

MAXIMUM LIKELIHOOD ESTIMATES OF TAG LOSS IN LEATHERBACK SEA TURTLES

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Abstract: Leatherback sea turtles (*Dermocheilus coriacea*) nesting in French Guiana have been the focus of a long-term monitoring and metal flipper-tagging program and were subjected to a double-tagging experiment starting in 1994. We developed a new method to estimate the rate of tag loss based on the number of days at liberty after tagging, using maximum likelihood function fitting. Metal tag loss in leatherback sea turtles is characterized by a high rate of loss just after tagging (>30% of turtles lose at least 1 tag within a year) and is followed by higher retention over a longer time period. Using additional data from permanent internal tags that were subsequently applied to turtles in French Guiana, we have shown that the rate of loss of the second metal tag was higher than that of the first metal tag. More accurate estimates of tag loss rates are essential for correctly generating demographic parameters from Capture–Mark–Recapture (CMR) analyses. We have developed a software package to facilitate the use of these models by others researchers in estimating tag loss.

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In wildlife studies, individual identification by way of external markers or tags is commonly used to provide information about demography, life history parameters, and behavior. The ability to recognize individuals is essential in CMR experiments that consist of releasing 1 or several groups of marked individuals and following them over time. The assessment of demographic parameters, such as survival rate or population size, is then based on the number of animals recovered with markers (see Pollock et al. 1990 for models review). In CMR models, individuals that have lost their tags are no longer recognizable and are indistinguishable from dead individuals. Therefore, tag loss can lead to biased estimates under CMR models (Arnason and Mills 1981, Seber 1982, Nichols and Hines 1993).

Tag loss has been quantified using double-tagging experiments that consist of releasing and subsequently monitoring 1 or several groups of double-tagged animals (Nichols et al. 1992). In the case of double-tagging with 2 temporary tags, 1 of the earliest models evaluated the tag reten-

tion rate (K_t) for time interval t from the proportion of animals that were recovered with 1 (r_{st}) and 2 (r_{dt}) tags (Seber 1982):

$$K_t = \frac{2 \times r_{dt}}{r_{st} + 2 \times r_{dt}} \quad (1)$$

When several double-tagged groups were considered together, this formula provided a time-dependent tag loss rate, whereas it was expected to depend on the age of the tag. Moreover, this formula assumed that the rate of loss was independent for both tags (i.e., that losing 1 tag did not affect the probability of losing the second tag). This assumption was found to be incorrect by Siniff and Ralls (1991) for sea otters, Diefenbach and Alt (1998) for black bears, and Bradshaw et al. (2000) for pinnipeds. Double-tagging experiments can be conducted for shorter periods relative to CMR studies. In this case, the rate of tag loss estimated by equation 1 only provided discrete rates of tag loss that cannot be easily extrapolated to the end of the CMR study. Recently, new methods have addressed some of these limitations. Diefenbach and Alt (1998) proposed a method that tested the independence of

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tag loss probabilities of the 2 tags. The cumulative probability that a tag was lost after a time t in individuals with 1 or 2 tags were modeled as logistic functions of time. Data were grouped by annual recaptures of animals with zero, 1, or 2 tags. When tag loss occurred between 2 capture events, the tag loss was arbitrarily dated to the time of the last capture with the corresponding tag (Diefenbach and Alt 1998). This overestimated the tag loss probability because it assumed the maximum possible time the tag was lost, when in fact the tag could have been lost at any time between the last time the individual was observed with the tag and the first time it was observed without it. In addition, the time spent between capture events (i.e., time at liberty) was pooled, requiring an assumption of a constant mortality rate that likely introduced some bias in the estimates (Xiao 1996).

Pistorius et al. (2000) proposed a continuous model for the probability of tag loss with an estimate of the instantaneous rate of loss of a single tag. This model resolved some problems encountered with the model of Diefenbach and Alt (1998), but it was limited because it considered only functions with analytical integrals such as linear functions. Data from different tagging studies suggested nonlinear rates of change in tag loss. For instance, Chevalier and Girondot (1999) observed after tagging leatherback sea turtles initial high rates of tag loss that then stabilized after a certain period. To circumvent this limitation, Pistorius et al. (2000) divided the recapture data into 2 categories: type A described the tag loss during the time from initial capture to the first resighting of the individual, and type B described the tag loss at all times after the first recapture event. Different functions were fitted for type A and B categories of tag loss. A limitation of this classification is that the time during which a tag was classified as type A varied with individuals, and thus, it was dependent on the recapture probability but not on the tag itself. Additionally, the linear function used in the Pistorius et al. (2000) study is inappropriate in cases when extrapolation is required because it does not ensure that the probability always remained between zero and 1. Finally, both methods lack available software to facilitate use of these models by other researchers.

