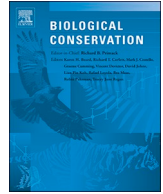




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The importance of passive integrated transponder (PIT) tags for measuring life-history traits of sea turtles

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ARTICLE INFO

Keywords:

Caretta caretta
Chelonia mydas
Flipper tag
Green turtle
Loggerhead turtle
Tag loss

ABSTRACT

Capture-mark-recapture studies rely on the identification of individuals through time, using markers or tags, which are assumed to be retained. This assumption, however, may be violated, having implications for population models. In sea turtles, individual identification is typically based on external flipper tags, which can be combined with internal passive integrated transponder (PIT) tags. Despite the extensive use of flipper tags, few studies have modelled tag loss using continuous functions. Using a 26-year dataset for sympatrically nesting green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles, this study aims to assess how PIT tag use increases the accuracy of estimates of life-history traits. The addition of PIT tags improved female identification: between 2000 and 2017, 53% of green turtles and 29% of loggerhead turtles were identified from PIT tags alone. We found flipper and PIT tag losses were best described by decreasing logistic curves with lower asymptotes. Excluding PIT tags from our dataset led to underestimation of flipper tag loss, reproductive periodicity, reproductive longevity and annual survival, and overestimation of female abundance and recruitment for both species. This shows the importance of PIT tags in improving the accuracy of estimates of life-history traits. Thus, estimates where tag loss has not been corrected for should be interpreted with caution and could bias IUCN Red List assessments. As such, long-term population monitoring programmes should aim to estimate tag loss and assess the impact of loss on life-history estimates, to provide robust estimates without which population models and stock assessments cannot be derived accurately.

1. Introduction

Population-based conservation is dependent on accurate estimates of life-history traits (Hernández-Camacho et al., 2015; Yokoi et al., 2017). Most population studies use capture-mark-recapture (CMR), which involves the release of tagged individuals and their subsequent recapture events over time. These studies rely on individual recognition to provide information about demography, behaviour and survival, assuming tags are correctly identified and retained over time (Pradel, 1996). This assumption, however, is often violated, having implications for the interpretation of demographic and survivorship data (Arnason and Mills, 1981; González-Vicente et al., 2012; Rotella and Hines, 2005). In CMR models, individuals having lost all tags are no longer identifiable and are indistinguishable from dead individuals, which can

lead to the overestimation of population abundance and underestimation of survival (Arnason and Mills, 1981; Cowen and Schwarz, 2006; Laake et al., 2014).

CMR has been used extensively in sea turtle research to study behaviour (e.g. Lazar et al., 2004) and to estimate life-history traits (e.g. Stokes et al., 2014). Such studies generally rely on tagging individuals with two external flipper tags, reducing the probability of individual loss from the identifiable population. Double tagging also allows tag loss estimation, the rate of which may be influenced by tag type and size, species and tagger experience (Casale et al., 2017; Limpus, 1992).

Flipper tags can be combined with subcutaneously injected passive integrated transponder (PIT) tags which are thought to be more durable, cannot be lost through abrasion or during courtship and have higher readability and retention than flipper tags (Gibbons and

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<https://doi.org/10.1016/j.biocon.2019.108248>

Received 19 May 2019; Received in revised form 20 August 2019; Accepted 9 September 2019

Available online 21 November 2019

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Andrews, 2004; Godley et al., 1999; McNeill et al., 2013; Rivalan et al., 2005). Thus, individuals having lost all external tags may nevertheless be re-identified. Detection failure can occur, however, if tags are expelled from the body before wound healing (Feldheim et al., 2002; Godley et al., 1999), if tags migrate within the animal's tissue (Van Dam and Diez, 1999; Wyneken et al., 2010) or if tags become unreadable (McNeill et al., 2013; Van Dam and Diez, 1999). Whilst PIT tags have very little negative impact on animals overall (Gibbons and Andrews, 2004), their benefits may be outweighed by their higher financial cost. Furthermore, the availability and necessity of PIT tag readers for tag detection (Gibbons and Andrews, 2004) may prohibit their use, especially when recapture probability is low or when non-project personnel, such as fishermen, encounter tagged animals.

