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Genetic determination of tag loss dynamics in nesting loggerhead turtles: a new chapter in "the tag loss problem"

Joseph B. Pfaller[1,2] · Kristina L. Williams[1] · Michael G. Frick[2] · Brian M. Shamblin[3] · Campbell J. Nairn[3] · Marc Girondot[4]

Abstract

Capture–mark–recapture studies that fail to account for the frequency and dynamics of marker loss risk generating biased demographic estimates. In this study, we used permanent multilocus genotypes (i.e., "genetic tags") and a new enhanced tag loss model to quantify the tag loss dynamics for both passive integrated transponder (PIT) and Inconel metal tags applied to loggerhead turtles (*Caretta caretta*) nesting on Wassaw Island, GA USA. Our results indicate that tag loss is most likely to occur within the nesting season in which tags were applied and is maximal just after tagging (maximum likelihood estimates): 0.00098 PIT tags day^{-1} and 0.007 Inconel tags day^{-1}. After that, PIT tag loss was negligible and Inconel tag loss remained low but constant at 0.00028 tags day^{-1}, such that after 5 years, the probability of losing one PIT tag was 0.06 and losing at least one Inconel tag was 0.46. The use of genetic tags in this study makes these the first truly accurate estimates of PIT and Inconel tag loss for marine turtles, and the new model of tag loss described herein represents an important advancement in the analytical methods used to estimate and compare tag loss dynamics.

Introduction

Capture–mark–recapture (CMR) studies provide fundamental information for estimating demographic parameters in animal populations, including abundance, survival, growth, migration and recruitment (Williams et al. 2002). Robust

✉ Joseph B. Pfaller
jpfaller@ufl.edu

1   Caretta Research Project, Savannah, GA 31412, USA

2   Archie Carr Center for Sea Turtle Research and Department of Biology, University of Florida, Gainesville, FL 32611, USA

3   Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

4   Laboratoire Écologie, Systématique, Évolution, Centre National de la Recherche Scientifique, Université Paris-Sud, AgroParisTech, Université Paris Saclay, 91400 Orsay, France

estimates of these parameters are critical for understanding individual- and population-level processes, which provide the basis for developing and implementing effective management strategies (Oosthuizen et al. 2010). A key assumption of CMR studies is that individual markings or markers are not lost, such that individuals are consistently identifiable upon subsequent recaptures (Seber 1973). Failure to recognize previously marked individuals (i.e., violating the no-marker-loss assumption) can severely bias demographic estimates under CMR models (Arnason and Mills 1981; McDonald et al. 2003). Because individuals that have lost their tags are indistinguishable from dead individuals, frequent marker loss can lead to overestimation of population abundance and recruitment and underestimation of survival and migration rates, including breeding frequency (Nichols and Hines 1993; Bjorndal et al. 1996). In the absence of truly permanent markings or markers, studies that fail to account for the frequency and dynamics of marker loss inherent to their system risk generating biased demographic estimates, leading to erroneous and potentially detrimental management decisions (Mrosovsky 1983; McMahon and White 2009; Unger et al. 2012).

Marine turtle populations, like those of other long-lived marine species, are inherently difficult to monitor, which increases their vulnerability to overexploitation (Heppell

et al. 1999; McClenachan et al. 2012). Long lifespans, cryptic life stages and wide-ranging migrations prevent direct monitoring of individuals, especially juveniles. Assessments of marine turtle populations, therefore, rely heavily on demographic estimates generated from CMR data (NRC 2010). Despite recent advances in photo-recognition technology (Schofield et al. 2008) and genetic identification (Shamblin et al. 2017), physical tags remain the primary tool for marking individual marine turtles. While the problem of premature tag loss in marine turtles is widely acknowledged (e.g., Mrosovsky 1976; Limpus 1992; Nishizawa et al. 2018), our ability to accurately quantify the complex dynamics of tag loss remains a challenge (Rivalan et al. 2005). Early studies relied on double-tagging experiments to estimate the proportion of external metal or plastic tags lost over time (e.g., Mrosovsky and Shettleworth 1982; Limpus 1992; van Dam and Diez 1999). However, without an accompanying form of permanent identification, these estimates are prone to underestimation and must assume tag loss independence due to an inability to identify individuals that have lost both tags (Wetherall 1982). The wide-spread implementation of internal passive integrated transponder devices (PIT tags) in marine turtle studies have provided a practical solution to these biases and facilitated the development of statistical tools for quantifying continuous tag loss dynamics (Rivalan et al. 2005; Girondot 2019a, b). Nevertheless, PIT tags are not infallible (e.g., Parmenter 1993; Godley et al. 1999; van Dam and Diez 1999; McNeill et al. 2013) and estimates of external tag loss—and resulting demographic estimates—that assume PIT tags to be permanent markers are still vulnerable to biases. Because small shifts in demographic rates can lead to large changes in population growth and stability over time (Crouse et al. 1987; Oosthuizen et al. 2010), it is important to quantify accurate measures of tag loss from truly permanent markers in marine turtle populations.

Genetic CMR techniques have emerged as valuable tools for generating demographic estimates in wildlife population (Palsbøll 1999), even in the absence of physically capturing individual animals (see Lampa et al. 2013 and references therein; Shamblin et al. 2011, 2017; Dutton and Stewart 2013). Moreover, genetic tagging has been used to determine both external and internal tag loss rates (Pearse et al. 2001; Feldheim et al. 2002; Unger et al. 2012), though this approach has never been applied to marine turtles. In this study, permanent multilocus genotypes (i.e., "genetic tags") of individual loggerhead turtles (*Caretta caretta*) nesting on Wassaw Island, GA USA were used to quantify tag loss dynamics for both PIT and Inconel metal tags. The goals of this study were to (1) generate robust estimates for the probability of PIT and Inconel metal tag loss over time and test for tag loss independence, (2) evaluate potential biases in tag loss estimates when PIT tags are assumed to be permanent, and (3) compare these new estimates with a comprehensive

review of all other estimates of tag loss in marine turtles. Results of this study provide the first truly accurate estimates of tag loss in marine turtles and highlight the importance of understanding tag loss dynamics when making assessments of marine turtle populations.

Methods

Tagging methodology

Tagging and monitoring of nesting loggerhead turtles (*C. caretta*) have been conducted on Wassaw Island, GA USA (31.89°N, 80.97°W) by the Caretta Research Project since 1973 (USFWS Permit No. 2018-25 and GADNR Licensee No. 1000527963). During the loggerhead nesting season (May–August), nocturnal patrols were conducted by at least two research staff and up to eight volunteers from 2100 to 0600 h to intercept nesting females. After oviposition or failed nesting, females were checked for and, if necessary, fitted with individualized tags. Starting in 1992, all untagged turtles were fitted with two Inconel metal tags (style 681, National Band and Tag Company, Newport, Kentucky, USA) and one PIT tag (Trovan, Douglas, UK or Destron Fearing, South St. Paul, Minnesota, USA). Metal tags were fitted within the first, second or third large scale along the posterior edge of both front flippers and PIT tags were implanted subcutaneously just proximal to the elbow region of the right front flipper. Tags were replaced if found to be lost upon recapture, such that every turtle (in most cases) returned to the water with the standard set of three tags. See Williams and Frick (2001) for additional patrolling and tagging details, including tagging procedures prior to 1992.

Genetic identification

Starting in 2008, genetic samples were collected from every female each season as part of larger regional and subpopulation-wide genetic studies (Shamblin et al. 2011, 2017). Following oviposition or failed nesting, one 6-mm skin biopsy was collected from the shoulder region of each female one time per season (i.e., genetic samples were not collected during within-season recaptures of previously sampled females identified based on tags; see above). All samples were stored in 95% ethanol prior to DNA extraction and/or long-term storage.

Each female was genotyped from samples collected during her first encounter of the study, which includes all untagged females and recaptured females tagged prior to 2008. Samples collected during subsequent recaptures of identifiable females (i.e., those with at least one tag) were not re-genotyped. DNA was extracted using Qiagen DNEasy tissue extraction kits with modifications previously

described (Shamblin et al. 2011). Selected samples were genotyped using 18 microsatellite loci (CcP1B03, CcP1F01, CcP1G02, CcP1G03, CcP1H11, CcP2G10, CcP2F11, CcP2H12, CcP5C08, CcP5F01, CcP5H07, CcP7B07, CcP7C04, CcP7E05, CcP7E11, CcP7G11, CcP7H10, CcP8E07; Shamblin et al. 2007, 2009), with fragment analysis conducted at the Georgia Genomics Facility using a 3730xl DNA Analyzer (Applied Biosystems™). Skin samples typically yielded high-quality and -quantity (> 20 ng/ μl) DNA extracts, such that genotyping error rates generated from blind re-genotyping were quite small (0.25%). Genotypes were compared using the program CERVUS (Kalinowski et al. 2010) and any that perfectly matched across a minimum of 14 loci and contained no mismatches were assigned to the same individual. This buffer allowed us to accommodate some genotyping failures (not mismatches) across samples without rerunning every sample until a complete genotype was obtained. The non-exclusion probability of sibling identity of the 14 least informative markers for these females was 9×10^{-8}, providing strong power for distinguishing even related individuals. See Shamblin et al. (2017) for more details on sample handling and genotyping methods.

