Survival and breeding interval of an endangered marine vertebrate, the leatherback turtle *Dermochelys coriacea*, in French Guiana

Damien Chevallier, Marc Girondot, Rachel Berzins, Johan Chevalier, Benoît de Thoisy, Jacques Fretey, Laurent Kelle, Jean-Dominique Lebreton*

*Corresponding author: jean-dominique.lebreton@cefe.cnrs.fr


Structure of the multi-event capture-recapture model

As explained in the main text, the capture-recapture model was based on Markovian transitions from one year to the next among 7 states: DEAD, PRE-M, PRE-P, PRE-MP, ABS-M, ABS-P, ABS-MP. To properly represent different types of transition, the annual transition was split in four successive phases, each represented by a transition submatrix: Survival (submatrix $S$), retention or Loss of Metal tags (submatrix $LM$), retention or Loss of PIT tag(s) (Submatrix $LP$), Movement (i.e. transition from PRE to ABS and from ABS to PRE) (submatrix $M$). Throughout, we use matrices with starting states as rows and arrival states as columns. As the states are a set of mutually exclusive alternatives, all matrices are as a consequence row-stochastic, i.e. the sum of their rows are all equal to 1, and time runs from left to right in matrix products. Therefore, the overall transition matrix among the 7 states was $T = S \times LM \times LP \times M$.

The annual survival probability was considered not to vary with the marks (M, P, or MP). As usual in models with temporary emigration to unobservable states (here ABSENT), the survival probability had to be considered not to vary with the presence status. This restrictive assumption cannot be avoided given the life cycle of the species. Altogether the survival probability was thus uniform among the six states PRE-M, PRE-P, PRE-MP, ABS-M, ABS-P, ABS-MP, and denoted as $s$. The resulting transition submatrix $S$ was thus:

<table>
<thead>
<tr>
<th></th>
<th>DEAD</th>
<th>PRE-M</th>
<th>PRE-P</th>
<th>PRE-MP</th>
<th>ABS-M</th>
<th>ABS-P</th>
<th>ABS-MP</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEAD</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-M</td>
<td>$1-s$</td>
<td>$s$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-P</td>
<td>$1-s$</td>
<td>$s$</td>
<td>$s$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-MP</td>
<td>$1-s$</td>
<td>0</td>
<td>0</td>
<td>$s$</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-M</td>
<td>$1-s$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>$s$</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-P</td>
<td>$1-s$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>$s$</td>
<td>0</td>
</tr>
<tr>
<td>ABS-MP</td>
<td>$1-s$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>$s$</td>
</tr>
</tbody>
</table>
We considered metal tag loss and PIT tag loss as independent by treating them as successive steps. This assumption is logical for marks as different as metal and PIT tags, but would not be tenable for marks of the same type. One should note that PIT tag loss means permanent loss of detectability, e.g. by migration of the tag far from the surface of the body, and does not necessarily imply the mark dropped from the individual. Metal tag loss generated non-null transition probabilities from M to DEAD, and MP to P according to the following submatrix \( \mathbf{LM} \), using a retention probability \( m \):

<table>
<thead>
<tr>
<th></th>
<th>DEAD</th>
<th>PRE-M</th>
<th>PRE-P</th>
<th>PRE-MP</th>
<th>ABS-M</th>
<th>ABS-P</th>
<th>ABS-MP</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEAD</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-M</td>
<td>(1-m)</td>
<td>(m)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-P</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-MP</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>(1-m)</td>
<td>(m)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-M</td>
<td>(1-m)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>(m)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-P</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>ABS-MP</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>(1-m)</td>
</tr>
</tbody>
</table>

Similarly, the loss of PIT tags, using a retention probability \( p \), lead to the transition submatrix \( \mathbf{LP} \):

<table>
<thead>
<tr>
<th></th>
<th>DEAD</th>
<th>PRE-M</th>
<th>PRE-P</th>
<th>PRE-MP</th>
<th>ABS-M</th>
<th>ABS-P</th>
<th>ABS-MP</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEAD</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-M</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-P</td>
<td>(1-p)</td>
<td>0</td>
<td>(p)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-MP</td>
<td>0</td>
<td>(1-p)</td>
<td>0</td>
<td>(p)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-M</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-P</td>
<td>(1-p)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>(p)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-MP</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>(1-p)</td>
<td>0</td>
<td>(p)</td>
<td>0</td>
</tr>
</tbody>
</table>

The two types of losses being assumed independent, their order did not matter, i.e. \( \mathbf{LP} \times \mathbf{LM} = \mathbf{LM} \times \mathbf{LP} \). The transition to DEAD accounted for permanent loss of marked individuals because they became unmarked. Assuming the same parameter for the transitions \( \text{PM} \rightarrow P \) and \( M \rightarrow \text{DEAD} \), and for the transitions \( \text{PM} \rightarrow M \) and \( P \rightarrow \text{DEAD} \), respectively, is the key feature that allowed us to estimate \( m \) and \( p \), respectively, separately from survival \( s \), correcting thus the estimation of survival for mark loss.

