the result of a joint effort by the organizations involved in sea turtle conservation in French Guiana (Direction Régionale de l'Environnement, Greenpeace, Kulalashi, Kwata, ONCFS, Sépanguy, WWF) and in Suriname (Biotopic, STINASU, WWF, IUCN-NL). We thank P.C.R. Barata for sending us a copy of his PhD thesis, and Claudine Briane and Julien Matsis for helping us with the English language. The comments and corrections of 4 anonymous referees and the editor (Jeffrey Seminoff) have greatly improved this manuscript.

LITERATURE CITED

- AKAIKE, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.
- ALVARADO, J. AND MURPHY, T.M. 1999. Nesting periodicity and interesting behavior. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). *Research and Management Techniques for the Conservation of Sea Turtles*. IUCN/SSC Marine Turtle Specialist Group, pp. 115–118.
- BARATA, P.C.R. 1998. Estimation of the number of sea turtles nesting on a beach in a season. University of Rio de Janeiro, Rio de Janeiro, Brazil.
- BRODERICK, A.C., GLEN, F., GODLEY, B.J., AND HAYS, G.C. 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* 36:227–236.
- BURNHAM, K.P. AND ANDERSON, D.R. 1998. *Model selection and inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- BURNHAM, K.P. AND ANDERSON, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- EFRON, B. 1993. *An introduction to the bootstrap*. New York: Chapman & Hall.
- FRAZER, N.B. AND RICHARDSON, J.I. 1985. Annual variation in clutch size and frequency for loggerhead turtles, *Caretta caretta*, nesting at Little Cumberland Island, Georgia, USA. *Herpetologica* 41:246–251.
- FRETEY, J. AND GIRONDOT, M. 1988. Nidification de la tortue luth sur le littoral de Guyane française pendant la saison 1987. *Annales des Sociétés de Sciences Naturelles de Charente-Maritime* 7:729–737.
- FRETEY, J. AND GIRONDOT, M. 1989a. L'activité de ponte de la tortue luth, *Dermochelys coriacea* (Vandelli, 1761), pendant la saison 1988 en Guyane française. *Revue d'Ecologie-La Terre et la Vie* 44:261–274.
- FRETEY, J. AND GIRONDOT, M. 1989b. Hydrodynamic factors involved in choice of nesting site and time of arrivals of leatherback in French Guiana. In: Eckert, S.A., Eckert, K.L., and Richardson, T.H. (Eds.). *Ninth annual workshop on sea turtle conservation and biology*. NOAA Tech. Memor. NMFS-SEFC-232, Jekyll Island, GA, pp. 227–229.
- GIRONDOT, M. AND FRETEY, J. 1996. Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978–1995. *Chelonian Conservation and Biology* 2:204–208.
- GIRONDOT, M., GODFREY, M.H., PONGE, L., AND RIVALAN, P. 2007. Modeling approaches to quantify leatherback nesting trends in French Guiana and Suriname. *Chelonian Conservation and Biology* 6(1):37–46.
- HILTERMAN, M. AND GOVERSE, E. 2007. Nesting and nest success of the leatherback turtle (*Dermochelys coriacea*) in Suriname, 1999–2005. *Chelonian Conservation and Biology* 6(1):87–100.

- JOHNSON, S.A. AND EHRHART, L.M. 1996. Reproductive ecology of the Florida green turtle: clutch frequency. *Journal of Herpetology* 30:407–410.
- KALB, H. 1999. Behavior and physiology of solitary and arribada nesting Olive Ridley sea turtles (*Lepidochelys olivacea*) during the interesting period. College Station: Texas A&M University, pp. 136.
- MILLER, J.D. 1997. Reproduction in sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). *The Biology of Sea Turtles*. New York: CRC Press, pp. 51–81.
- RAPPACHI, B. 1994. Une introduction au Bootstrap. Centre Interuniversitaire de Calcul de l'Université de Grenoble, Grenoble, France.
- RIVALAN, P. 2003. La dynamique des populations de tortues luths de Guyane française: recherche des facteurs impliqués et application à la mise en place de stratégies de conservation. Université Paris Sud, Orsay, France, pp. 248
- RIVALAN, P., GODFREY, M.H., PRÉVOT-JULLIARD, A.-C., AND GIRONDOT, M. 2005. Maximum likelihood estimates of tag loss in leatherback sea turtles. *Journal of Wildlife Management* 69:540–548.
- RIVALAN, P., PRADEL, R., CHOQUET, R., GIRONDOT, M., AND PRÉVOT-JULLIARD, A.-C. 2006. Estimating clutch frequency in the sea turtle *Dermochelys coriacea* using stopover duration. *Marine Ecology-Progress Series* 317:285–295.
- SANATHANIAN, L. 1972. Estimating the size of a multinomial population. *The Annals of Mathematical Statistics* 43:142–152.
- SATO, K., MATSUZAWA, Y., TANAKA, H., BANDO, T., MINAMIKAWA, S., SAKAMOTO, W., AND NAITO, Y. 1998. Interesting intervals of loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. *Canadian Journal of Zoology* 76:1651–1662.
- SCHAUB, M., PRADEL, R., JENNI, L., AND LEBRETON, J.-D. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. *Ecology* 82:852–859.
- SOKAL, R.R. AND ROHLF, F.J. 1981. *Biometry: the Principles and Practice of Statistics in Biological Research*. New York: W.H. Freeman and Co.
- STEYERMARK, A.C., WILLIAMS, K., SPOTILA, J.R., PALADINO, F.V., ROSTAL, D.C., MORREALE, S.J., KOBERG, M.T., AND ARAUZ, R. 1996. Nesting leatherback turtles at Las Baulas National Park, Costa Rica. *Chelonian Conservation and Biology* 2:173–183.

Received: 28 December 2004

Revised and Accepted: 9 January 2007