Modeling tag loss dynamics

Tag loss histories were assembled for all "new" untagged individuals that received three new tags (two Inconel and one PIT) and a permanent genetic tag during their first encounter between 2008 and 2016. Individuals tagged prior to 2008 and recaptured during or after 2008 were excluded. These data were separated into three datasets to address the goals of this study: (1) genetic–PIT to estimate the probability of PIT tag loss over time, (2) genetic–Inconel to estimate the probability of Inconel tag loss over time and test for tag loss independence, and (3) PIT–Inconel to compare with genetic–Inconel to test for biases when PIT tags are assumed to be permanent. Tag loss histories were converted into the number of days that a turtle retained both metal tags (N_{22}), the number of days during which the first metal tag was lost (N_{21}), the number of days that the second metal tag or PIT tag was retained (N_{11}), the number of days during which the second metal tag or the PIT tag was lost (N_{10}), and the number of days during which both metal tags were lost (N_{20}) depending on the dataset. For calculating N_{10} and N_{20}, we used permanent genetic markers in the Genetic–PIT and Genetic–Inconel datasets, and PIT tags in the PIT–Inconel dataset. Tagging datasets can be made available from the corresponding author on reasonable request.

Tag loss estimates were generated using a new enhanced version of the full individual-based approach described by Rivalan et al. (2005), which was shown to produce more stable and less biased results when compared with other methods

(Venerus et al. 2013). Like the model described in Rivalan et al. (2005), this new model uses a likelihood estimate of time at liberty to estimate the daily probability of tag loss, $p(t)$. However, the new model includes to three computational improvements. First, both maximum likelihood (ML) and Bayesian models were implemented (see below for details). Second, we have corrected the assumption made in Rivalan et al. (2005) that the probability of losing both tags at day t can be simplified to zero [$p(t)^2 = 0$]. This simplification was used to limit the computing time because $p(t)$, and therefore $p(t)^2$ are often very low. However, this could bias estimates when $p(t)$ is not very low just after tagging, a common pattern among marine turtle studies (Casale et al. 2017; Nishizawa et al. 2018; this study). We have changed Eq. 4 in Rivalan et al. (2005), and consequently downstream Eqs. 5–9, to restore the full probability that an individual has retained both tags at day t, $(1 - p(t))^2$. Third, we have developed a new, more versatile function for modeling daily rates of tag loss that allows standard errors to be estimated directly without losing the identifiability of parameters, the condition needed for consistency of ML estimation (Wald 1949). Rivalan et al. (2005) used a single formula with up to 6 parameters to describe the daily tag loss rate. However, a similar shape for daily tag loss rate could be obtained from different set of parameters because some parameters compensate each other. Therefore, identifiability of parameters could not be assured, and the standard error of parameters could be not calculated. Unlike the function described in Rivalan et al. (2005), the function of daily tag loss rates in the new model maintains the identifiability of parameters. This new enhanced approach is outlined below and the statistics for both ML and Bayesian models are implemented in R package *phenology* (v.7.3.2 and higher) (Girondot 2019b).

Tag loss dynamics were modeled using a new 6-parameter function with A, B and C being daily tag loss rate-scaling parameters and D_1, D_2 and D_3 being time-scaling parameters (Fig. 1). Daily tag loss rates in the full model were defined in four segments:

$$\begin{cases} t < D_1 & \left(1 + \cos\left(\pi\left(\frac{t+D_1}{2D_1}\right)\right)\right)(A-B) + B \\ D_1 \le t < D_2 & B \\ D_2 \le t < D_3 & \left(1 + \cos\left(\pi\left(\frac{t-D_2}{D_3-D_2}\right)\right)\right)\frac{1}{2}(B-C) + C \\ t \ge D_3 & C, \end{cases}$$

where the daily tag loss rate goes from A to B between day 0 and day D_1 and remains constant at rate B until day D_2. Then, the rate changes from B to C between days D_2 and D_3, and remains constant at rate C thereafter. To ensure a time progression ($D_1 \le D_2 \le D_3$), two new variables were fitted for D_2 and D_3: D_2D_1 and D_3D_2 with $D_2 = D_1 + |D_2D_1|$ and $D_3 = D_2 + |D_3D_2|$. To ensure that A, B, and C remain between 0 and 1, we fitted their negative logit. This versatile
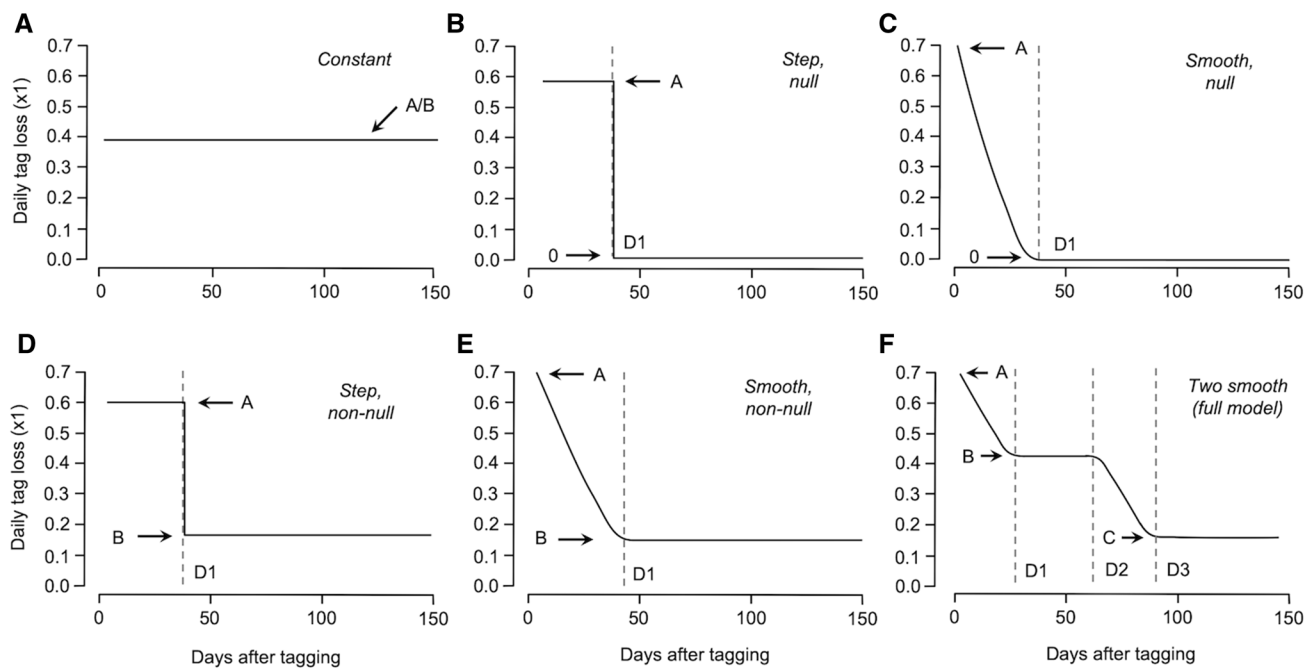
Fig. 1 Six different models of tag loss that were tested using a new 6-parameter function with A, B and C being daily tag loss rate-scaling parameters and D_1, D_2 and D_3 being time-scaling parameters: **a** Constant tag loss (*Constant*), **b** constant initial tag loss followed by null long-term loss (*Step, null*), **c** decreasing initial tag loss rate followed by null long-term loss (*Smooth, null*), **d** constant initial tag loss fol- lowed by non-null long-term loss (*Step, non-null*), **e** decreasing initial tag loss rate followed by non-null long-term lost (*Smooth, non-null*), and **f** full model with two smooth tag loss transitions (*Two smooth (full)*). Fitted parameters are shown on each figure and fixed parameters are listed in Tables 1 and 2

function allows for high rates of initial tag loss ($A > B$) followed by long-term tag senescence ($B > C$) or short- or long-term tag senescence with $B > A$ or $C > B$. Moreover, the full model (6 parameters) can be used to derive other more simplified models, including a model of constant daily tag loss over time (1 parameter).