Movement was considered as not depending on the type of marks, leading thus to the transition submatrix \( \mathbf{M} \), using generic parameters \( \alpha \) and \( \beta \). The probability of departure \( \alpha \) was the probability of not coming back to lay eggs next year.
The split into four successive phases made it possible to represent complex transitions in a straightforward way, as the overall transition matrix \( T = S \times LM \times LP \times A \times M \):

<table>
<thead>
<tr>
<th></th>
<th>DEAD</th>
<th>PRE-M</th>
<th>PRE-P</th>
<th>PRE-MP</th>
<th>ABS-M</th>
<th>ABS-P</th>
<th>ABS-MP</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEAD</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-M</td>
<td>1-sm</td>
<td>sm(1-(\alpha))</td>
<td>0</td>
<td>0</td>
<td>sm(\alpha)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-P</td>
<td>1-sp</td>
<td>0</td>
<td>sp(1-(\alpha))</td>
<td>0</td>
<td>0</td>
<td>sp(\alpha)</td>
<td>0</td>
</tr>
<tr>
<td>PRE-MP</td>
<td>l-s +s(1-m)(1-p)</td>
<td>sm(1-p)(1-(\alpha))</td>
<td>sp(1-m)(1-(\alpha))</td>
<td>sm(\alpha)</td>
<td>sp(1-m)(\alpha)</td>
<td>smp(\alpha)</td>
<td></td>
</tr>
<tr>
<td>ABS-M</td>
<td>1-sm</td>
<td>sm(\beta)</td>
<td>0</td>
<td>0</td>
<td>sm(1-(\beta))</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-P</td>
<td>1-sp</td>
<td>0</td>
<td>sp(\beta)</td>
<td>0</td>
<td>0</td>
<td>sp(1-(\beta))</td>
<td>0</td>
</tr>
<tr>
<td>ABS-MP</td>
<td>l-s +s(1-m)(1-p)</td>
<td>sm(1-p)(\beta)</td>
<td>sp(1-m)(\beta)</td>
<td>smp(\beta)</td>
<td>sm(1-p)(1-(\beta))</td>
<td>sp(1-m)(1-(\beta))</td>
<td>spm(1-(\beta))</td>
</tr>
</tbody>
</table>

Each season an individual was detected, it was necessarily in one of the three PRE states (i.e. individuals DEAD or ABSent had a detection probability of 0, an event denoted as U for Unrecorded), and noted with Metal and/or PIT tag(s). However, all marks present were not uniformly recorded, would it be only for field sessions done without PIT tag reader. As a consequence, an individual with both metal and PIT tags (state PRE-MP) could be unrecorded (event U) or noted with metal tag only, PIT tag only or both (i.e. events M,P, MP, respectively). The relationship of the 4 events U, M, P, MP (coded as 0, 1, 2, 3 in the data file) with the 7 underlying states was thus necessarily probabilistic, expressed by a matrix of detection probabilities.

<table>
<thead>
<tr>
<th></th>
<th>U (0)</th>
<th>M (1)</th>
<th>P (2)</th>
<th>MP (3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEAD</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-M</td>
<td>1-g</td>
<td>g</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PRE-P</td>
<td>1-h</td>
<td>0</td>
<td>h</td>
<td>0</td>
</tr>
<tr>
<td>PRE-MP</td>
<td>1-j-k-l</td>
<td>j</td>
<td>k</td>
<td>1</td>
</tr>
<tr>
<td>ABS-M</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-P</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ABS-MP</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

The transition parameters were of five types \((s, m, p, \alpha, \beta)\). These 5 parameters were considered as constant, or varying according to various effects such as time, based on the classical philosophy of modern capture-recapture models (Lebreton et al. 1992), with the following rules. Survival \(s\) and probabilities of movement \(\alpha\) and \(\beta\) were considered either as constant or time dependent. For survival we also considered an effect of time since marking (with two “age” levels: first year after marking and the following years) to represent potential transience. Considering any more complex effects (such as time since last presence, or effect of Presence/Absence) induced pervasive identifiability problems, preventing from estimating separately these parameters. For the probabilities of mark retention \(m\) and \(p\), constancy or variation over time were combined in various fashion with the “age” of the mark, again with two levels (first year after marking, and the following years).
By considering the detection of a band and that of a PIT tag were independent, the 4 types of detection parameters were reduced to 2, each of which being considered as necessarily varying over time, as a direct consequence of the variation in effort over the years.

