Oecologia (2005) 145: 564–574
DOI 10.1007/s00442-005-0159-4

POPULATION ECOLOGY

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Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle

Received: 20 January 2005 / Accepted: 9 May 2005 /

Abstract The trade-off between current and future reproduction plays an important role in demographic analyses. This can be revealed by the relationship between the number of years without reproduction and reproductive investment within a reproductive year. However, estimating both the duration between two successive breeding season and reproductive effort is often limited by variable recapture or resighting effort. Moreover, a supplementary difficulty is raised when nonbreeder individuals are not present sampling breeding grounds, and are therefore unobservable. We used capture–recapture (CR) models to investigate intermittent breeding and reproductive effort to test a putative physiological trade-off in a long-lived species with intermittent breeding, the leatherback sea turtle. We used CR data collected on breeding females on Awa:la-Ya:lima:po beach (French Guiana, South America) from 1995 to 2002. By adding specific constraints in multistate (MS) CR models incorporating several nonobservable states, we modelled the breeding cycle in leatherbacks and then estimated the reproductive effort according to the number of years elapsed since the last nesting season. Using this MS CR framework, the mean survival rate was estimated to 0.91 and the average resighting probability to 0.58 (ranged from 0.30 to 0.99). The breeding cycle was found to be limited to 3 years. These results therefore suggested that animals whose observed breeding intervals are greater than 3 years were most likely animals that escaped detection during their previous nesting season(s). CR data collected in 2001 and 2002 allowed us to compare the individual reproductive effort between females that skipped one breeding season and females that skipped two breeding seasons. These inferences led us to conclude that a trade-off between current and future reproduction exists in leatherbacks nesting in French Guiana, likely linked to the resource provisioning required to invest in reproduction.

Keywords Reproductive skipping · Reproductive trade-off · Capture–recapture models · Multistate-model · *Dermochelys coriacea*

Communicated by Roland Brandl

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Introduction

A central assumption in life-history theory is that trade-offs occur between fitness-related characters (Stearns 1989), where an increase in some is associated with a decrease in others (Reznick 1985). The cost of reproduction, often conceptualized in terms of reduced survival, may also be expressed as a trade-off between current and future reproduction. A high current investment may lead to the skipping of a subsequent reproductive event, inducing an alternation between reproductive and nonreproductive seasons (Clutton-Brock 1988). As such, reproductive skipping could be a breeding strategy that maximizes lifetime reproductive success *LRS* (Schaffer 1974).

Although reproductive skipping is a widespread phenomenon, found in many taxa including amphibians (Husting 1965), birds (Cam et al. 1998; Coulson 1984; Wooller et al. 1990), snakes (Lourdais et al. 2002; Naulleau and Bonnet 1996) or turtles (Chevalier et al. 1998; Hughes 1982), its importance in population biology and evolutionary ecology has rarely been studied (but see Danchin and Cam 2002). The few studies that have addressed reproductive skipping at an individual level mainly focused on the relationship between nonbreeding and survival probability. To date, these studies provided contradictory conclusions: According to William's (1966) expectation under reproductive cost theory, Coulson (1984) showed that in order to maximize reproductive output during their lifespan, Eider ducks skipped a reproductive season when their survival is potentially poor. However, Cam et al. (1998) reported that nonbreeding kittiwakes had both lower survival rate and lower breeding probability in subsequent years in comparison to current breeders, suggesting a variation in individual quality rather than a reproductive cost.

The aim of the present study is to address the relationship between reproductive skipping and future reproduction in the leatherback sea turtle (*Dermochelys coriacea*, Vandelli 1761) nesting in French Guiana. Marine turtles are good subjects for studying reproductive skipping since they do not breed every year (Bull and Shine 1979; Carr and Carr 1970) and because their extended lifespan (Zug and Parham 1996) facilitates observations across several breeding intervals per individual. Breeding females are easily identified when they are nesting on the beach, whereas nonbreeding females remain at sea on feeding grounds located several thousand kilometers from nesting beaches (Ferraroli et al. 2004). During a single reproductive season, breeding females lay a variable number of clutches that can be used as an index of current reproductive output.

Addressing the relationship between reproductive skipping and future reproduction required knowledge of the number of years elapsed between two successive nesting seasons and the knowledge of the reproductive effort, regardless of capture probability. To achieve this aim, we first addressed reproductive skipping in leatherbacks by modeling reproductive cycles (i.e., number of years since last breeding season) using multistate (MS) capture–recapture (CR) models (Nichols et al. 1994). MS CR models have been used to estimate transition between reproductive states (e.g., breeders vs. nonbreeders) when all states are observable simultaneously on the sampling area (Cam et al. 1998; Nichols et al. 1994). More recently, Lebreton et al. (2002), Kendall and Nichols (2002), Fujiwara and Caswel (2002) and Schaub et al. (2004) incorporated unobservable states in MS modeling. In this paper, we have built on these latter approaches and developed a new method to investigate breeding cycles, by adding specific constraints on transition probabilities.

In a second step, we assessed annual reproductive effort of breeding females, expressed as the number of clutches laid per female during the nesting season, for the different breeding intervals revealed by MS CR model (i.e., 2 and 3 years). For leatherbacks nesting in French Guiana, reproductive effort cannot be directly measured since breeding females are not all observed every time they come ashore for laying eggs. We therefore evaluated the number of clutches from the stopover duration (i.e., duration an animal is present in the sampling area) using CR models initially developed for migratory birds (Schaub et al. 2001). This method estimates the number of times a female lays eggs after it was detected for the last time, as well as the number of times it came ashore before it was first detected. The number of clutches laid by an average individual was then assessed by dividing the estimated stopover duration by the interval between two egg-layings.