Using this new function, six different models of tag loss were fitted to each dataset: (a) Constant tag loss [*Constant*; fitted: $B (=A)$; fixed: $C = 0$, $D_1 = 0$, $D_2 D_1 = +\infty$, $D_3 D_2 = +\infty$; Fig. 1a], (b) Constant initial tag loss followed by null long-term loss [*Step, null*; fitted: $B (=A)$, D_1; fixed: $C = 0$, $D_1 = 0$, $D_2 D_1 = +\infty$, $D_3 D_2 = +\infty$; Fig. 1b], (c) Decreasing initial tag loss rate followed by null long-term loss (*Smooth, null*; fitted: A, D_1; fixed: $B = C = 0$, $D_2 D_1 = +\infty$, $D_3 D_2 = +\infty$; Fig. 1c), (d) Constant initial tag loss followed by non-null long-term loss (*Step, non-null*; fitted: $A (=B)$, C, D_1; fixed: $D_2 D_1 = +\infty$, $D_3 D_2 = +\infty$; Fig. 1d), (e) Decreasing initial tag loss rate followed by non-null long-term lost (*Smooth, non-null*; fitted: A, B, D_1; fixed: $C = 0$, $D_2 D_1 = +\infty$, $D_3 D_2 = +\infty$; Fig. 1e), and (f) Full model with two smooth tag loss transitions (*Two smooth (full)*; fitted: A, B, C, D_1, $D_2 D_1$, $D_3 D_2$; fixed: none; Fig. 1f). When fitting each model to data on metal tags (i.e., two metal with permanent genetic or PIT), the probability of losing the first tag, $p(t)$, was first assumed to equal to the probability of losing the second tag, $p^*(t)$.

Then, $p(t)$ and $p^*(t)$ were assumed to be unequal, $p(t) \neq p^*(t)$, and were fitted to the same model of tag loss (Rivalan et al. 2005). Using the structure and parameter estimates of the best-fitting model for each dataset, the likelihood of different tag loss histories and the cumulative probability of tag loss after 2 and 5 years were estimated.

Maximum likelihood estimates of tag loss parameters were generated using the simplex search method (Nelder and Mead 1965). Among the set of 12 candidate models, the best-fitting model for each dataset was selected based on the minimum Akaike's Information Criteria (AIC; Akaike 1974). If L was the ML for a specific model fitted using P independently estimated model parameters, then AIC $= -2 \ln L + 2P$. We also measured the statistical support for each model by computing relative Akaike weights (normalized to sum to 1; Burnham and Anderson 2002). For each dataset, fitted parameters were estimated for each model, including the daily tag loss rate [$p(t)$ and $p^*(t)$ when applicable]. Standard error for parameters was obtained from the square-root of the diagonal of the inverse of the Hessian matrix, while standard error for a combination of parameters was obtained using the delta method (Rice 2007).

Bayesian parameter estimates were modeled using Metropolis–Hastings algorithm with Monte-Carlo Markov chain with uniform priors. Only the best-fitting model based

on AIC was used due to high computing time. The adaptive proposal distribution (Rosenthal 2011) as implemented in R package *HelpersMG* (Girondot 2019a) was used to ensure that the acceptance rate was close to 0.234. The burn-in value and number of iterations were defined after an initial run of 10,000 iterations (Raftery and Lewis 1992). If the estimated computing time for the recommended number of iterations was higher that 48 h, 50,000 iterations were chosen. Convergence and stability of the total run were tested (Heidelberger and Welch 1983; Plummer et al. 2018). The posterior distributions of tag loss parameters were estimated from the output of the MCMC.

Results

Between 2008 and 2016, 506 untagged females each received three new tags (one PIT and two Inconel) and a permanent genetic tag during their first encounter. Of these females, 186 (36.8%) were subsequently recaptured and identified using their genetic tag (range 1–22 recaptures/female; mean ± SD 5.03 ± 4.22). The time between first tagging and last recapture ranged from 0 to 2938 days (mean ± SD 550.7 ± 786.8), and recapture intervals ranged from 1 to 53 days within seasons (mean ± SD 9.92 ± 8.03) and 651 to 2891 days between seasons (mean ± SD 1089.3 ± 407.6). Among the 186 recaptured females, 125 (67.2%) retained all three tags between 0 and 2542 days after tagging (mean ± SD 200.8 ± 445.6), 34 (18.3%) lost only one Inconel tag between 1 and 2938 days after tagging (mean ± SD 1146.9 ± 921.2), 17 (9.1%) lost both Inconel tags between 25 and 2219 days after tagging (mean ± SD 1211.0 ± 717.9), 14 (7.5%) lost their single

PIT tag between 2 and 1108 days after tagging (mean ± SD 522.9 ± 533.1), and 5 (2.7%) lost all three tags between 18 and 1482 days after tagging (mean ± SD 858.2 ± 553.1). The five females that lost all three tags lost all three within one recapture interval, making them unidentifiable without their genetic tags.

The best-fitting model for PIT tag loss when using a permanent genetic tag (Genetic–PIT dataset) was a *Step, null* modality (Fig. 1b) in which the daily tag loss rate was initially constant at 0.00099 tags day^{-1} (95% CI 0.00057–0.00169) for the first 67 days, then dropped to ~0 tag day^{-1} after that (Table 1; Fig. 2a; Akaike weight = 0.35). Table 1 and Fig. 3a, b show the Bayesian estimates for the best-fitting model of PIT tag loss dynamics when using a permanent genetic tag. There was also support for a *Smooth, null* modality for PIT tag loss (Fig. 1c) in which the daily tag loss rate started at 0.0011 tags day^{-1} (95% CI 0.00045–0.0028) just after tagging, then decreased to ~0 tag day^{-1} after 163.5 days (Table 1; Akaike weight = 0.32). From the best-fitting *Step, null* model, the estimated cumulative probability of an individual losing a single PIT tag after 2 and 5 years is 0.06 (95% CI 0.03–0.09) (Table 3; Fig. 2b), which means that approximately 6% of females (95% CI 3–9%) will be unidentifiable after 2 and 5 years when only one PIT tag is applied.

The best-fitting model for Inconel tag loss when using a permanent genetic tag (Genetic–Inconel dataset) was a *Smooth, non-null* modality (Fig. 1e) in which the probability of losing the first tag was not equal to (i.e., independent from) the probability of losing the second tag, $p(t) \neq p^*(t)$ (Table 2; Akaike weight = 0.995). The daily tag loss rate for the first tag started at 0.007 tags day^{-1} (95%

Table 1 Parameter estimates and model fits for PIT tag loss with permanent genetic tag (Empty fields "–"are filled using $D_1 = 0$; $D_2D_1 = \max(t) + 1$; $D_3D_2 = \max(t) + 1$; $A = 0$; $B = 0$; $C = 0$)

Dataset	Parameters						Model fit	
	$p(t)$						AIC	Weight
Model	D_1	D_2D_1	D_3D_2	A	B	C		
Genetic–PIT (ML)								
(a) Constant	–	–	–	–	0.00007	–	257.5	0.00
(b) Step, null	66.8	–	–	0.00099	–	–	231.2	0.35
(lower 95% CI)	(–18918)			(0.00057)				
(upper 95% CI)	(19,052)			(0.00169)				
(c) Smooth, null	163.5	–	–	0.0011	–	–	231.3	0.32
(d) Step, non-null	66.4	–	–	0.00098	–	0.0	233.2	0.13
(e) Smooth, non-null	163.5	–	–	0.0011	0.0	–	232.4	0.19
(f) Two smooth (full)	3.1	0.0	122.5	0.0	0.00104	0.0	239.3	0.01
Genetic–PIT (Bayesian)[a]								
(b) Step, null	94.2	–	–	0.00074	–	–		
(lower 95% CI)	(45.2)	–	–	(0.00026)	–	–		
(upper 95% CI)	(301.1)	–	–	(0.00156)	–	–		