We propose an integrative model of tag loss that reveals temporal patterns of tag loss from a double-tagging experiment data. This method provides an estimate of quasi-continuous tag loss

probability and tests for several tag shedding modalities (e.g., constancy over time, time-linear loss) using a newly developed function to describe tag loss. Moreover, our study population of leatherback turtles included some double-tagged individuals that also had an internal permanent marker (Passive Integrated Transponders [PIT] tags), independent of the external metal tags. Therefore, we were able to estimate 2 different rates of tag loss (from 2 tags to 1 tag and from 1 tag to zero tags) and, consequently, to test for tag loss dependency. We based this individual-focused approach on the number of days that each animal kept its tags. Subsequently, we assessed the tag loss probability that provided the most likely description of the data (i.e., possible days of loss) by the maximum likelihood method. We applied this method to leatherback sea turtles nesting in French Guiana. The model presented required double-tagged individuals, some of which also had a permanent tag. We then applied the derived function of tag loss to other cohorts only identified with nonpermanent tags.

METHODS

Tagging and Recapture of Leatherback Sea Turtles

French Guiana is one of the principal nesting grounds for leatherback sea turtles worldwide (Girondot and Fretey 1996). Leatherbacks nest all along the French Guiana coast, with the highest density found within the Amana Natural Reserve at Awa:la-Ya:lima:po beach.

In 1994 on Awa:la-Ya:lima:po beach, conservation workers placed 2 self-piercing, numbered Monel tags, style 4-1005 size 49 (National Band and Tag, Newport, Kentucky, USA) on the rear flippers of 2,053 leatherbacks. From 1995 to 2000, conservation workers have also permanently marked leatherbacks with an ID-100 PIT tag (Trovan Euroid, Courbevoie, France). This small (14×2 mm diameter), glass-encased microchip was injected into the turtle's right shoulder muscle and read with a portable, battery-powered scanner (Dutton and Mac Donald 1994). Among the females that were double-tagged in 1994, 41 were also PIT-tagged during the following years.

From 1994 to 2000, conservation workers on Awa:la-Yalima:po beach surveyed for turtles nearly every night during the main nesting season (mid-Apr to mid-Aug). They recorded tag information and the number of tags remaining on leatherback's flippers for each observation and

Table 1. Tag loss histories of leatherbacks sea turtles tagged in 1994 within the Amana Natural Reserve at Awa:la-Ya:lima:po beach, French Guiana.

Tagged females	Tag histories (see Fig.1)				
	A	B	C	D	E
2053	760	925	327	41	0

identified PIT tags using scanners (see summary in Table 1). Among the 2,053 double-tagged turtles in 1994 (Table 1), 760 turtles (37%) were never observed after the initial tagging. However, 55 % ± 4.8% (SE) of PIT (permanent) tagged females marked yearly from 1995 to 2001 were also seen only once (on the day of application), despite a retention rate assumed to be close to 100% (McDonald and Dutton 1996). As there is likely to be no difference in the effect of PIT or Monel tags on turtle survival, we conclude that the 37% of individuals not seen after the Monel double-tagging was not a result of rapid tag loss. Consequently, excluding these individuals from our calculation should not have affected our estimates of tag loss.

Describing the Daily Tag Loss Rate Function

We considered a function describing the time-dependent daily probability of tag loss, $p(t)$, based on a logistic equation but with a parameter called min_t that allowed the daily tag loss to converge to an asymptotic daily tag loss value ≠ zero:

$$p(t) = \frac{a_4}{1 + e^{(a_0 \times (a_1 - t))}} + min_t \tag{2}$$

where a_0 and a_1 are fitted model parameters.

However, the rate of tag loss can increase over the long term, a phenomenon called tag senescence (Chevalier and Girondot 1999). To allow min_t to change over time, we defined it as another logistic function to ensure that the resulting $p(t)$ value remained between 0-1 :

$$min_t = \frac{1 - min_t}{1 + e^{(a_2 \times (a_3 - t))}} \tag{3}$$

where a_2 and a_3 are fitted model parameters.