Finally, we compared the LRS (Clutton-Brock 1988) of two different breeding behaviors (i.e., breeding every 2 years and breeding every 3 years) in order to assess their respective fitness. Linking long-term breeding phenology and intra-annual reproductive effort has not been previously possible for species such as marine turtles.

Materials and methods

Some natural history features of leatherback turtles

The leatherback sea turtle is a pelagic reptile distributed worldwide (Spotila et al. 1996). During the nesting season, which lasts from mid-April to Mid-August in the northern hemisphere (Miller 1996), breeding female leatherbacks come ashore at night to lay eggs on tropical and subtropical sandy beaches (Spotila et al. 1996). Between two consecutive intra-annual laying events, females stay approximately 20 miles off the coast for 6–12 days (Fig. 1a, Girondot and Fretey 1996). After laying their last nest, females definitively leave the nesting area (Ferraroli et al. 2000). Monitoring on nesting beaches has revealed that breeding interval (i.e., duration between two consecutive nesting seasons) ranges from 1 year to more than 6 years, with a modal class for 2–3 years (Fig. 1b, Girondot and Fretey 1996). Because resighting probabilities of nesting turtles are usually below 1.0, observed breeding intervals likely overestimate the real breeding interval. Therefore, CR modeling is required to estimate a more accurate breeding interval.

Study area and data collection

Data on reproductive leatherbacks were collected at Awa:la-Ya:lima:po beach (French Guiana, Fig. 2), home of one of the largest leatherback sea turtle nesting populations, which has been intensively monitored since the early 1990s (Girondot and Fretey 1996). From 1995 to 2002 (1997 excluded), nesting females were tagged with encoded microchips (PITs). Each year, from April to mid-August, the beach was patrolled at night from 2 h before, until 2 h after, the high tide (Girondot and Fretey 1996). Nesting females that were encountered during patrols were scanned for tags. If a tag was present, their identity was recorded; if no tag was present, a new PIT microchip was injected into the left shoulder of

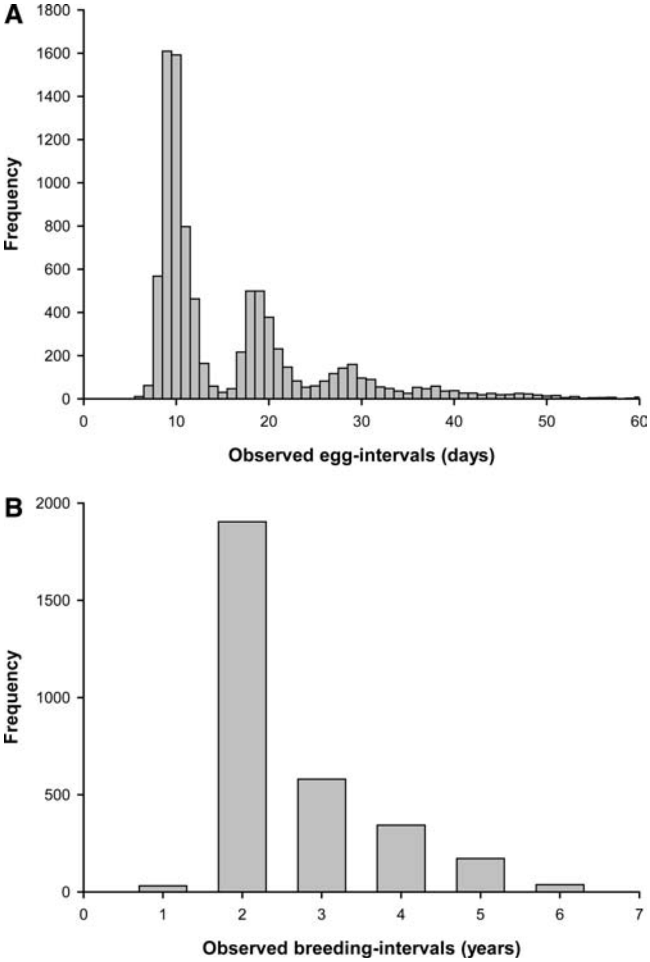


Fig. 1 **a** Distribution of observed egg-laying interval (i.e., number of days between two clutches within a single breeding season) and **b** distribution of observed breeding interval (i.e., duration between two successive breeding season) in leatherback females observed on Awa:la-Ya:lima:po beach from 1995 to 2002. Note that on **a**, only intervals lower than 13 days corresponds to the duration between two successive egg-layings

the turtles (Table 1). Contrary to metal tags, PIT tags are considered as permanent markers in marine turtles (Godley et al. 1999; Rivalan et al. 2005) and thus provide valuable data for demographic analyses with CR modeling. Because of the high density of females on Awa:la-Ya:lima:po beach, no other reproductive variables were measured.