[a]Bayesian parameter estimates were modeled only for the best-fitting model based on AIC
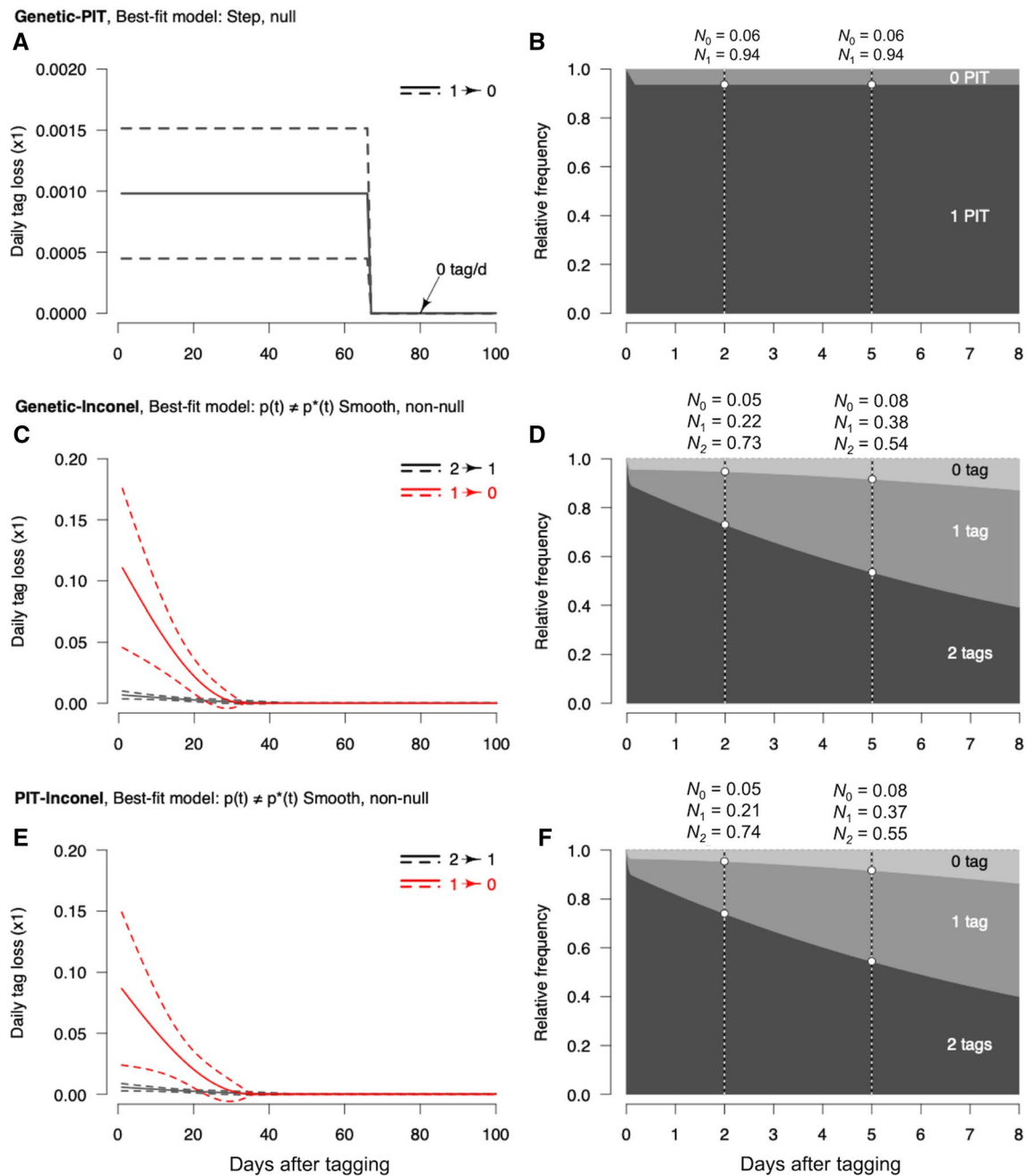
Fig. 2 Maximum likelihood estimates of tag loss dynamics in nesting loggerhead turtles. **a** Best-fit model of PIT tag loss when using a permanent genetic tag and **b** estimated cumulative probabilities of individuals retaining 1 or zero PIT tags at two and 5 years after tagging. **c** Best-fit model of first and second Inconel tag loss when using a permanent genetic tag and **d** estimated cumulative probabilities of individuals retaining 2, 1 or zero Inconel tags at 2 and 5 years after tagging. **e** Best-fit model of first and second Inconel tag loss when PIT tags are assumed to be permanent and **f** estimated cumulative probabilities of individuals retaining 2, 1 or zero Inconel tags at 2 and 5 years after tagging when PIT tags are assumed to be permanent

CI 0.004–0.011) just after tagging and then decreased to an asymptote value of 0.00028 tags day^{-1} (95% CI 0.00019–0.00043) after 44.9 days (95% CI 22.1–67.6), while the daily tag loss rate for the second tag started at 0.116 tags day^{-1} (95% CI 0.063–0.204) just after tagging and then decreased to an asymptote value of 0.00009 tags day^{-1} (95% CI 0.00003–0.00029) after 33.2 days (95% CI 25.8–40.7) (Table 2; Fig. 2c). Table 2 and Fig. 3c, d show the Bayesian estimates for the best-fitting model of Inconel tag loss dynamics when using a permanent genetic tag. The estimated cumulative probability of an individual losing just one Inconel tag—while retaining the
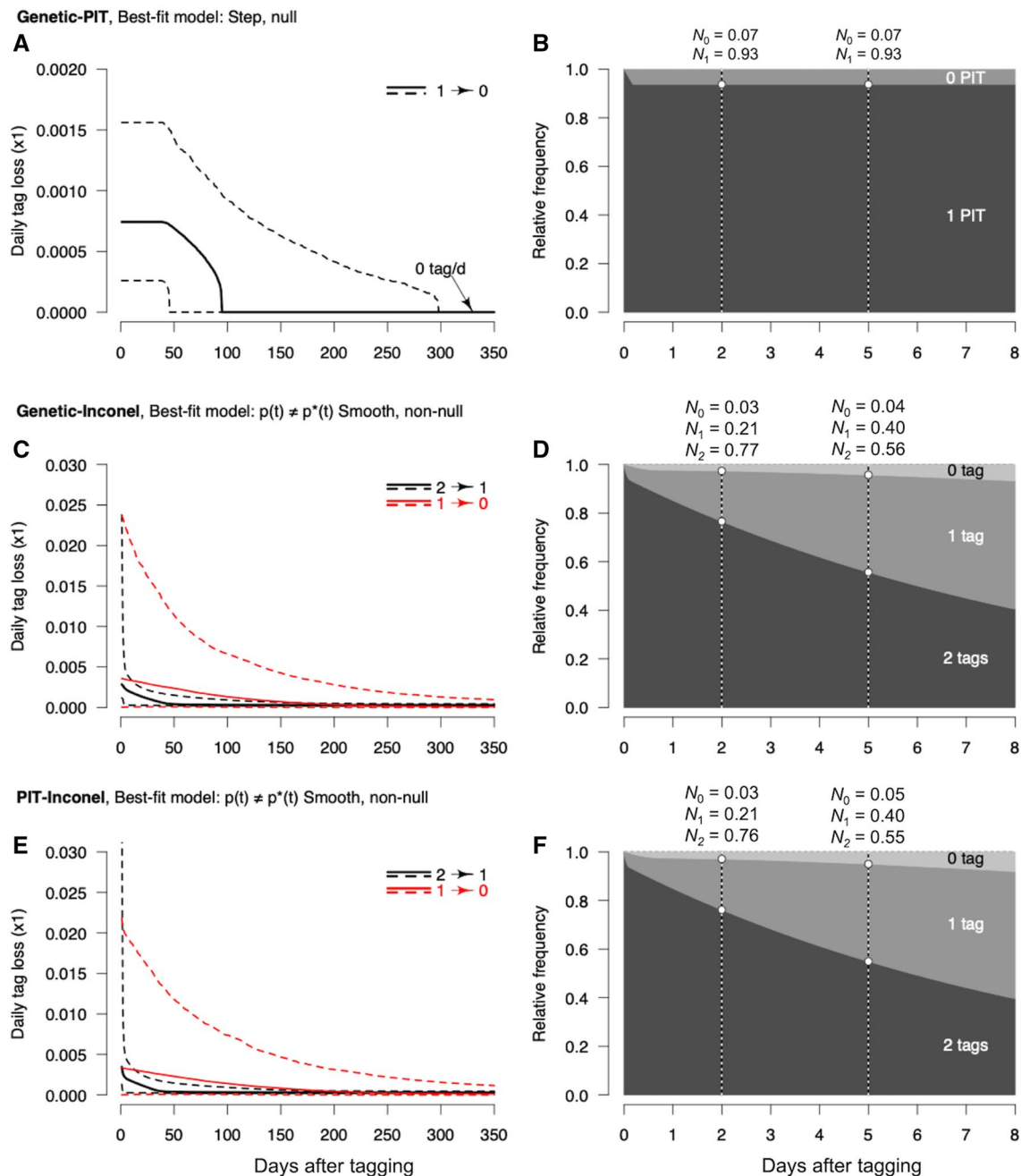
Fig. 3 Bayesian estimates of tag loss dynamics in nesting loggerhead turtles. **a** Model of PIT tag loss when using a permanent genetic tag and **b** estimated cumulative probabilities of individuals retaining 1 or zero PIT tags at 2 and 5 years after tagging. **c** Model of first and second Inconel tag loss when using a permanent genetic tag and **d** estimated cumulative probabilities of individuals retaining 2, 1 or zero Inconel tags at 2 and 5 years after tagging. **e** Model of first and second Inconel tag loss when PIT tags are assumed to be permanent and **f** estimated cumulative probabilities of individuals retaining 2, 1 or zero Inconel tags at 2 and 5 years after tagging when PIT tags are assumed to be permanent

other—is 0.22 (95% CI 0.15–0.28) after 2 years and 0.38 (95% CI 0.27–0.49) after 5 years, while the probability of losing both the Inconel tags is 0.05 (95% CI 0.03–0.08) after 2 years and 0.08 (95% CI 0.03–0.13) after 5 years (Table 3; Fig. 2d). This means that when two Inconel tags are applied, 5% of females (95% CI 3–8%) will be unidentifiable after 2 years and 8% of females (95% CI 3–13%) will be unidentifiable after 5 years. Additionally, if only one Inconel tag is applied, approximately 27% of females (95% CI 20–34%) will be unidentifiable after 2 years and 46% of females (95% CI 35–58%) will be unidentifiable after 5 years.