We defined the daily probability of loss of the second tag given that the first tag was already lost, $p^*(t)$, identically except with corresponding parameters a_0^* to a_4^* . The rate of daily tag loss estimated in this way encompassed a wide variety of forms from a constant rate of tag loss to a 2-step function (Fig. 1).

Assessing the Likelihood of Tag Loss Histories

We assumed that an individual was tagged with 2 identical temporary tags and a permanent tag (tattoo or PIT tag) on day zero. Five histories were possible for this individual (Fig. 2): (1) We never subsequently observed the individual after initial capture and hence we could not include it in the estimates of tag loss; (2) We subsequently observed the individual with its 2 tags always intact and hence we calculated the minimum number of days that the individual kept the 2 tags (N_{22}); (3) We subsequently observed the turtle once with 2 tags and later with only 1 tag, hence we calculated N_{22} , the length of the interval during which 1 tag was lost (N_{21}), and the minimum number of days that the second tag remained (N_{11}); (4) We subsequently observed the individual with 2 tags, then with only 1 tag, and at the end of the study without any tags, hence we calculated N_{22} , N_{21} , N_{11} , and the length of the interval during which the last tag was lost (N_{10}); (5) We subsequently observed the turtle with 2 tags and then with no tags (but was still identifiable with its permanent PIT tag), hence we calculated N_{22} and the number of days between the last observation with 2 tags and the first observation without any external tags (N_{20}).

Based on the probability, $p(t)$, of losing the first tag at day t , and the probability, $p^*(t)$, of losing the second tag at day t (Appendix A), we calculated the individual likelihood for each tag loss history. We correctly estimated the probability of losing the first tag, $p(t)$, during the entire experiment. On the other hand, we were able to identify the transition from 1 to zero tags, $p^*(t)$, only after the application of the permanent tag (i.e., 1,414 days after the beginning of the double-tagging experiment). We maximized the sum of the individual log-likelihoods over the model parameter values a_i and a_i^* (i from zero to 4) by using the downhill simplex method (Nelder and Mead 1965) as implemented in Numerical Recipes (Press et al. 1992) followed by a steepest descent gradient search (Greenstadt 1967). We estimated the standard error for the parameters using the delta method, a standard procedure to estimate the variance of a function about a point (Rice 1995). When we applied this procedure to the error in the location of a point, it was directly related to the uncertainty in the model regarding the position of the peak (mathematically represented by the standard error in the estimation of the point where the first derivative was zero). The error was inversely related to the value of the sec-