Modeling breeding intervals

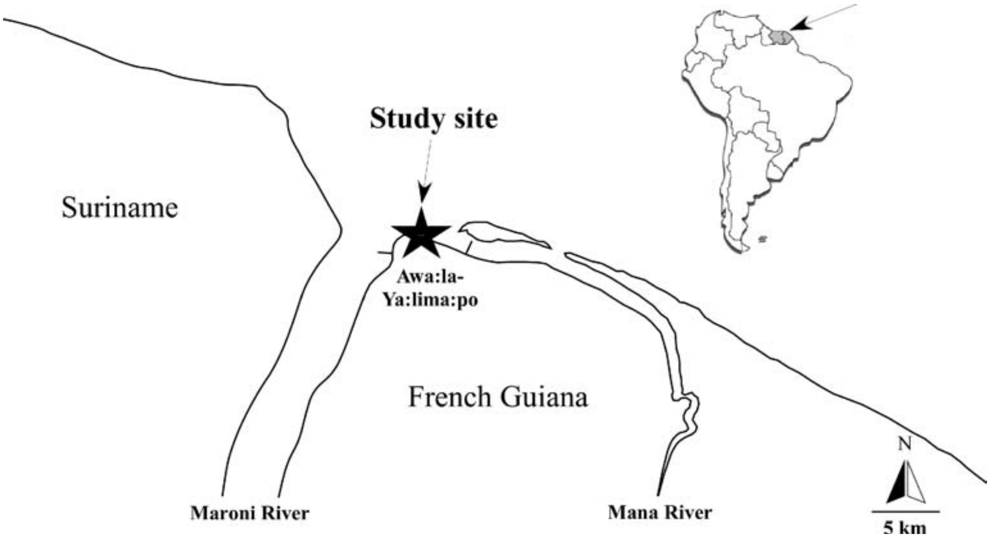
Given two observable states, namely breeders "*B*" and nonbreeders "*NB*", a MS CR model can be expressed as a transition matrix and associated vectors of survival and resighting probabilities (Nichols et al. 1994):

$$\begin{bmatrix} \psi^{BB} & 1-\psi^{BB} \\ 1-\psi^{NBB} & \psi^{NBB} \end{bmatrix}_t \begin{bmatrix} S^{B} \\ S^{NB} \end{bmatrix}_t \begin{bmatrix} P^{B} \\ P^{NB} \end{bmatrix}_t \qquad (1)$$

where ${S^r}_i$ is the probability that a marked animal in state r (r = "B" or "NB") has survived from time i to $i+1$, ψ_i^{rs} is the conditional transition probability that an animal in state r at time i is in state s at time $i+1$, given that animal survived until $i+1$, and P_i^r is the probability that an animal is recaptured at time i in state r, given that it is alive and present at time i.

Our main interest in using the MS model was to describe the breeding cycle through the distribution and the range of the breeding interval (i.e., number of years between two consecutive nesting seasons). The knowledge of the breeding cycle will enable us to compute the reproductive effort for each biologically meaningful breeding interval rather than computing reproductive effort for each observed one (that are possibly overestimated because of the capture probability). In our MS model, states were therefore defined as the number of years elapsed since an individual last nested. The number of states varied with the maximum breeding interval allowed in the model. For example, a maximum

Fig. 2 Map showing the location of the study site



breeding interval of 4 years indicates that the duration between two successive nesting seasons ranges from 1 year to 4 years within the population. Then, we considered four states: (1) state 'B': breeder, (2) state 'NB_1': nonbreeder 1 year after the previous nesting attempt, (3) state 'NB_2': nonbreeder 2 years after the previous nesting attempt and (4) state 'NB_3': nonbreeder 3 years after the previous nesting attempt. The only biologically meaningful transitions were $\psi^{BB}, \psi^{BNB_1}, \psi^{NB_dB}$ and $\psi^{NB_dNB_{d+1}} = 1 - \psi^{NB_dB} (d = 1, 2)$. Since the nonbreeder states were not all available for detection of sampling area, Eq. 1 became

$$\begin{bmatrix} \psi^{BB} & 1-\psi^{BB} & 0 & 0 \\ \psi^{NB_1B} & 0 & 1-\psi^{NB_1B} & 0 \\ \psi^{NB_2B} & 0 & 0 & 1-\psi^{NB_2B} \\ 1 & 0 & 0 & 0 \end{bmatrix}_t \begin{bmatrix} S^B \\ S^{NB_1} \\ S^{NB_2} \\ S^{NB_3} \end{bmatrix}_t \begin{bmatrix} P \\ 0 \\ 0 \\ 0 \end{bmatrix}_t \tag{2}$$

Note that in order to constrain the maximal breeding interval to 4 years, we constrained the conditional transition ψ^{NB_3B} to be equal to 1.

Kendall and Nichols (2002), and more recently Schaub et al. (2004), computed the estimability of demographical parameters (i.e., survival rates, capture rates and transitions rates) using MS CR models with one observable and one unobservable states. Kendall and Nichols (2002) pointed out that, in the absence of robust design [i.e., multiple secondary sampling periods within each primary time period (Pollock 1982)], some parameters have to be constrained to be estimable. Relying on Kendall and Nichols' conclusions, our most general model included (1) time-dependent survival probability, (2) time-dependent capture probability and (3) constant transition between states. Our sampling design did not allow us to test a model where the survival rate was different between breeders and nonbreeders. Testing this assumption would have required sampling in other areas (e.g., foraging grounds), which was beyond the scope of this study. We also fixed the resighting probability in 1997 to 0 because no sampling was performed on this year.

According to these constraints, the most general model for a hypothetical breeding interval limited to 4 years deviated from Eq. 2 as follows:

$$\begin{bmatrix} \psi^{BB} & 1-\psi^{BB} & 0 & 0 \\ \psi^{NB_1B} & 0 & 1-\psi^{NB_1B} & 0 \\ \psi^{NB_2B} & 0 & 0 & 1-\psi^{NB_2B} \\ 1 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} S \\ S \\ S \\ S \end{bmatrix}_t \begin{bmatrix} P \\ 0 \\ 0 \\ 0 \end{bmatrix}_t \tag{3}$$

The type of models we want to fit belong to the class of MS models with unobservable states (Lebreton and Pradel 2002) for which there are no goodness-of-fit tests (GOF) currently available. However, because only one state is observable in our data set (namely breeders), an ad hoc GOF test can be derived from the unistate models GOF test. Although these latter models are not well suited to the biological question we want to address, they are more thoroughly studied and provide a first step toward more relevant models for which GOF tests are available.