Table 2 Parameter estimates and model fits for Inconel tag loss with permanent genetic tag and when PIT tags are assumed to be permanent (empty fields "–"are filled using $D_1 = 0$; $D_2D_1 = \max(t)+1$; $D_3D_2 = \max(t)+1$; $A = 0$; $B = 0$; $C = 0$)

Dataset		Parameters												Model fit	
		$p(t)$						$p(t)*$							
Model	Assumption	D_1	D_2D_1	D_3D_2	A	B	C	D_1	D_2D_1	D_3D_2	A	B	C	AIC	Weight
Genetic–Inconel (ML)															
(a) Constant	$p(t) = p(t)*$	–	–	–	–	0.00057	–							1230.3	0.00
(a) Constant	$p(t) \neq p(t)*$	–	–	–	–	0.00053	–	–	–	–	–	0.00068	–	1231.6	0.00
(b) Step, null	$p(t) = p(t)*$	98.1	–	–	0.0043	–	–							1345.9	0.00
(b) Step, null	$p(t) \neq p(t)*$	200.8	–	–	0.0023	–	–	52.9	–	–	0.037	–	–	1321.0	0.00
(c) Smooth, null	$p(t) = p(t)*$	217.4	–	–	0.0052	–	–							1319.9	0.00
(c) Smooth, null	$p(t) \neq p(t)*$	282.9	–	–	0.0038	–	–	67.9	–	–	0.068	–	–	1317.0	0.00
(d) Step, non-null	$p(t) = p(t)*$	71.2	–	–	0.0044	–	0.00016							1159.5	0.00
(d) Step, non-null	$p(t) \neq p(t)*$	78.0	–	–	0.0026	–	0.00027	74.5	–	–	0.025	–	0.00003	1129.0	0.002
(e) Smooth, non-null	$p(t) = p(t)*$	41.7	–	–	0.0111	0.00023	–							1157.2	0.00
(e) Smooth, non-null	$p(t) \neq p(t)*$	44.9	–	–	0.007	0.00028	–	33.2	–	–	0.116	9.3e^{-05}	–	1116.1	0.995
(lower 95% CI)		(22.1)			(0.004)	(0.00019)		(25.8)			(0.063)	(2.9e^{-05})			
(upper 95% CI)		(67.6)			(0.011)	(0.00043)		(40.7)			(0.204)	(2.9e^{-04})			
(f) Two smooth (full)	$p(t) = p(t)*$	45.1	450.9	0.01	0.0109	0.0	0.00034							1160.4	0.00
Genetic–Inconel (Bayesian)[†]															
(e) Smooth, non-null	$p(t) \neq p(t)*$	58.3	–	–	0.0029	0.00029	–	299.8	–	–	3.6e^{-03}	4.8e^{-05}	–		
(lower 95% CI)		(2.6)			(0.0012)	(0.00017)		(45.0)			(8.9e^{-06})	(1.8e^{-06})			
(upper 95% CI)		(314.4)			(0.053)	(0.00043)		(911.9)			(2.3e^{-02})	(2.4e^{-04})			
PIT–Inconel (ML)															
(a) Constant	$p(t) = p(t)*$	–	–	–	–	0.00055	–							1010.0	0.00
(a) Constant	$p(t) \neq p(t)*$	–	–	–	–	0.00053	–	–	–	–	–	0.00061	–	1011.8	0.00
(b) Step, null	$p(t) = p(t)*$	107.4	–	–	0.0037	–	–							1119.9	0.00
(b) Step, null	$p(t) \neq p(t)*$	131.0	–	–	0.0029	–	–	49.0	–	–	0.032	–	–	1101.5	0.00
(c) Smooth, null	$p(t) = p(t)*$	244.6	–	–	0.0044	–	–							1097.0	0.00
(c) Smooth, null	$p(t) \neq p(t)*$	307.0	–	–	0.0033	–	–	80.3	–	–	0.049	–	–	1075.4	0.00
(d) Step, non-null	$p(t) = p(t)*$	71.9	–	–	0.0038	–	0.00017							958.7	0.00
(d) Step, non-null	$p(t) \neq p(t)*$	89.3	–	–	0.0005	–	0.00006	93.3	–	–	0.00061	–	0.0	1019.8	0.00
(e) Smooth, non-null	$p(t) = p(t)*$	51.0	–	–	0.0084	0.00023	–							960.9	0.00
(e) Smooth, non-null	$p(t) \neq p(t)*$	47.4	–	–	0.006	0.00028	–	35.4	–	–	0.090	0.00011	–	932.8	0.993
(lower 95% CI)		(21.2)			(0.004)	(0.0002)		(23.8)			(0.042)	(0.00004)			
(upper 95% CI)		(73.6)			(0.010)	(0.0004)		(47.0)			(0.182)	(0.00036)			
(f) Two smooth (full)	$p(t) = p(t)*$	51.0	487.0	0.61	0.0084	0.0	0.00038							960.9	0.00

Table 2 (continued)

Dataset Model	Assumption	Parameters p(t)						Parameters p(t)*						Model fit	
		D_1	D_2D_1	D_3D_2	A	B	C	D_1	D_2D_1	D_3D_2	A	B	C	AIC	Weight
(f) Two smooth (full)	$p(t) \neq p(t)*$	54.3	302.4	382.2	0.0058	0.0	0.00049	0.0	0.0	35.2	0.0	0.063	0.00013	942.8	0.007
PIT–Inconel (Bayesian)†															
(e) Smooth, non-null	$p(t) \neq p(t)*$	46.3	–	–	0.004	0.00029	–	320.7	–	–	$3.4e^{-03}$	$6.1e^{-05}$	–		
(lower 95% CI)		(1.2)			(0.001)	(0.0002)		(13.9)			$(1.0e^{-06})$	$(2.3e^{-06})$			
(upper 95% CI)		(293.8)			(1.0)	(0.0005)		(904.5)			$(2.5e^{-02})$	$(3.0e^{-04})$			

$p(t)$ probability of losing the first tag, $p(t)*$ probability of losing the second tag

†Bayesian parameter estimates were modeled only for the best-fitting model based on AIC

The best-fitting model for Inconel tag loss when the PIT tag was assumed to be permanent (PIT–Inconel dataset) was a *Smooth, non-null* modality (Fig. 1e) in which the probability of losing the first tag was not equal to (i.e., independent from) the probability of losing the second tag, $p(t) \neq p*(t)$ (Table 2; Akaike weight = 0.993). The daily tag loss rate for the first tag started at 0.006 tags day^{-1} (95% CI 0.004–0.010) just after tagging and then decreased to an asymptote value of 0.00028 tags day^{-1} (95% CI 0.00017–0.00043) after 47.4 days (95% CI 21.2–73.6), while the daily tag loss rate for the second tag started at 0.090 tags day^{-1} (95% CI 0.042–0.182) just after tagging and then decreased to an asymptote value of 0.00011 tags day^{-1} (95% CI 0.00004–0.00036) after 35.4 days (95% CI 23.8–47.0) (Table 2; Fig. 2e). Table 2 and Fig. 3e, f show the Bayesian estimates for the best-fitting model of Inconel tag loss dynamics when PIT tags are assumed to be permanent. The overall dynamics of Inconel tag loss over time (modality and dependency) were the same when PIT tags were assumed to be permanent (Genetic–Inconel *versus* PIT–Inconel) (Figs. 2d, f, 3d, f). Moreover, parameter estimates for the timing and rate of Inconel tag loss were not significantly different when PIT tags were assumed to permanent (Table 2).

Maximum likelihood and Bayesian estimates were similar for each dataset. However, there were three differences. First, the standard error of parameter D1 for the ML estimate of PIT tag loss was huge (95% CI 18,918.40428–19,052.01001), indicating a lack of information to adequately fit this parameter. This problem was not observed for the Bayesian method. Second, the lower limit for the ML estimate of tag loss rate using delta method was negative (see Fig. 2), whereas it was not negative using Bayesian method. Third, Bayesian estimation was computationally more intensive than ML: the ML search using Nelder–Mead algorithm required approximately 1000 estimations of likelihood, whereas the Bayesian MCMC using 100,000 iterations and 6 parameters required 600,000 estimations of likelihood. When N_{20} individuals were present in the dataset, Bayesian estimation was not computationally feasible (run time > 2 years).