To these detection probabilities (which concern only recaptures and thus do not exist for the first year), one should add the probabilities that the females captured for the first time each year and marked (i.e. in one of the three states PRE-M, PRE-P, and PRE-MP) are in one of the other of these three states. These parameters reflected only the proportions of the various types of marks used each year and were necessarily time-dependent. The sum of the proportions being 1, there were only two parameters for each of the 28 years of recapture. These 56 parameters were necessary in the model but do not bring any useful information and were not displayed or discussed.
Implementation of Capture-Mark-Recapture models in E-SURGE

To implement the models in E-SURGE (as explained in the main text), we had to define a pattern and a structure of parameters. The elements below are sufficient to run models similar to ours.

The file for the pattern of parameters (step GEPAT in E-SURGE) is a text file as follows:

```plaintext
%%%% VERSION 2.0 %%%%%%
3
%%%% Initial state %%%%%%
1
1 6 IS
p p * - -
%%%% Transition %%%%%%
4
7 7 SURVIVAL
y - - - - *
 - y - - - *
 - - y - - *
 - - - y - *
 - - - - y *
 - - - - - *
7 7 PIT RETENTION
a - - - - *
 - * - - - -
 - * a - - -
 - - a - - *
 - - - * -
 - - - - a -
 - - - - - *
7 7 METAL TAG RETENTION
* - - - - -
 - b - - - *
 - * - b - -
 - - * - b -
 - - - * - b -
 - - - - * - b -
7 7 MOVEMENT
* - - q - -
 - * - q - -
 - - * - q -
r - - * - -
 - r - * - -
 - - r - * -
 - - - * -
%%%% Event %%%%%%
2
7 4 DETECT PIT
* a - -
 - * -
 - - * a
* - -
* - -
* - -
* - -
4 4 DETECT_METAL
* - -
 - * -
 - - b -
 - * - b
```
The file for the structure (Step GEMACO in E-SURGE) of the final model in the paper (time dependent survival, departure and return probabilities, constant PIT tag and Metal tag retention probabilities) is as follows:

```
%%% VERSION 3.1 %%%
3
-------- INIT --------
1
  = STEP 1 =
1
to.time
0
1 6
p p * - -
defaultfile
-------- TRANSITION --------
4
  = STEP 1 =
1
time
0
7 7
  y - - - *
  - y - - *
  - - y - *
  - - - y *
  - - - - y*
  - - - - - *
  = STEP 2 =
1
i
0
7 7
  a - - - *
  * - - -
  * - a - -
  ----- a -
  ------ *
  = STEP 3 =
1
i
0
7 7
  * - - - -
  - b - - - *
  * - b - - -
  ----- *
  ---- b -*
  ---- * - b-
  ------ *-
  = STEP 4 =
1
from(1 2 3, 4 5 6).time
0
7 7
  * - q - -
  * - q -
  * - q -
  r - * -
  r - * -
```
defaultfile

---------- CAPTURE ----------

2
  = STEP 1 =
  1
  firste+a(2 3).time
  0
  7 4
  * a - -
  - - * -
  - - * a
  * - -
  * - -
  * - -
  = STEP 2 =
  1
  firste+a(2 3).time
  0
  4 4
  * - -
  - * -
  * * b -
  * * b
  defaultfile
Calculation of time interval between two seasons of reproduction

We detail here the calculation of various compound demographic parameters, such as the time interval between two reproductive events, derived from the primary parameters estimated by capture-recapture. Although derived for the specific case of the leatherback, these calculations may be applicable and of general interest for all populations with intermittent reproduction.