Goodness-of-fit tests based on bootstrap procedures are known to perform poorly (Lebreton and Pradel 2002), especially for the estimation of the variance inflation factor required in the application of the quasi-likelihood approach recommended by Anderson et al. (1994). Therefore, we relied on tests (Burnham et al. 1987; Pradel 1993) based on the decomposition of the likelihood of the Cormack–Jolly–Seber model (CJS Cormack 1964; Jolly 1965; Seber 1965). Because of the heterogeneity of capture probabilities resulting from the mixture of individuals with different cycles, two test components were highly significant: (1) test 3.SR, which tests whether newly marked individuals have the same probability of being recaptured in subsequent years as previously marked individuals recaptured simultaneously; it is usually interpreted as testing for the presence of transients in the population (Pradel et al. 1997; Prévot-Julliard et al. 1998). (2) test 2.CT that is sensitive to whether recapture probability depends on an animal having been caught on the previous occasion (i.e., immediate trap-dependence; (Pradel 1993)). An approximate GOF for models allowing for transients (Pradel et al. 1997; Prévot-Julliard et al. 1998), trap-dependence (Pradel 1993) and reproductive skipping, is obtained by discounting three components (Viallefont et al. 1995):

$$\mathrm{GOF}_m = \chi^2_{\mathrm{total}} - \chi^2_{\mathrm{test2.}CT} - \chi^2_{\mathrm{test3.}SR} - \Delta\mathrm{dev}$$

with

$$df_m = df_{\mathrm{total}} - df_{\mathrm{test2.}CT} - df_{\mathrm{test3.}SR} - 1.$$

where Δdev was the change of deviance between models that accounted for reproductive skipping (denoted $[S_{t\,*\,\tau}, \Psi_{cycle=2}, P_{t\,*m}]$) and models that did not account for reproductive skipping (denoted $[S_{t\,*\,\tau}, P_{t\,*m}]$).

Our most general model included a distinct parameter accounting for survival of the individual immediately after first capture (i.e the model therefore account for transients; Cam et al. 2004; Pradel et al. 1997; Prévot-Julliard et al. 1998). In this model, we also accounted for the possibility of trap-dependence on resighting probability. As above, ignoring such an effect may lead to biased estimates of survival. Incorporating trap-dependence required modification of the data following the approach specified by (Pradel 1993) to account for the time elapsed since last capture. We used a separate parameter for the capture at occasion $i + 1$ of animals captured at occasion i. The starting model had the following structure $[S_{t\,*\,\tau}, \Psi_{cycle=2}, P_{t\,*m}]$: where S stands for survival probability, P for recapture probability, and Ψ for breeding state transition. The subscript τ represents the transient effect. Subscripts t and m stand for 'time' (year) and the trap-dependent effect, respectively. Subscript $cycle = x$ associated with Ψ indicates that breeding cycle was limited to x years.

Four lengths of breeding cycles were tested (i.e., maximal breeding interval limited to 2, 3, 4 and 5 years, noted as $\Psi_{cycle=2}$, $\Psi_{cycle=3}$, $\Psi_{cycle=4}$ and $\Psi_{cycle=5}$). For each length, several models were considered for survival (i.e., time-dependent S_t, time-dependent with transients $S_{\tau * t}$, and constant with transience S_τ) and resighting probabilities (i.e., time-dependent P_t, time-dependent with trap-dependence P_{t+m} and $P_{t\,*m}$) by using software MSURGE (Choquet et al. 2004). Model selection was performed by selecting the model with the lowest QAIC, a modified Akaike's Information Criterion (Akaike 1974; Burnham and Anderson 1998) defined as

$$\mathrm{QAIC} = 2 \times np + \left(\frac{\text{deviance}}{\hat{c}}\right)$$

with np as the number of identifiable parameters and $\hat{c}$, the variance inflation factor, given by $\hat{c} = \mathrm{GOF}_m/df_m$. The Hessian matrix of second order derivatives of the likelihood was used to obtain the number of identifiable parameters (Viallefont et al. 1995) using MSURGE. The identifiability of each parameter was estimated from the deviance profiles (i.e., deviance values obtained for variation of a given parameter from 0 to 1 with a step of 0.1). A flat profile deviance is a proof of redundancy for the considered parameter (Choquet et al. 2004).

Correlation between annual reproductive effort and breeding interval

Because of the high density of females on Awa:la-Ya:lima:po beach, reproductive information on leatherbacks were limited to CR data. Indeed, measuring other reproductive variables (e.g., number of eggs per nest, body mass ...) is time-consuming and logistically demanding and would have decreased the resighting probability. In the absence of such data, the reproductive effort can only be estimated from the annual number of nests laid per female. However, because all individuals present in the sampling area on a given occasion were not observed, the observed annual number of nests per female was a biased index. Using CR data, we estimated the number of nests per female through the total duration an animal is present in the sampling area, also known as stopover duration (Schaub et al. 2001). To estimate the total duration of presence, sequences of individual resightings were analyzed using classical CR methods to compute the duration of stay from the first observation and the duration of stay before the last observation. The sum of both is an estimate of the expected individual duration of presence on that capture occasion (see Schaub et al. 2001). By defining the duration between two capture occasions, inside of which a female only nests once, the stopover duration approximates the reproductive effort. Stopover durations were estimated with SODA software (Schaub et al. 2001). Confidence intervals of total stopover duration were obtained using nonparametric bootstrap (10,000 iterations each time) on the individual capture histories (Schaub et al. 2001).