Discussion

In this study, permanent genetic markers were used to estimate the first truly accurate rates of tag loss in marine turtles. In particular, this approach has provided the first direct estimates of the frequency and dynamics of PIT tag loss. Herein, we discuss the patterns that were observed, as well as the potential reasons and relevance of their occurrence, and incorporate the findings of this study into the history and future narrative of the "tag loss problem" in research

Table 3 Comparison between model-based estimates of tag loss in marine turtles (values in parentheses are 95% confidence intervals)

Species					Daily asymptotic tag loss		Long-term probability of tag loss			
							$P_{2\text{-}1}$		$P_{2\text{-}0/1\text{-}0}$	
References	Site	Habitat	Tag	Best-fitting model	$N_{2\text{-}1}$	$N_{1\text{-}0}$	2 years	5 years	2 years	5 years
Caretta caretta										
This study	Georgia, USA	N	PIT	*Step, null*	–	$<10^{-9}$	–	–	0.06 (0.03–0.09)	0.06 (0.03–0.09)
This study (Bayesian)	Georgia, USA	N	PIT	*Step, null*	–	$<10^{-9}$	–	–	0.07 (0.04–0.12)	0.07 (0.04–0.12)
This study	Georgia, USA	N	I	*Smooth, non-null, $p(t) \neq p(t)*$*	2.8e^{-4} (1.9–4.3e^{-4})	9.3e^{-5} (2.9e^{-5}–2.9e^{-4})	0.22 (0.15–0.28)	0.38 (0.27–0.49)	0.05 (0.03–0.08)	0.08 (0.03–0.13)
This study (Bayesian)	Georgia, USA	N	I	*Smooth, non-null, $p(t) \neq p(t)*$*	2.9e^{-4} (1.7–4.3e^{-4})	4.8e^{-5} (1.8e^{-6}–2.4e^{-4})	0.21 (0.14–0.29)	0.40 (0.28–0.52)	0.03 (0.00–0.07)	0.05 (0.01–0.12)
McNeill et al. (2013)[a]	N. Carolina, USA	F	I	*Smooth, non-null, $p(t) \neq p(t)*$*	0.00038 (3.2–4.3e^{-4})	0.00044 (2.7–6.3e^{-4})	0.19 (0.16–0.23)	0.32 (0.26–0.38)	0.05 (0.03–0.06)	0.17 (0.12–0.23)
Casale et al. (2017)[a]	Mediterranean	F	I	*Smooth, non-null, $p(t) = p(t)*$*	1.4e^{-4}	1.4e^{-4}	0.17	0.26	0.02	0.05
Chelonia mydas										
Reisser et al. (2008)[a,b]	Brazil	F	I-PS	*Constant $p(t) = p(t)*$*	0.00039 (7.6e^{-5}–7.0e^{-4})	0.00039 (6.3e^{-5}–7.0e^{-4})	0.21 (0.05–0.37)	0.35 (0.12–0.57)	0.03 (0.00–0.07)	0.16 (0.00–0.31)
Reisser et al. (2008)[a,b]	Brazil	F	I-BS	*Constant $p(t) = p(t)*$*	0.0021 (9.0e^{-4}–3.3e^{-3})	0.0021 (9.0e^{-4}–3.3e^{-3})	0.33 (0.18–0.66)	0.08 (0.00–0.17)	0.46 (0.26–0.66)	0.90 (0.78–1.0)
Nishizawa et al. (2018)[a]	Malaysia	N	I	*Smooth, non-null, $p(t) \neq p(t)*$*	0.00028 (2.1–3.4e^{-4})	0.00016 (7.4e^{-5}–2.4e^{-4})	0.21 (0.17–0.24)	0.36 (0.30–0.42)	0.03 (0.01–0.04)	0.08 (0.04–0.11)
Nishizawa et al. (2018)[a]	Malaysia	N	T	*Smooth, non-null, $p(t) \neq p(t)*$*	0.00016 (9.7e^{-7}–3.1e^{-4})	0.00022 (6.3e^{-5}–3.8e^{-4})	0.29 (0.18–0.42)	0.31 (0.15–0.46)	0.13 (0.03–0.23)	0.20 (0.08–0.33)
Dermochelys coriacea										
Rivalan et al. (2005)	French Guiana	N	M	*Smooth, non-null, $p(t) \neq p(t)*$*	0.00028	0.00060	0.18	0.24	0.06	0.20
Rivalan et al. (2005)[a]	French Guiana	N	M	*Smooth, non-null, $p(t) \neq p(t)*$*	0.00027 (2.2–3.1e^{-4})	0.00016 (1.0–2.1e^{-4})	0.22 (0.20–0.24)	0.36 (0.32–0.40)	0.02 (0.01–0.03)	0.07 (0.05–0.09)

Habitat (*N* nesting, *F* foraging), tag (*BS* between scales, *I* inconel, *M* monel, *PS* pre-scale, *PIT* passive integrated transponder, *T* titanium)

Tag loss metrics: $N_{2\text{-}1}$ and $N_{1\text{-}0}$ are daily asymptotic tag loss rates for losing the first of two tags and losing second of two tags, respectively. $P_{2\text{-}1}$ is the probability of losing one out of two Inconel metal tag, thereby maintaining individual identifiability between recapture events. $P_{2\text{-}0/1\text{-}0}$ is the probability of losing two out of two Inconel metal tags or one out of one PIT tag, thereby losing individual identifiability for each tag type respectively. $P_{2\text{-}2}$ (not shown) or $1 - (P_{2\text{-}1} + P_{2\text{-}0/1\text{-}0})$ is the probability of retaining both Inconel tags or the single PIT tag at each time period

[a]Estimates recalculated here, either not provided or calculated incorrectly in the original article

[b]Includes one hawksbill recapture. Only one model was used (no model selection)

on marine turtles (Mrosovsky 1976; summarized in Table 4 and Online Resource 1).

Despite their frequent use as permanent markers, a small percentage of PIT tags applied in this study were lost (7.5% of 186 PIT tags). Results from our modeling approach suggest that PIT tag loss is most likely to occur within the season in which the tag was applied (< 70 days post-tagging) and is essentially non-existent after that. The prevalence of short-term PIT tag loss is attributable to application error (i.e., user failing to properly insert tag) or to tags being expelled through the tagging wound soon after application (Feldheim et al. 2002; McNeill et al. 2013). Although long-term PIT loss was relatively infrequent in our study, these instances remain important. Of the five females that lost all three tags (one PIT and two Inconel tags) within one recapture interval and were subsequently only identified by their genetic tag, four lost their tags/identity between nesting seasons (656–1482 days). Long-term PIT tag "loss" is attributable to failures in detection resulting from internal tag migration, changes in scanner frequency, or failures in tag transmission (Eckert and Beggs 2006; Wyneken et al. 2010). Understanding both the short- and long-term dynamics of PIT tag loss will help to direct future efforts and incentive to reduce PIT tag loss in the field. Clearly, providing adequate training of field staff remains a critical step towards reducing preventable PIT tag loss. However, field managers might also consider using a temporary, fast-drying adhesive or patch at the tagging site to reduce the likelihood of PIT tag expulsion soon after tagging.

Similar rates of PIT tag loss (5–15%) have been documented in other studies of marine turtle around the world (Table 4). However, given that PIT tags are frequently assumed to be permanent markers in CMR studies (i.e., 0% tag loss), the question remains whether PIT tag loss is frequent enough to bias estimates of external tag loss, as well as other important demographic rates. The use of permanent genetic tags provides the first opportunity to evaluate this assumption. Results from our comparative modeling approach (Genetic–Inconel versus PIT–Inconel) suggest that while the short-term rates of external tag loss might be slightly different, the overall dynamics (i.e., modality and dependency; see below) were the same and long-term estimates of tag loss were not significantly different. At least in our analyses of external tag loss, estimates were not substantially biased by assuming that PIT tags were permanent, even when in fact 7.5% were lost. However, this may not be the case in other locations or for other demographic rates that are more sensitive to the no-marker-loss assumption (e.g., adult survival, population abundance). Acknowledging and accounting for the frequency and dynamics of PIT tag loss, therefore, will help future efforts to estimate demographic rates avoid biases when permanent tags or markers are unavailable.

External tags have revolutionized the study of marine turtles but are well known for their tendencies to be lost (Balazs 1999; Table 4). For this reason, understanding and accounting for the dynamics of external tag loss are critical in CMR studies, especially in the absence of PIT tags or permanent markers (McMahon and White 2009; Unger et al. 2012). Studies that model the long-term probability of tag loss highlight the limitations of using metal tags alone (Table 3). At the estimated rates of tag loss, single-tagging studies would fail to recognize 18–29% of previously tagged individuals after 2 years and 24–40% after 5 years, while double-tagging studies would fail to recognize 2–13% of previously tagged individuals after 2 years and 8–20% after 5 years (excluding the extremely high rates estimated for the BS position by Reisser et al. 2008; Table 3). Without the inclusion of permanent tags, single-tagging studies in marine turtles would likely significantly overestimate population abundance and recruitment, and underestimate rates of survival and migration (Nichols and Hines 1993; Bjorndal et al. 1996). To a lesser degree, the same can be said for double-tagging studies in which only metal tags are applied. However, more work is needed to quantify the extent to which important demographic estimates and the population models to which they are applied are affected by a typical range of tag loss rates estimated for marine turtles.