Although tagging, and particularly flipper tagging, is considered standard practice in sea turtle research, few studies have estimated tag loss. Two approaches have been used to do so: proportion of tags lost (e.g. Bjørndal et al., 1996; Limpus, 1992) and, recently, modelling (e.g. Casale et al., 2017). Typically, individuals are tagged with two flipper tags and the shedding of one of the two tags is used to model tag loss using different scenarios. Only five studies have modelled flipper tag loss in such a manner at foraging (timeframe: 11 yr, McNeill et al., 2013, timeframe: 14 yr, Casale et al., 2017) and nesting (timeframe: 22 yr, Nishizawa et al., 2017; timeframe: 9 yr, Pfaller et al., 2019) grounds for loggerhead turtles (*Caretta caretta*), and only at nesting grounds for leatherback turtles (*Dermochelys coriacea*, timeframe: 7 yr, Rivalan et al., 2005). Tag loss was best described by a high initial loss before remaining constant thereafter (Casale et al., 2017; Nishizawa et al., 2017; Pfaller et al., 2019; Rivalan et al., 2005), except in McNeill et al. (2013), where it was constant over time. Only one study has used its findings to adjust survival estimates and to compare them to non-adjusted estimates (Nishizawa et al., 2017). Similarly, only one study has modelled PIT tag loss using continuous functions indicating that PIT tag loss is negligible in nesting loggerhead turtles (timeframe: 9 yr, Pfaller et al., 2019).

The need for more accurate data on life-history parameters for demographic models and population assessments has been highlighted as a research priority for sea turtles globally (Hamann et al., 2010; Rees et al., 2016) and, in particular, for green turtles (*Chelonia mydas*) in the Mediterranean (Casale et al., 2018). For example, although annual survival has been calculated for subset groups of green and loggerhead nesting females in the Mediterranean (Omeyer et al., 2019; Snape et al., 2016), no estimates are available for nesting populations as a whole in the region.

Saturation flipper tagging has been carried out since 1992 at Alagadi Beach, North Cyprus, and PIT tags were introduced in 1997. Using the resulting 26-year individual-based monitoring dataset for green and loggerhead turtles, this study aims (1) to accurately estimate long-term flipper and PIT tag loss for green and loggerhead turtles; and (2) to assess how the use of PIT tags has increased the accuracy of estimates of flipper tag loss, population abundance and recruitment, survival, and reproductive periodicity and longevity.

2. Material and methods

2.1. Data collection

Since 1992, sea turtle monitoring at Alagadi Beach has been carried out by the Marine Turtle Conservation Project (University of Exeter, UK), a collaboration between the Marine Turtle Research Group, the North Cyprus Department for Environmental Protection and the North Cyprus Society for the Protection of Turtles. Alagadi Beach, situated on the north coast of Cyprus (35°33' N, 33°47' E), consists of two coves of 0.8 and 1.2 km in length, separated by a rocky headland (Broderick and Godley, 1996). On average, 217 green and 65 loggerhead turtle clutches are laid annually (2014–2018). Satellite tracking of females of both species at this study site has revealed foraging sites in Syria, Egypt,

Libya, Lebanon, Tunisia, Turkey and Cyprus (Bradshaw et al., 2017; Snape et al., 2016).

Data were collected between early May and mid-August (encompassing the entire nesting season) from 1993 to 2017, except in 1992 when monitoring began in early July. Flipper tags were fitted on the trailing edge of the fore-flippers between the proximal second and third scales (after Balazs, 1999) during the covering phase, immediately after oviposition. From 1992 to 1999, plastic flipper tags were used (1992–1994: Dalton Jumbotags®, 1994–1999: Dalton Supertag®; Dalton Tags, UK). Because these tags became unreadable after a few years, from 1999 to 2015, titanium Stockbrands® (Australia) flipper tags were used, except in 2013, where Inconel 681/C tags were used (National Band & Tag Company, Kentucky, USA). In 2016 and 2017, Inconel and titanium flipper tags were used because it was decided to stop using titanium tags when females reacted negatively to the new design. The estimation of Inconel flipper tag loss was not possible due to their recent introduction and the resultant low level of tag returns to date.