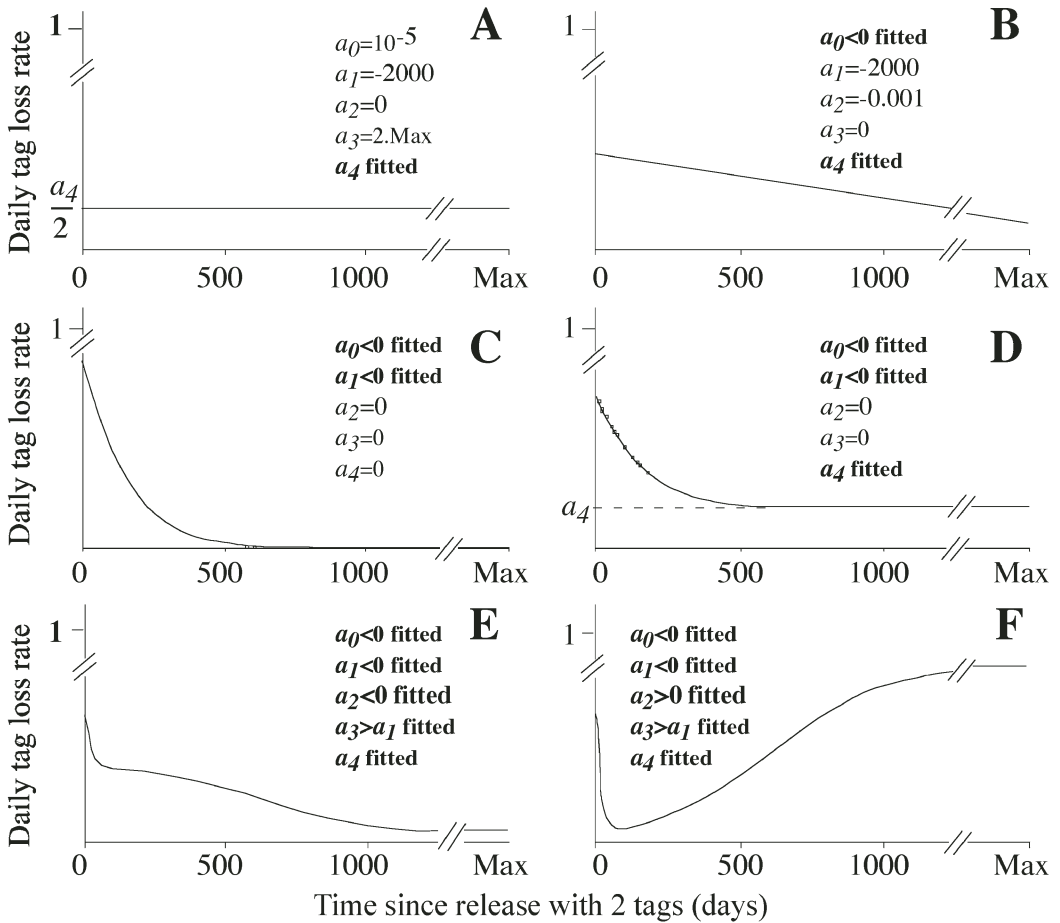


Fig. 1. Examples of tag loss patterns for several model parameterizations: (A) constant tag loss rate, (B) quasi-linear tag loss rate over time – possibly due to tag loss heterogeneity, (C) 1-step function, null asymptote – rapid initial tag loss rate and remaining tags not lost, (D) 1-step function, non null asymptote – rapid initial tag loss rate followed by a constant tag loss rate on a long time scale, (E) 2-step decreasing function – rapid initial tag loss rate followed by a decreasing long-term tag loss rate possibly due to heterogeneity, and (F) 2-step function up and down – rapid initial tag loss rate and long-term tag loss increasing possibly due to tag senescence.

ond derivative about the minimum, and we approximated the value using a second order polynomial around the fitted value for each parameter. For the maximum likelihood model, we calculated the confidence intervals of $p(t)$ and $p^*(t)$ by examining all possible combinations of the parameters varied by ± 2 standard errors and searching for minimum and maximum $p(t)$ and $p^*(t)$ values.

We reduced the most general model (10 parameters) by assuming tag loss independence ($p[t] = p^*[t]$) or by setting some parameters to constant values (Fig. 1). We tested all pertinent combinations of parameters involved in the modeling of $p(t)$ (i.e., 6 models; Fig. 1). Because of a lack of data prior to permanent PIT tag application (i.e., 1,414 days after the first day of double-tagging experi-

ment), we fit models in 2 stages. First, we used the most complex model (5 parameters; Fig. 1 E, F) for the $p^*(t)$ parameters together with all alternative models for $p(t)$. We then constructed a second set of models in which the parameters included in the best model for $p(t)$ from the first stage of model selection were assumed to be the same (but with possibly different values) for modeling $p^*(t)$, but we nevertheless considered again all alternatives for modeling $p(t)$. We fitted the parameter values of $p(t)$ and $p^*(t)$ simultaneously, and model selection was repeated on this set of models.

We adopted the model selection strategy recommended by Burnham and Anderson (1998) for selecting the best approximating model from a set of candidate models based on the minimum