Denoting as $D$ and $R$ the probabilities of departure and return, respectively, and assuming them as constant, the distribution of time to next reproduction after a season of reproduction is as follows:

<table>
<thead>
<tr>
<th>time to next reproduction</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>...</th>
<th>i</th>
<th>...</th>
</tr>
</thead>
<tbody>
<tr>
<td>probability</td>
<td>$1-D$</td>
<td>$DR$</td>
<td>$D(1-R)R$</td>
<td>...</td>
<td>$D(1-R)^{i-2}R$</td>
<td>...</td>
</tr>
<tr>
<td>Terms for expectation</td>
<td>$1-D$</td>
<td>$2DR$</td>
<td>$3D(1-R)R$</td>
<td>...</td>
<td>$iD(1-R)^{i-2}R$</td>
<td>...</td>
</tr>
</tbody>
</table>

This distribution is valid for a female turtle surviving until its next reproduction. One can easily check that the sum of these probabilities is equal to 1:

$$
\text{Sum} = 1 - D + DR \sum_{i=2}^{\infty} (1-R)^{i-2} = 1 - D + DR \sum_{j=0}^{\infty} (1-R)^j = 1 - D + \frac{DR}{R} = 1
$$

The expectation, i.e. the mean time until next reproduction for an individual still alive is:

$$
M = 1 - D + \sum_{i=2}^{\infty} iD(1-R)^{i-2}R = 1 - D + \frac{DR}{1-R} \sum_{i=2}^{\infty} i(1-R)^{i-1}
$$

The sum simplifies to

$$
- \sum_{i=2}^{\infty} \frac{\partial (1-R)^i}{\partial R} = - \frac{\partial}{\partial R} \sum_{i=2}^{\infty} (1-R)^i = - \frac{\partial}{\partial R} \left( \frac{1}{R} - 1 - (1-R) \right) = - \frac{\partial}{\partial R} \left( (1-R)^2 / R \right)
$$

i.e.:

$$
\frac{(1+R)(1-R)}{R^2}
$$

In turn:

$$
M = 1 - D + D \left( \frac{1}{R} + 1 \right) = 1 + \frac{D}{R}
$$

One sees in particular that if there is no departure (i.e., $D = 0$), then $M = 1$, i.e. all individuals reproduce next year, and if everybody departs (i.e., $D = 1$), then, individuals come back at the earliest 2 years after their reproduction, and, as $\frac{1}{R} \geq 1$ necessarily, $M \geq 2$. If both $D$ and $R$ are equal to 1, the individual always skip a year and come back, i.e. reproduction is biennial: $M = 2$ with a null variance.

In the case of the French Guyana leatherbacks, for the average estimates $D = 0.942$ and $R = 0.530$, one gets $M = 2.777$. 

The delta method provides an estimate of the variance of $M$ as:

$$\text{var}(M) \approx \left( \frac{\partial M}{\partial D} \right)^2 \text{var}(D) + \left( \frac{\partial M}{\partial R} \right)^2 \text{var}(R) + 2 \left( \frac{\partial M}{\partial D} \right) \left( \frac{\partial M}{\partial R} \right) \text{cov}(R, D) =$$

$$= \frac{1}{R^2} \text{var}(D) + \frac{D^2}{R^4} \text{var}(R) - \frac{2}{R^2} \text{cov}(R, D)$$

The variances and covariance of the average departure and return probabilities $R$ and $D$ are obtained in a straightforward fashion as variances and covariance of linear combinations of the time dependent estimates in the CMR model:

From the estimates $\text{var}(D) = 0.000417$ (Standard error 0.0204), $\text{var}(R) = 0.0009942$ (standard error 0.0315); and $\text{cov}(R, D) = -0.0001801$, one gets $\text{var}(m) = 0.0139$ (standard error 0.118) leading to 95% C1 (2.547 - 3.008).

A similar calculation accounting for survival makes it possible to estimate the probability that a leatherback that just reproduced will have one more reproductive event at successive times.

<table>
<thead>
<tr>
<th>next reproduction</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>…</th>
<th>i</th>
<th>…</th>
</tr>
</thead>
<tbody>
<tr>
<td>probability</td>
<td>$(1 - D)S$</td>
<td>$DRS^2$</td>
<td>$D(1 - R)RS^3$</td>
<td>…</td>
<td>$D(1 - R)^i - 2 RS^i$</td>
<td>…</td>
</tr>
</tbody>
</table>

The sum of these probabilities is the probability $P$ that a leatherback that just reproduced will have one more reproductive event. The calculations are closely parallel to the earlier ones:

$$P = (1 - D)S + DRS^2 \sum_{j=0}^{\infty} ((1 - R)S)^j = (1 - D)S + \frac{DRS^2}{1 - (1 - R)S}$$

As the system is supposed to have no memory (i.e. no dependency among successive events, and no senescence), the number of reproductive events for a leatherback that just reproduced follows a geometric distribution, of which the expectation is $1/P$.

Bases on the above estimates, one gets the estimates $P = 0.5469$ and $1/P = 1.7039$. After some algebra, the application of the delta method leads to $\text{var}(P) = 0.0012$ (S.E. 0.0347).