Similar to other modeling studies, our results suggest that Inconel tag loss was initially high soon after tagging, then decreased to a non-zero asymptote after ~50 days such that the long-term probability of tag loss increased over time (Table 3). Moreover, we found that the probability of losing the second Inconel tag was significantly higher than the probability of losing the first tag (i.e., tag loss dependence), which was also found in these other modeling studies. The consistency of these short-term patterns across studies suggests that tag application error is a ubiquitous phenomenon affecting long-term tag retention rates in CMR studies of marine turtles. When one tag is not applied correctly through human error or mechanical failure and is lost prematurely, then there is a greater likelihood that that other tag was not applied correctly and will also be lost prematurely (McNeill et al. 2013). The same is likely true for tags that are applied correctly—if the first tag is applied correctly, so is the second. As with PIT tags, providing thorough training of new field staff and regular quality-control assessments of all staff, tagging equipment and procedures are all critical steps for reducing preventable loss of external tags.

Once an external tag is applied correctly, its long-term retention is likely then dependent on the combination of tag type, tag position, turtle species and habitat (Table 4 and Online Resource 1). Among studies that provide direct comparisons between tag types, Monel metal and plastic tags generally exhibit higher tag loss rates over time compared to Inconel and Titanium metal tags, with Titanium typically

Table 4 Summary of tag loss estimates for marine turtles (see Online Resource 1 for additional details)

Species RMU	Habitat	Stage	Tag	Position	Perm. mark	Method	Tag loss	Time unit	References
Caretta caretta									
A-NW	N	A	I	FF	G	ML	0.22/0.38*	2 years/5 years	This study
A-NW	N	A	I	FF	G	BAY	0.21/0.40*	2 years/5 years	This study
A-NW	N	A	PIT	FF	G	ML	0.06/0.06	2 years/5 years	This study
A-NW	N	A	PIT	FF	G	BAY	0.07/0.07	2 years/5 years	This study
A-NW	N	A	I	FF	N	P	0.62	3 years	Williams and Frick (2000)
A-NW	N	A	P	FF	N	P	0.59	3 years	Williams and Frick (2000)
A-NW	N	A	P	RF	N	P	0.38	3 years	Williams and Frick (2000)
A-NW	N	A	PIT	FF	N	P	0.21	3 years	Williams and Frick (2000)
A-NW	F	J,A	M	FF	N	P	0.08	99 days	Henwood (1986)
A-NW	F	A	P	FF	N	P	> 0.50	~1 year	Gorham et al. (1998)
A-NW	F	A	I	FF	N	P	> 0.50	~1 year	Gorham et al. (1998)
A-NW	F	J,A	I	RF	PIT	ML	0.19/0.32*	2 years/5 years	McNeill et al. (2013)
A-NW	F	J,A	PIT	FF	N	ML	0.08	15 years	McNeill et al. (2013)
A-NW	C	J	CW	FF,RF	C	P	0.15	1 year	Schwartz (1981)
MED	N	A	PIT	SH	N	P	0.11	3 months	Godley et al. (1999)
MED	F	J	I	FF	N	ML	0.17/0.26*	2 years/5 years	Casale et al. (2017)
P-S	N	A	M	FF	N	P	0.16/0.37	2 years/5 years	Limpus (1992)
P-S	N	A	T	FF	N	P	0.07/0.23	2 years/5 years	Limpus (1992)
P-S	N	A	T	RF	N	P	0.21/0.33	2 years/5 years	Limpus (1992)
P-S	F	J,A	M	FF	N	P	0.16/0.12	2 years/5 years	Limpus (1992)
P-S	F	J,A	T	FF	N	P	0.06/0.20	2 years/5 years	Limpus (1992)
Lepidochelys kempii									
A-NW	N	A	M	FF	PIT	P	0.054	3 months	Jiménez-Quiroz and Márquez-Millán (2002)
A-NW	N	A	I	FF	PIT	P	0.057	3 months	Jiménez-Quiroz and Márquez-Millán (2002)
A-NW	C	J	PIT	FF	N	P	0.0	5 months	Fontaine et al. (1987)
Lepidochelys olivacea									
P-E	N	A	M	FF	N	P	0.54	–	Cornelius and Robinson (1982)
P-E	N	A	P	FF	N	P	0.60	–	Cornelius and Robinson (1982)
Eretmochelys imbricata									
A-W	F	J,A	M	FF	PIT	P	0.22/0.40	2 years/5 years	van Dam and Diez (1999)
A-W	F	J,A	I	FF	PIT	P	0.14/––	2 years/5 years	van Dam and Diez (1999)
A-W	F	J,A	P	FF	PIT	P	0.00/–	2 years/5 years	van Dam and Diez (1999)
A-W	F	J,S	PIT	FF	N	P	0.10/0.17	2 years/5 years	van Dam and Diez (1999)
A-W	F	J,S	M	FF	N	P	0.57/0.54	1 year/2 years	Bellini et al. (2001)
A-W	F	J,S	I	FF	N	P	0.05/0.00	1 year/2 years	Bellini et al. (2001)
Natator depressus									
P-SW	N	A	M	FF	N	P	0.09/0.47	2 years/5 years	Parmenter (1993)
P-SW	N	A	PIT	SH	N	P	0.08	2 years	Parmenter (1993)
P-SW	N	A	P	FF	PIT	P	0.59/0.79	2 years/5 years	Parmenter (2003)
I-SE	N	A	T	FF	TS	P	0.24	≥1 year	Schäuble et al. (2006)
Chelonia mydas									
A-NW	N	A	M	FF	N	P	0.15	1 month	Schulz (1975)
A-NW	N	A	M	FF	TS	P	0.26	~3 years	Carr (1980)
A-NW	N	A	M	FF	TS	P	0.20	~3 years	Bjorndal (1980)
A-NW	N	A	M	FF	N	P	0.06/0.20	4 months/3 years	Bjorndal et al. (1996)
A-NW	N	A	I	FF	N	P	0.24/0.14	4 months/3 years	Bjorndal et al. (1996)
A-NW	N	A	M	FF	N	P	0.11/0.25	4 months/2 years	Troëng et al. (2003)

Table 4 (continued)

Species RMU	Habitat	Stage	Tag	Position	Perm. mark	Method	Tag loss	Time unit	References
A-NW	N	A	I	FF	N	P	0.04/0.13	4 months/2 years	Troëng et al. (2003)
A-NW	N	A	I	FF	N	P	0.03	4 months	Campbell and Lagueux (2005)
A-NW	N	A	I	FF	N	P	0.13/0.20	2 years/5 years	Troëng and Chaloupka (2007)
A-NW	N	A	I	FF	N	P	0.03	≥1 year	Velez-Espino et al. (2018)
A-NW	N	A	P	FF	N	P	>0.50	~1 year	Gorham et al. (1998)
A-NW	N	A	I	FF	N	P	>0.50	~1 year	Gorham et al. (1998)
A-NW	F	J	M	FF	N	P	0.0-0.04	~1 year	Labrada-Martagón et al. (2017)
A-NW	C	J	CW	FF,RF	C	P	0.83	1 year	Schwartz (1981)
A-NW	C	J	M	RF	C	P	0.05/0.71	4 weeks/5 weeks	Owens (1977)
A-S	F	J	I	FF	PR	P	0.10	3 years	Reisser et al. (2008)
A-S	F	J	I	FF	PR	BAY	0.21/0.35*	2 years/5 years	Reisser et al. (2008)
MED	N	A	PIT	SH	N	P	0.07	3 months	Godley et al. (1999)
P-E	N	A	M	FF	N	P	0.44	4 months	Alvarado et al. (1988)
P-E	N	A	P	RF	N	P	0.03	4 months	Alvarado et al. (1988)
P –WS	N	A	I	FF	N	P	0.40	~3 years	Liew and Chan (2002)
P-WS	N	A	T	FF	N	P	0.20	~3 years	Liew and Chan (2002)
P-WS	N	A	I	FF	N	ML	0.21/0.36*	2 years/5 years	Nishizawa et al. (2018)
P-WS	N	A	T	FF	N	ML	0.29/0.31*	2 years/5 years	Nishizawa et al. (2018)
P-SW	N	A	M	FF	N	P	–/0.56	2 years/5 years	Limpus (1992)
P-SW	N	A	T	FF	N	P	–/0.25	2 years/5 years	Limpus (1992)
P-E	F	J,A	M	FF	N	P	0.42	4 years	Green (1979)
P-E	F	J,A	P	RF	N	P	0.06	4 years	Green (1979)
P-SW	F	J,A	M	FF	N	P	0.02/0.34	2 years/5 years	Limpus (1992)
P-SW	F	J,A	T	FF	N	P	0.00/0.00	2 years/5 years	Limpus (1992)
P-SW	F	J,A	P	RF	N	P	0.08/0.86	2 years/5 years	Limpus (1992)
P-WC	F	J,A	I	FF	PIT	P	0.02	7.6 years	Summers et al. (2017)
P-WC	F	J,A	T	FF	PIT	P	0.00	7.6 years	Summers et al. (2017)
P-WC	F	J,A	PIT	RF	N	P	0.01	7.6 years	Summers et al. (2017)
Dermochelys coriacea									
A-NW	N	A	M	FF	N	P	0.16	2 years	Eckert and Eckert (1989)
A-NW	N	A	P	FF	N	P	0.88	2 years	Eckert and Eckert (1989)
A-NW	N	A	PIT	SH	N	P	~1%	4 months	Dutton and McDonald (1994)
A-NW	N	A	M	RF	N	P	0.15/0.88	2 years/5 years	McDonald and Dutton (1994)
A-NW	N	A	T	RF	N	P	0.33/0.88	2 years/5 years	McDonald and Dutton (1994)
A-NW	N	A	PIT	SH	N	P	0.02	5 months	McDonald and Dutton (1994)
A-NW	N	A	M,T	RF	PIT	P	~0.40	2–3 years	McDonald and Dutton (1996)
A-NW	N	A	PIT	SH	N	P	0.0	2–3 years	McDonald and Dutton (1996)
A-NW	N	A	M	RF	PIT	P	0.25/0.45	2 years/3 years	Chevalier and Girondot (1999)
A-NW	N	A	M	RF	PIT	ML	0.22/0.36*	2 years/5 years	Rivalan et al. (2005)
P-E	N	A	PIT	SH	N	P	> 0.0	>1 year	Santidrián Tomillo et al. (2017)