The correlation between the previous breeding interval (i.e., number of years elapsed since last breeding season) and reproductive effort (i.e., mean number of nests laid per female in a single season) was calculated using data collected in 2001 and 2002. The other resighting years were excluded due to insufficient data. The proportion of animals that nested 2 years in a row was too small to be used in the analysis (Fig. 1a) and we limited the maximum breeding interval to 3 years (see results section). We then split the 2001 and 2002 data sets into the two following groups of turtles: (1) turtles that nested 2 years before (group 1 Table 1), and (2): turtles that nested 3 years before (group 2 Table 1).

Finally, we compared these durations between years and among groups with repeated measure ANOVAs, using Statview. Repeated measure ANOVAs were performed on bootstrap resamplings (50 individuals within each group were simulated to keep the test conservative with respect to the number of field observations that are always >50; Table 1).

Comparison of two breeding behaviors

We calculated the *LRS* (total number of offspring produced by an individual over its lifetime; Clutton-Brock, 1988) associated with the two following breeding behaviors: animals that nest every 2 years ("behavior 1") and animals that nested every 3 years ("behavior 2"). A third breeding behavior occurs in wild where animals nest alternatively every 2 years or every 3 years. In animals with this "mixed behavior", the succession of 2-year and 3-year intervals is not predictable and it is therefore not possible to estimate properly the *LRS* at individual level. However, *LRS* associated with "behavior 1" and "behavior 2" can be respectively

Table 1 Annual number of resighted nesting leatherback females, and the respective numbers of observed animals that skipped 1 year between breeding seasons (group 1) and animals that skipped 2 years between breeding seasons (group 2)

	1995	1996	1998	1999	2000	2001	2002
Number of observations	248	208	1,123	1,343	1,702	2,311	1,272
Group 1						459	172
Group 2						289	63
Mean number of resightings per female (range)	1.16 (1–6)	1.11 (1–7)	1.63 (1–6)	1.59 (1–6)	1.39 (1–6)	2.25 (1–11)	2.36 (1–9)

considered as the upper and lower boundaries of *LRS* for "mixed behaviors".

In order to estimate *LRS*, the fecundity was approximated as being the number of nests laid per female per year. The estimated stopover duration was used as an index of this nest number. We also assumed that each nest contained the same number of eggs (Rostal et al. 2001). We assumed that the annual survival rate and the survival to first reproduction did not dependent on breeding behavior. We thus calculated the LRS_i associated with behavior *i* with the following formula:

$$L\hat{R}S_i = \sum_{n=0}^{\infty} S_0.\hat{F}_i.(\hat{S}_i)^n = \frac{S_0.\hat{F}_i}{1-\hat{S}_i} \tag{4}$$

where S_0 is the survival to first reproduction, $\hat{F}$ is the estimated annual stopover duration for breeding behavior *i* ($i=1, 2$) and $\hat{S}_i$ is the estimated survival between two successive breeding seasons for breeding behavior ($\hat{S}_1 = \hat{S} \times \hat{S}$ and $\hat{S}_2 = \hat{S} \times \hat{S} \times \hat{S}$). In the leatherback sea turtle, survival until reproduction remains unknown. Assuming that S_0 is common to both breeding behaviors, we eliminated it from the calculations of *LRS*.

LRS values for the two breeding behaviors were estimated from randomly sampling survival rates from normal distributions (mean and SD derived from MS CR model estimators) and fecundity from the nonparametric bootstraps values previously used for estimating confidence intervals associated with total stopover durations (see previous section). In order to account for inter-annual variability in demographic parameters in the computation of LRS, distributions of demographic parameters were pooled over years. Differences in *LRS* were assessed with a nonparametric Mann and Whitney test (Zar 1999).

Results

Breeding intervals

Before performing the model selection, we estimated the variance inflation factor $\hat{c}_m$ for the most general MS model denoted $[S_{t\ *\ \tau}, \Psi_{cycle=2}, P_{t\ *\ m}]$. The variance inflation factor for the model was estimated to $\hat{c} = 3.47$. Because the QAIC of the model that took into account reproductive skipping (i.e., $[S_{t\ *\ \tau}, \Psi_{\text{cycle}=2}, P_{t\ *\ m}]$), was lower than the QAIC of the model that did not (*i.e.*, $[S_{t\ *\ \tau}, P_{t\ *\ m}]$), we were confident about the adequacy of the former as a general model (QAIC were respectively equal to 2024.85 and 2029.72).

The model with the lowest QAIC was denoted $[S_\tau, \Psi_{\text{cycle}=3}, P_t]$ (Table 2). Another model, denoted $[S_\tau, \Psi_{\text{cycle}=2}, P_{t+m}]$, presented a similar QAIC (Table 2). Since the number of parameters was the same, the principle of parsimony was not helpful in model selection. Whereas the model selection (based on QAIC) highlighted that two relative age-classes constant over years were required in survival modeling regardless of the breeding interval, trap-dependence modeling on capture rate was required when breeding interval was limited to 2 years (i.e., animals bred every other year; Table 2). Therefore, it is likely that trap-dependence in this model corrected partially for the inappropriately short duration of the breeding cycle but was not necessary when a correct duration of the breeding cycle was used. We therefore considered that the model denoted $[S_\tau, \Psi_{\text{cycle}=3}, P_t]$ was the best model.