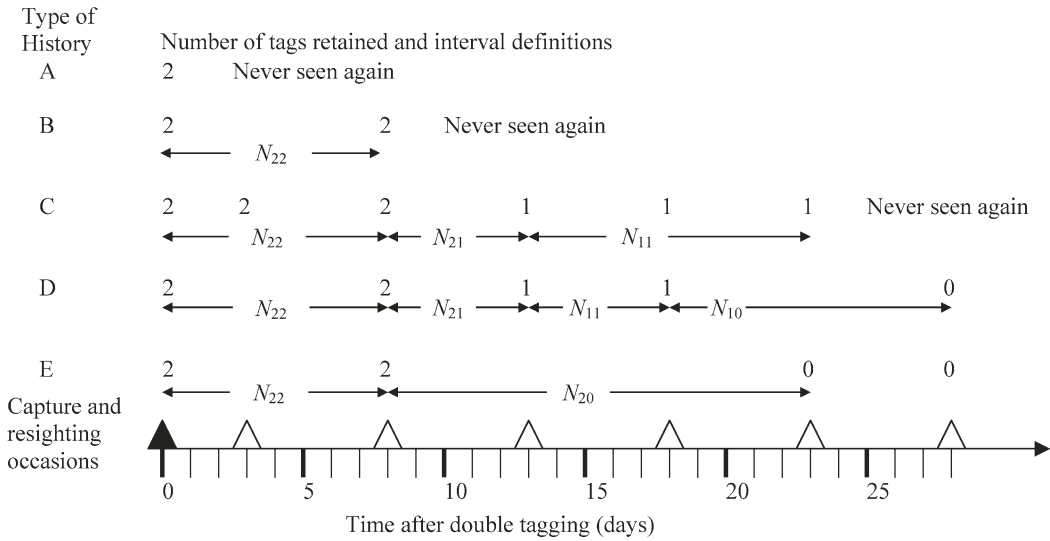


Fig. 2. Hypothetical tag loss histories during capture-mark-recapture experiment and associated time-intervals. Values indicate the number of intact tags at each observation. Double-tagging occurred at $t = 0$ (solid triangle). Grey triangles on the time scale correspond to capture and resighting occasions. Note that N_{20} can only be calculated for history E.

Akaike’s Information Criteria (AIC; Akaike 1974). If L was the maximum likelihood for a specific model using n independently estimated model parameters, then $AIC = -2 \ln L + 2n$. We also computed relative (normalized to sum to 1.0) Akaike weights, w_i , that measured the evidence supporting each model (Burnham and Anderson 1998).

We programmed the models in Realbasic 5.2. TAG_LOSS, a computer software application, is available for MacOS classic, MacOS X, as well as for Windows (9x, Me and XP) at the URL: http://www.es.e.u-psud.fr/epc/conservation/Tag_Loss/Tag_Loss.html.

Testing for the Quality of Fit by Computer Simulations

We used the observed deviance for the selected model based on AIC as a measure of the quality of fit (Burnham and Anderson 1998). We compared the observed deviance to computer simulation generated deviances using conditions similar to those observed in tagged leatherbacks in French Guiana. In our simulation, we discarded from analyses the 760 individuals seen only once with 2 tags on the day of tagging (Fig. 2A) because they provided no information about tag loss. Consequently, we considered that a total of 1,293 individuals were double tagged and followed for 2,569 days. Within this period, females were resighted a mean of 1.3 times. Therefore, we set the daily probability of being observed to

0.0005 ($1.3/2,569$). After the first recapture, we raised this probability to 0.02 for the next 100 days to mimic the observation that females nest several times during the nesting season. We then lowered to zero the daily probability of being observed for the next 600 days to mimic the observation that females nest, on average, every 2 years. On day 1,400 of the simulation, we assumed that 40 permanent tags were applied. We first generated 10 replicate simulations using the software TAG_LOSS, and we performed a model selection based on AIC. In all 10 cases, the selected model was the same one we used to generate data. We then generated 89 replicate simulations using the same procedure, and then parameters were fitted using the model selected on the first 10 datasets. We did not perform the complete model selection for these 89 replicates due to the high computing time; instead we searched only for the maximum likelihood of the parameters values.

RESULTS

Based on AIC, the model for $p(t)$ with only 3 parameters (8 total parameters, including the 5 for $p^*[t]$) was the most strongly supported ($w_i = 58\%$, Table 2). Under this model, the long-term daily tag loss rate was constant. The 2 models with 5 parameters for $p(t)$ received virtually all of the remaining support. However, the global shape of $p(t)$ for these 2 models was similar because in both cases $a_2 \approx 0$. The 3 remaining models received essentially

Table 2. Results of model fitting for model of first tag loss, $p(t)$, in leatherback sea turtles in French Guiana (1994–2000). Second tag loss, $p^*(t)$, was modeled with 5 parameters in every case (not shown).