RMU Regional Management Unit, *A-NW* Atlantic-Northwest, *A-W* Atlantic-Western Caribbean/USA, *A-S* Atlantic-Southwest and South Caribbean, *I-SE* Indian-Southeast, *MED* Mediterranean, *P-E* Pacific-East, *P-S* Pacific-South, *P-SW* Pacific-Southwest, *P-WS* Pacific-West Pacific/Southeast Asia, *P-WC* Pacific-West Central), habitat (*C* captivity; *F* foraging, *N* nesting), stage (*A* adult; *J* juvenile), tag (*CW* coded wire, *I* inconel, *M* monel, *P* plastic, *PIT* passive integrated transponder, *T* titanium), position (*FF* front flippers, *RF* rear flippers, *SH* shoulder), permanent (Perm) mark (*C* captivity, *G* genetic, *N* none, *PR* photo recognition, *PIT* passive integrated transponder, *TS* tag scars); method (*BAY* Bayesian, *ML* maximum likelihood, *P* proportion)

*Model-based estimates reflect the cumulative likelihood of losing just one tag at 2 and 5 years—making these estimates comparable to past studies that cannot account for double tag loss in the absence of a permanent tag (see Table 3 and Online Resource 1 for more details)

outperforming Inconel. An exception being plastic tags in foraging habitats, which maintain low rates of tag loss over time (Green 1979; Limpus 1992; van Dam and Diez 1999) but have also been linked to fisheries entanglement (Nichols and Seminoff 1998). The use of Monel tags has been widely discontinued due to their tendency to corrode in seawater (Balazs 1982, 1999). Among studies that directly compare tag position, tags applied to more distal positions on the front flippers consistently exhibit higher tag loss rates than more proximal positions (Limpus 1992; Reisser et al. 2008), while tags applied to the rear flippers sometimes but not always outperform tags applied to the front flippers (Green 1979; Alvarado et al. 1988; Limpus 1992). Although there is considerable co-variation among tag type and position, and turtle species and habitat, some generalities in tag loss rates do emerge. Tag loss rates estimated on nesting beaches tend to be higher than those estimated in foraging areas, which suggests that the added stresses of courting, mating and nesting exacerbate tag loss. Leatherbacks tend to exhibit relatively high rates of tag loss, but estimates are only from nesting beach studies, while hawksbills tend to exhibit relatively low rates of tag loss, but estimates are only from foraging-ground studies. Nesting loggerhead, flatback and green turtles seem to exhibit similar, but highly variable, rates of tag loss that are largely dependent on tag type and position (Table 4). Because quantifying tag loss is often not the primary focus of CMR studies, the biological factors that drive difference is tag loss remain poorly understood. More rigorous studies that isolate the effect that different factors have on tag loss would be highly informative for directing the best field methodologies.

The new model of tag loss described in this study represents an important progression in the analytical methods used to understand and compare tag loss dynamics. Early studies relied on double-tagging experiments to estimate tag loss rates based on the proportion of animals that were recaptured with one and two tags (Seber 1973; Nichols et al. 1992). However, this approach is prone to underestimation because it does not account for individuals that have lost both tags (Wetherall 1982) or for tag loss dependence, a phenomenon that is supported by our study as well as other studies of marine turtles (e.g., Nishizawa et al. 2018) and mammals (Siniff and Ralls 1991; Bradshaw et al. 2000; McMahon and White 2009). Subsequent efforts to test for tag loss dependence and extrapolate discrete rates of tag loss over time were biased by an inability to account for the continuous nature of tag loss (Xiao 1996; Diefenbach and Alt 1998), which is especially problematic when recapture intervals are long (Rivalan et al. 2005). A continuous model of tag loss probability was proposed that estimated an instantaneous rate of loss that could be more easily extrapolated to the end of CMR studies (Pistorius et al. 2000), but was limited because it considered only linear functions of tag loss. In response to these limitations, Rivalan et al. (2005) developed a new individual-based model of tag loss that uses double-tagging data to estimate quasi-continuous tag loss probability and a new tag loss function to compare different modalities of tag loss (linear and non-linear) in a maximum likelihood framework. The incorporation of "permanent" PIT tag data also allowed this study to model first and second tag losses separately, thereby providing the first test for tag loss dependency. Tag loss estimates generated using this approach have been shown to produce more stable and less biased results when compared with other methods (Venerus et al. 2013) and has now been applied to three sea turtle species in five countries (Table 3).

The new enhanced model of tag loss described in this study builds on the Rivalan et al. (2005) approach. Daily tag loss rates in this new model are defined in time segments, but all segments are in continuity. Therefore, unlike Rivalan et al. (2005), this updated function allows standard errors to be estimated directly using the inverse of the Hessian matrix because parameters were all identifiable (Wald 1949). Alternatively, when computing time was not too high, Bayesian estimation of parameters was used, and posterior distribution could be evaluated. The main advantages of these new approaches are that model parameters for daily rates of tag loss (A, B and C) and timing of tag loss (D_1, D_2 and D_3) have direct biological interpretations (units: tags day^{-1} and days, respectively) and are also directly comparable across studies (Table 3). If one were interested in testing for differences in tag loss dynamics between datasets or studies, one would need only to compare confidence intervals of like parameters. Moreover, this framework allows tag loss estimates to be more easily and accurately extrapolated to the end of CMR studies. Future studies that apply this new more versatile function and enhanced analytical approach will draw stronger inferences about tag loss, thereby directing the most robust tagging methods and leading to more accurate demographic estimates from CMR data.

The widespread implementation of genetic tagging in studies of marine turtles will likely continue to improve our ability to estimate many demographic parameters. Methods for non-invasive genetic tagging of nesting females have already exposed important biases in past estimates of reproductive characteristics (Shamblin et al. 2017) and genetic tagging of hatchlings has the potential to reveal basic life history characteristics, such as age-to-maturity, survivorship and dispersal, that have eluded scientists for decades (Dutton and Stewart 2013). Our study used genetic tagging to generate the first truly accurate estimates of metal and PIT tag loss. Nevertheless, prior to universal genetic tagging or other forms of permanent identification (e.g., McDonald et al. 1996; Reisser et al. 2008), most CMR studies of marine turtles around the world will continue to rely on physical tags as the primary tool for marking individuals.

Consequently, the accuracy of demographic estimates from CMR data will continue to depend on our ability to account for the methodological biases associated with the "tag loss problem" (Mrosovsky 1976). Because methodological biases—in the field and in analytical tools—can stymy accurate assessments of population stability (Crouse et al. 1987; Oosthuizen et al. 2010) and mask important biological patterns (Pfaller et al. 2018), efforts to account for and eliminate biases in methodology are critical for avoiding erroneous and potentially detrimental management decisions (McMahon and White 2009; Unger et al. 2012).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Human and animal rights statement All elements of this research followed ethical standards that were approved and permitted by the United States Fish and Wildlife Service and Georgia Department of Natural Resources, Wildlife Resources Division.

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