According to the deviance profiles, all 11 parameters involved in this model were estimable independently (results not shown). In this model, survival was designed as two relative age classes constant over time, while the capture rate varied over years and the breeding interval was limited to 3 years (i.e., $\hat{\psi}^{BB} = 0.009$ (CI, 0.006–0.014); $\hat{\psi}^{NB_1B} = 0.71$ (CI, 0.68–0.74) and ψ^{NB_2B} fixed equal to 1.00). The two "age-dependent" survival rates were estimated respectively at 0.50 (CI 0.45–0.54) and 0.91 (CI 0.75–0.97). Resighting probabilities varied over years from 0.30 in 2000 to almost 1.00 in 2001 (Table 3). In 1996, the resighting probability was estimated at 0.00 because no animals tagged in 1995 were recaptured in 1996.

Correlation between annual reproductive effort and breeding interval

The annual reproductive effort was estimated through the stopover duration from CR data. The number of

Table 2 Selection model statistics for each model tested based on QAIC (number of identifiable parameters)

Capture probability modeling	Survival probability modeling					
	$S_{\tau * t}$	S_τ	S_t	$S_{\tau * t}$	S_τ	S_t
	Breeding interval limited to 2 years			Breeding interval limited to 3 years		
$P_{t\ *m}$	2024.85 (25)	2010.80 (15)	2037.31 (20)	2028.89 (26)	2012.32 (16)	2038.61 (21)
P_{t+m}	2018.89 (20)	2007.94 (11)	2031.69 (16)	2020.89 (21)	2009.03 (12)	2031.65 (17)
P_t	2115.81 (19)	2126.55 (10)	2133.60 (13)	2020.21 (20)	**2007.23**(11)	2027.18 (14)
	Breeding interval limited to 4 years			Breeding interval limited to 5 years		
$P_{t\ *m}$	2026.85 (27)	2014.32 (17)	2039.70 (22)	2028.85 (28)	2016.32 (18)	2041.70 (23)
P_{t+m}	2024.09 (22)	2011.03 (13)	2032.74 (18)	2022.09 (23)	2013.03 (14)	2034.71 (19)
P_t	2022.21 (21)	2009.23 (12)	2027.92 (15)	2024.21 (22)	2011.23 (13)	2029.92 (16)

The model with the smallest QAIC $[S_\tau, \Psi_{\text{cycle}=3}, P_\text{t}]$ is in bold

Table 3 Estimates and 95% confidence intervals (CI) of resighting probability in the leatherback adult female population under model $[S_\tau, \Psi_{\text{cycle}=3}, P_t]$

Year	Resigthing rate (CI)
1996	0.000 (0.000–0.000)
1998	0.537 (0.231–0.817)
1999	0.666 (0.279–0.912)
2000	0.304 (0.186–0.456)
2001	0.999 (0.999–0.999)
2002	0.426 (0.306–0.543)

The resighting probability in 1997 was constrained to 0.00 (cf. text). In 1996, the resighting probability was estimated to 0.00 because no animals tagged in 1995 were recaptured in 1996

days between two successive egg-laying required to estimate the number of nests per female from stopover duration, was estimated from nest intervals at 6–12 days (Fig. 1b, Girondot and Fretey 1996). Thus, estimators were not biased by resighting effort because only one clutch can be physiologically laid during this time interval (Davenport 1991). No difference was found in the number of days between two successive nests between 2001 and 2002 ($P = 0.234$; Fig. 3). The number of years elapsed since last breeding did not affect the duration between two successive nests ($P = 0.536$; Fig. 3): individuals come ashore for nesting in average every 9.879 days (SE = 0.041).

Based on these inferences, the average stopover duration varied significantly across groups in the 2002 cohort (repeated measures ANOVA: $F_{1,18} = 330.98$; $P < 0.001$): animals that nested 3 years before stayed longer near the nesting beach than those that nested 2 years before (Table 4). Although not significant (repeated ANOVA: $F_{1,18} = 0.113$; $P = 0.74$), there was a tendency toward a greater stopover duration for females that nested 3 years before (Table 4). Within a given group, the stopover duration varied over years (repeated measures ANOVA: $F_{1,36} = 15.82$; $P = 0.003$; Table 4).

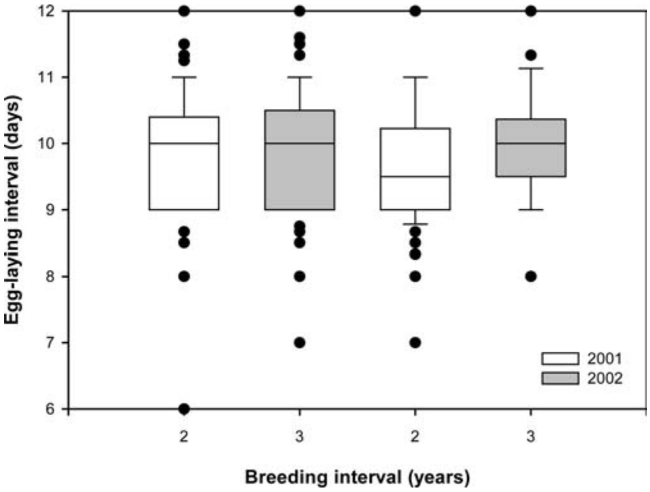


Fig. 3 Egg-laying interval (i.e., duration between two successive clutches) in 2001 and 2002 in relation with breeding interval (i.e., the number of years elapsed since last breeding seasons). In accordance with the results of MS modeling, only breeding interval equal to 2 and 3 years were tested. *Boxes* represent the inter-quartile range (*IQR*), *vertical lines* represent the median, *whiskers* represent 1.5×IQR and *dots* represent the outliers

Table 4 Mean annual stopover duration for group 1 (animals that skipped 1 year between breeding seasons) and group 2 (animals that skipped 2 years between breeding seasons) in leatherback sea turtles nesting in French Guiana

Years	Group 1	Group 2
2001	9.08 (1.09)	9.93 (1.68)
2002	8.66 (0.82)	11.43 (1.87)

Comparison of two breeding behaviors

The LRS in females that nest every 2 years was significantly different from the one in females that nest every 3 years (Mann–Whitney test, $U = 529$; $P < 0.05$): females that nest every 2 years had a larger *LRS* than females that nest every 3 years (Fig. 4).