Model type	Deviance	df	AIC	Δ AIC	Akaike weights, w_i	Model parameter estimates ¹				
						a_0	a_1	a_2	a_3	a_4
One-step function, non-null asymptote (Fig. 1D)	6452.84	8	6468.84	0	0.68	-5.43×10^{-2}	-103.52	— ^a	—	5.62×10^{-4}
Two-step decreasing function (Fig. 1E)	6451.20	10	6471.20	2.36	0.21	-6.80×10^{-2}	-81.15	-2.20×10^{-4}	-6348.01	1.65×10^{-3}
Two-step function up and down (Fig. 1F)	6452.66	10	6472.66	3.81	0.10	-6.93×10^{-2}	-78.92	8.45×10^{-4}	-16272.76	2.87×10^{-4}
One-step function, null asymptote (Fig. 1C)	6576.32	7	6590.32	121.74	2.88×10^{-27}	-1.68×10^{-3}	-4141.68	—	—	—
Quasi-linear tag loss rate (Fig. 1B)	6622.93	7	6636.93	168.09	2.17×10^{-37}	-3.77×10^{-4}	—	—	—	5.00×10^{-8}
Constant tag loss rate (Fig. 1A)	6667.28	6	6679.28	210.43	1.38×10^{-46}	—	—	—	—	8.34×10^{-4}

^a Fixed parameters are represented by dash (see Fig. 1 for details).

no support (Table 2); therefore, the data were inconsistent with a constant tag loss rate (model A) or a continuous decline in tag loss rate to 0.0 (models B, C). Only models with an initial decline in loss rate and a long-term rate >0 were supported.

The most strongly supported model indicated that the change in average daily rate of tag loss was very rapid immediately after tag application; it declined from $3.7 \times 10^{-3} \pm 5.9 \times 10^{-4}$ (SE) tags/day to $2.8 \times 10^{-4} \pm 1.9 \times 10^{-5}$ (SE) tags/day after 180 days, where it remained stable thereafter. The fitted model for $p^*(t)$ showed a constant daily tag loss rate after PIT tag application (i.e., 1,414 days after the beginning of double-tagging experiment). For this period, we estimated $p^*(t) = 6.0 \times 10^{-4} \pm 1.4 \times 10^{-4}$ (SE) tags/day. It was significantly higher than $p(t)$ (the confidence intervals of ± 2 SE for $p[t]$ and $p^*[t]$ do not overlap; Fig. 3). Therefore, the rates of

tag loss for each tag on double-tagged animals were not independent. An adequate model fit could not be rejected when we compared the observed deviance to the 99 simulated deviances ($P = 0.57$).

Assuming that the shapes of $p(t)$ and $p^*(t)$ were similar and therefore the shift between $p(t)$ and $p^*(t)$ was constant over time ($p^*[t] = p[t] + 3.2 \times 10^{-4}$), we calculated the cumulative probabilities

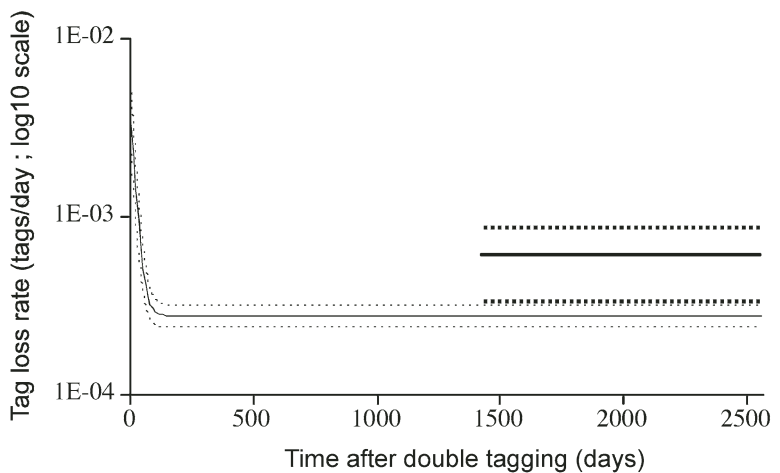


Fig. 3. Maximum likelihood model for first tag loss rate function, $p(t)$ (thin line) and second tag loss rate function, $p^*(t)$ (bold line) with their respective confidence intervals (± 2 SE) in dashed lines for the model most strongly supported by AIC for explaining the daily tag loss rate in leatherback sea turtles in French Guiana (1994–2000). The model of $p^*(t)$ for $t < 1414$ could not be estimated.