Discussion

In this paper, we linked two aspects of breeding phenology: breeding interval (i.e., duration between two successive breeding seasons) and annual reproductive effort during the subsequent nesting season. To do this, we adapted recently developed CR methodologies, which partially solve problems of indetectability of nonbreeders during the nesting season. The different results of our study are discussed below.

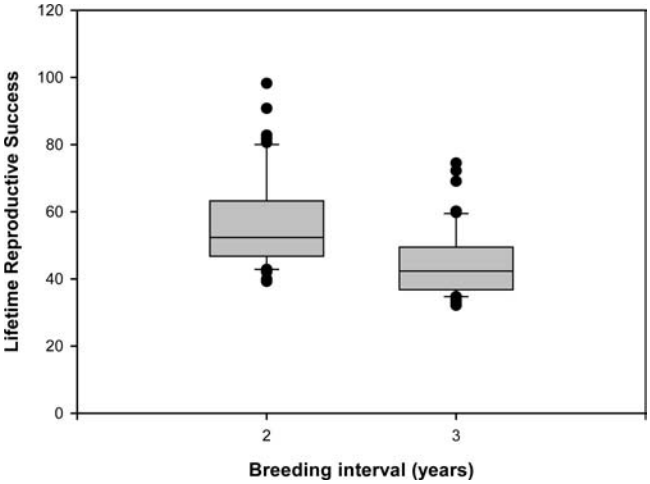


Fig. 4 Lifetime reproductive success according to breeding interval (i.e., the number of years elapsed since last breeding seasons). *Boxes* represent the inter-quartile range (*IQR*), *vertical lines* represent the median, *whiskers* represent 1.5×IQR and *dots* represent the outliers

Annual survival probability

The transient effect was expressed by a lower survival probability the year following tagging (i.e., 0.50) in comparison with the survival probability in the subsequent years (i.e., 0.91). Annual survival probability for females nesting in Awa:la-Ya:lima:po was estimated as constant over time. Although this estimate is high, it remains rather low for a long-lived species such as the leatherback sea turtle (Lebreton and Clobert 1991; Zug and Parham 1996). Two main factors are known to affect demographic estimators using CR methodology: tag-loss and permanent emigration (Lebreton et al. 1992). Because PIT tags can be considered as permanent makers in sea turtles (Godley et al. 1999), the tag-loss unlikely explains the low survival rate. However, our data collection was performed at local scale (i.e., Awa:la-Ya:lima:po beach). We therefore suspect that the estimated survival still remains an underestimation of the real survival probability since we have no access to permanent emigrants.

Breeding cycle modeling

We used MS methodology to study intermittent breeding. Similar methods were previously used to estimate breeding proportions and test hypotheses about reproductive cost (Nichols et al. 1994). However, in earlier studies both states were detectable in a given time on the study site. Breeders were notably distinguishable from nonbreeders through morphological characteristics or behavior associated with reproduction, or by the presence of eggs or young. In our study, based on a new model written in the MS framework, we produced estimates about breeding interval in species where animals do not breed every year and nonbreeders are not available for detection. We found that a 3-year breeding interval was long enough to adequately explain the breeding interval of leatherback nesting in French Guiana. Therefore, it appears that animals whose observed breeding intervals are greater than 3 years are most likely animals that escaped detection during their previous nesting season(s).

The probability for a female to nest in consecutive seasons was very low ($\hat{\psi}_i^{BB} = 0.009$). The rarity of females breeding two consecutive years is probably due to physiological and behavioral constraints. Satellite telemetry data show that leatherbacks nesting in French Guiana travel several thousand kilometers away from the nesting beaches to foraging grounds located off Newfoundland and off the western coast of Africa (Ferraroli et al. 2000, 2004). As other marine turtles, leatherbacks are considered capital breeders, i.e., energy invested in reproduction is gathered prior to reproduction (Drent and Daan 1980). Female capital breeders have to reach a fixed body condition threshold in order to engage in reproduction (Lourdais et al. 2002). The migration from nesting to foraging grounds takes approximately 4 months (Ferraroli et al. 2000; Girondot and Fretey 1996). Therefore, in order to nest in consecutive seasons, leatherback turtles have only from 1 months to 2 months to replenish their energy reserves and migrate back to the nesting grounds. Unfortunately, the low number of females observed exhibiting this migration pattern ($n = 14$) was not conducive to accurate estimation of their reproductive effort.

Stopover duration as an index of reproductive effort

The use of stopover duration as an index of reproductive effort assumes that females do not nest outside sampling season. The main nesting season for leatherback turtles in French Guiana extends from early March to mid-August but some females are observed nesting before and after this period (Girondot and Fretey 1996). However, based on daily nest counts performed in 2002, about 95% of nests are laid between 1 April and 15 August. We are thus confident that our assumption would have little impact on the results.

Based on data collected during nesting season 1988, Girondot and Fretey (1996) estimated that a female leatherback lays on average 7.52 nests per season. Considering that the total stopover duration is directly related to the number of clutches (one clutch is laid per 9-day period), our estimate of mean annual reproductive effort (8.66–11.43 nests; Table 4) was greater than the estimate of Fretey and Girondot (Fretey and Girondot 1988). We showed that reproductive effort varies over years, explaining partly the difference between the two estimates. This difference might also result from their assumption that considered the first and last captures as the true times of arrival and departure, which would lead to an underestimation (see Fretey and Girondot 1988). Our estimate of the number of nests laid per year per female, based on stopover duration estimate, relaxed this assumption that is likely unrealistic since all egg-laying events are not observed.

Nesting strategies and LRS

In 2002, a significant difference in stopover duration with respect to the time elapsed since the last nesting season was found: females that skipped two breeding seasons before nesting in 2002 exhibited longer stopover duration in subsequent season than animals that skipped only one breeding season. Although not significant, the same tendency was observed in 2001. Two hypotheses compete for explaining the negative correlation between annual reproductive effort and the number of reproductive seasons per lifetime uncovered in 2002: an individual quality hypothesis versus a physiological trade-off hypothesis. The individual quality hypothesis would assume that some “bad-quality” females gather energy slower that “good-quality” females and produce less clutches when they reach the nesting area because of a longer interval between two successive clutches. However, our data did not sustain this hypothesis because the duration between two successive egg-layings was not significantly related to the number of years elapsed since last breeding season (i.e., 2 and 3 years). Therefore, the negative correlation between annual reproductive effort and number of reproductive seasons likely suggests a trade-off between current and future reproduction (as observed in sooty shearwaters Weimerskirch 1998).

Our conclusion about the existence of trade-off strongly depends on the ability to accurately estimate the number of years elapsed since the last breeding (2 or 3 years). For instance, a female with an apparent 3-year breeding cycle might have indeed skipped one and two breeding seasons, but might have escaped to detection on a nesting season. However, given the very low probability of nesting 2 years in a row ($<1\%$) and the fairly high probability of observation, such misclassification is unlikely. If misclassification actually occurred, it would tend to produce low power in comparing the number of nests laid by each category of individuals. Since we found a significant difference in the reproductive effort regarding the time elapsed since last breeding, the biases are probably not large enough to affect our conclusions that a tradeoff exists.

The coexistence of two patterns of breeding phenology within the same population (i.e., breeding interval limited to 2 and 3 years) can be interpreted within two different contexts: capital breeding theory or life history strategies. In terrestrial capital breeders, animals must surpass a fixed body threshold to engage in reproduction. A certain level of flexibility in resource acquisition exists, with some females eating rapidly enough to ‘overshoot’ the body condition threshold, thus accumulating body reserves above the fixed threshold. The ‘extra’ storage, invested in reproduction, is positively correlated with litter size (Bonnet et al. 2001). In marine turtles, females that do not reach the body condition threshold within 1 year after the previous nesting season must stay on the feeding grounds whereas others can start migration to nesting grounds. During the second year spent on the feeding grounds, females will overshoot the body condition threshold and accumulate large ‘extra’ reserves. They will thus invest more in reproduction in the following year.

Based on data gathered in 2001 and 2002, *LRS* expressed in number of nests produced per female over its lifetime, appeared to be significantly larger for females that skip one breeding season (LRS_1 for “behavior 1”) compared with females that skip two breeding seasons (LRS_2 for “behavior 2”). Because of the unpredictability of the succession of nesting intervals in females that exhibit “mixed behavior” (i.e., skip alternatively 1 or 2 years), we were not able to compute *LRS* for “mixed behavior”. However, this *LRS* is likely included between LRS_1 and LRS_2. Since the *LRS* value is related to fitness, those results suggested that skipping only one breeding seasons maximized the individual fitness. However, extrapolation based on *LRS* must be done carefully because of the underlying assumptions we made. Indeed, we assumed that both breeders and nonbreeders have the same survival probability. We were not able to test this hypothesis because it would have required sampling in wintering or feeding grounds (Brownie et al. 1993). Moreover, the number of eggs per nests might be affected by the age of females and by the breeding interval.

In a study performed in the same site, Girondot et al. (2002) demonstrated density dependence in hatching success. The nesting beach appears to have a threshold carrying capacity: above a critical density, the hatching success reaches a threshold with increasing number of nesting females. In the context where the population is composed of two pools of individuals (some always skip 1 breeding season and others always skip two breeding seasons) a year with a high density of nesting females will be succeeded by another high-density season lagged by 6 years (i.e., the time period needed to re-synchronize the population). An individual whose phenotypic plasticity allows for changing breeding interval will increase its reproductive value, by avoiding the subsequent high-density nesting season. Therefore, rather than selection favoring one behavior over the other, the ability for an animal to switch between skipping one or two breeding seasons might be selected.

Finally, instead of separating the two hypotheses involved to explain the observed pattern (capital breeding vs. life history strategies), we think that these two hypotheses are not exclusive and can be joined. Indeed, they explain the same phenomenon from two different points of view: on an evolutionary time scale, these two behaviors may have been selected and represent life history strategies. Capital breeding can be seen as the functional mechanism leading to these two strategies. Resource provisioning may be the proximal cause of intermittent breeding, and reproductive success its ultimate cause.

Acknowledgments For data used in this study, we are indebted to everyone that has participated in the Kawana project in French Guiana and especially to J. Fretey and J. Lescure, who were in charge of this project from 1977 to 1996. We also thank the authorities and inhabitants of Awa:la and Ya:lima:po villages for their active participation in the marine turtle study and conservation program. The tag database used for this study is the result of a joint effort of the organizations involved in sea turtles conservation in French Guiana (Direction Régionale de l’Environnement, Greenpeace, Kulalashi, Kwata, ONCFS, Sépanguy, WWF) and in Suriname (Biotopic, STINASU, WWF). Finally, we thank E. Baudry, D. Drolet, J.-S. Lauzon-Guay, M. Godfrey, T. Giraud, E. Johannesen, R. Julliard, and J. Shykoff for their comments on the manuscript.

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