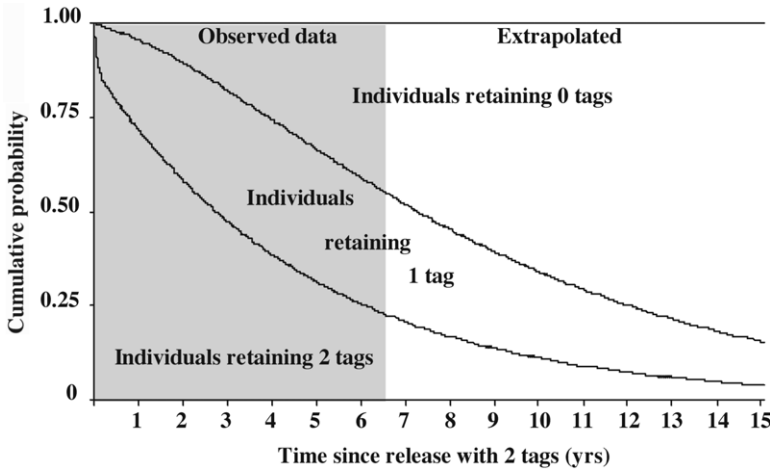


Fig. 4. Estimated cumulative probabilities of individuals retaining 2, 1, or zero tags using the best AIC model selected for data on leatherback sea turtles in French Guiana (1994–2000).

of the different kinds of individuals in the population. Projections indicated that 1 year after double tagging only 70% of double-tagged individuals still had both tags and that $\approx 50\%$ of double-tagged individuals had lost both tags after 8 years (Fig. 4). A similar conclusion was reached if we constrained $p(t) = p^*(t)$ just after the tagging process ($a_0^* = a_0$ and $a_1^* = a_1$) where the difference between 2 functions was due to a change of the asymptote value ($a_4^* \neq a_4$).

DISCUSSION

Tag loss for this species was dependent on the age of the tag and on tag number (i.e., the probability of losing the second tag was different if the individual had already lost 1 tag). The selected model provided 2 tag loss probabilities: (1) probability, $p(t)$, of losing the first tag, and (2) probability, $p^*(t)$, of losing the second tag, given the loss of the first. For $p(t)$, 2 temporal components were highlighted by the model: (1) a short term tag loss, that occurred within 180 days after tag application (called type A), and (2) a long-term tag loss, that occurred from 180 days after tag application (called type B, after Wetherall 1982).

For leatherback sea turtles in French Guiana, the initial tag loss rate was very high, and the probabilities of loss decreased rapidly immediately after application. Tag loss within such a short time scale could have been due to tagging failure, either caused by human error (i.e., improper application) or mechanical error (i.e., failure of the tag's locking mechanism). The lower rate of

tag loss after 6 months can be interpreted as an indication of heterogeneity in the loss rate: the tags that were more subject to shedding were initially lost, and the remaining tags were probably well applied, and hence their loss was lower over time. The long-term tag loss probability was constant but significantly different for $p(t)$ and $p^*(t)$ (Fig. 2); the rate of second-tag loss was significantly higher than for first-tag loss. We lack information on the first part of $p^*(t)$ because permanent

PIT tags were applied only 1,414 days after the beginning of double-tagging experiment.

For elephant seals *Mirounga leonina*, Pistorious et al. (2000) observed an increase in tag loss over a long period that could be due to the rapid growth of the animal. For leatherback sea turtles, our model did not highlight such an increase in long-term tag loss, consistent with the slow growth rate after sexual maturity in Chelonians (Zug and Parham 1996). However, the lack of an age effect could be due to the relatively small sampling time compared to the potential longevity of leatherback sea turtles. Eckert and Eckert (1989) suggested that the primary reason for flipper tag loss in leatherbacks in the U.S. Virgin Islands was tissue necrosis. This hypothesis seems to be consistent with the results provided by our model; if tissue necrosis is a characteristic that is differentially expressed by individuals in the population, it could explain the tag loss dependency (illustrated by the dissimilarity in long-term patterns of $p[t]$ and $p^*[t]$ values). When an individual loses the first tag, the probability of loss of the second tag is higher because tissue necrosis is a characteristic of the individual marked with both tags. Tag loss dependency, revealed here in female leatherbacks tagged in French Guiana and also shown previously for black bears (*Ursus americanus*; Diefenbach and Alt 1998), sea otters (*Enhydra lutris*; Siniff and Ralls 1991), and fur seals (*Arctocephalus forsteri*; Bradshaw et al. 2000), also could be caused by others factors, such as the variable experience of field workers.

MANAGEMENT IMPLICATIONS

Testing for tag loss and its modalities (time-dependency and tag-dependency) should be the first step in analyzing capture-recapture models. If survival rate is under-estimated by misspecification of tag-loss rate, population viability analysis models (Caswell 2001) used to evaluate the status of the population will bias management conclusions because of the associated artificially inflated extinction probability.

Tag loss should be estimated with methods based on the exact time at liberty rather than those based on pooled times at liberty. In marine turtle studies, the use of estimates based on the exact time at liberty is particularly important because the temporal scales of demographic parameters are large. Thus, an estimation of the number of nests laid in 1 season (clutch frequency) requires the observation of an animal during 1 reproductive season, whereas the estimation of inter-nesting interval requires the ability to observe animals for several years. The flexibility of our tag loss model design, expressed as a daily probability of loss, increases the sensitivity to short time scale tag loss phenomena but also provides long time scale extrapolation.

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APPENDIX A: TAG HISTORY PROBABILITIES

If the probabilities of tag loss on day t is $p(t)$ and $p^*(t)$ for first and second tags, respectively, then the probability (Q_{22}) that an individual retained both tags for at least N_{22} days is expressed as:

$$Q_{22} = \prod_{t=1}^{N_{22}} (1 - p(t) \times p^*(t) - 2p(t) \times (1 - p^*(t))) \quad (4)$$

During the interval N_{21} , the first tag was lost. Nevertheless, the exact day of loss was not known and can be any time from the first day of the N_{21} interval ($N_{22} + 1$) to the last day ($N_{22} + N_{21}$). Let us suppose that the first tag was lost at day d . The probability that both tags are retained from day ($N_{22} + 1$) until $(d - 1)$ was:

$$\prod_{j=N_{22}+1}^{d-1} (1 - p(j) \times p^*(j) - 2p(j) \times (1 - p^*(j))) \quad (5)$$

The probability that only 1 tag was lost on a particular day d in this interval is $2 \times p(d) \times (1 - p^*(d))$. The probability of the remaining tag being retained from the day $(d + 1)$ until $(N_{22} + N_{21})$ was:

$$\prod_{j=d+1}^{N_{22}+N_{21}} (1 - p^*(j)) \quad (6)$$

Therefore, the probability Q_{21} that only 1 tag was lost during the N_{21} interval while the second was kept until the end of N_{21} was the sum of these probabilities during N_{21} days:

$$Q_{21} = \sum_{d=N_{22}+1}^{N_{22}+N_{21}} \left\{ \prod_{j=N_{22}+1}^{d-1} [1 - p_j p_j^* - 2p_j(1 - p_j^*)] \times 2p_d(1 - p_d^*) \times \prod_{j=d+1}^{N_{22}+N_{21}} (1 - p_j^*) \right\} / N_{21} \quad (7)$$

We know that the remaining tag was not lost in the N_{11} interval, i.e. from the day $(N_{22} + N_{21} + 1)$ to $(N_{22} + N_{21} + N_{11})$. This probability Q_{11} was:

$$Q_{11} = \prod_{j=N_{22}+N_{21}+1}^{N_{22}+N_{21}+N_{11}} (1 - p^*(j)) \quad (8)$$

Note the special cases when d is the first or the last day of interval N_{21} . In these respective cases, the first product (equation 5) or the last (equation 6) must not be used.

And finally, the remaining tag has been lost during the interval N_{10} and the corresponding probability Q_{10} was:

$$Q_{10} = \frac{\sum_{d=N_{22}+N_{21}+N_{11}+1}^{N_{22}+N_{21}+N_{11}+N_{10}} \left(\prod_{j=N_{22}+N_{21}+N_{11}+1}^{d-1} (1 - p_j^*) \times p_d^* \right)}{N_{10}} \quad (9)$$

The individual likelihood function, L_i , for individual, i , for tag loss history was therefore:

$$L_i = Q_{22} \times Q_{21} \times Q_{11} \times Q_{10} \quad (10)$$

If an interval was not known for an individual, the corresponding Q value was not used for the estimation of L_i . Note the particular case where an individual was seen with 2 tags and then again with zero tags but was still identifiable with its permanent marker. The resulting equation was simply a combination of the equations 7 and 9.

Note two typographical errors in the original text:

Equation 2

$$p(t) = \frac{1 - \min_t}{1 + e^{(a_0 \cdot (a_1 - t))}} + \min_t$$

Equation 3

$$\min_t = \frac{a}{1 + e^{(a_2 \cdot (a_3 - t))}}$$