PIT tags were injected from 1997 onwards, as per Godley et al. (1999), to increase recapture rates of females having lost all flipper tags. Prior to 2014, Trovan microchips (11.50 × 2.12 mm, 0.10 g) were used, after which the newly available Trovan mini-transponders (8.00 × 1.40 mm, 0.06 g) were used due to their smaller, less invasive gauge needle. Until 2013, one PIT tag was given in each shoulder where time permitted, whereas from 2014 onwards, only one PIT tag was given, in preference, in the right shoulder, both to reduce costs and limit the number of invasive procedures. Checks of both shoulders were nevertheless maintained as standard. Effects of flipper and PIT tagging have been investigated at Alagadi Beach, showing no significant effects on post-ovipositional behaviour and reproductive success (Broderick and Godley, 1999).

2.2. Data handling

Two datasets were compared to assess the error associated with tag loss and to determine whether the use of PIT tags resulted in more accurate estimates of life-history parameters and flipper tag loss. In the 'PIT tag' dataset, flipper and PIT tag readings were used, whereas, in the 'no PIT tag' dataset, PIT tags were omitted and female identification was based solely on flipper tags. In the 'no PIT tag' dataset, if a previously known female returned to nest and was identified by PIT tag(s) alone, having lost all flipper tags, she was given a new identification number and thus treated as a neophyte female (first-time nester). Reproductive periodicity and longevity were calculated for each new female, except for females that were identified by PIT tag(s) alone on their first recapture at their second nesting season, as these females will not have successfully completed one remigration interval with both flipper tags. A new encounter history was created for each female and the process was repeated each time females had lost both flipper tags, meaning that a known female could have multiple identification numbers and thus multiple encounter histories in the 'no PIT tag' dataset. Finally, for the tag loss analysis of the 'no PIT tag' dataset, tag histories in which all tags were lost were excluded, as these could not be determined without the use of PIT tags (TH20 and TH10, see Section 2.5 for further details).

2.3. Reproductive periodicity and longevity

While reproductive periodicity is the number of years elapsed between two consecutive nesting seasons, reproductive longevity is the time span since recruitment (year of first capture) to the nesting population, with neophytes being given year 0. The annual number of neophyte females and the annual proportion of misidentified remigrant females were calculated from 2000 onwards because of the increased accuracy of neophyte classification following one modal breeding cycle (3 yr) after the introduction of PIT tags.

Linear models and generalised linear mixed effect models were used

to determine whether PIT tags significantly improved estimates of reproductive longevity and periodicity respectively, using the package 'nlme' in R (R Core Team, 2018). Female ID was included to account for pseudoreplication and temporal effects were controlled for.

2.4. Annual survival

Encounter histories were created based on nesting events. Survival probability was estimated using the multi-state model in MARK (White and Burnham, 1999), assuming a breeding state (B; observable state) and a non-breeding state (NB; unobservable state). The parameters estimated were annual survival probability (S), encounter probability (p) and transition probabilities between states ($\psi_{B \rightarrow NB}$ and $\psi_{NB \rightarrow B}$). A 'time-since-marking' approach with two 'age' classes was used to allow survival the first year after initial tagging (hereafter S1) to differ from that in subsequent years (hereafter S2; Chaloupka and Limpus, 2002; Kendall et al., 2018; Pradel et al., 1997; Sasso et al., 2006). This allows us to account for imperfect fidelity, assuming that some neophytes are transient individuals, i.e. those being individuals that are never seen again after their initial capture. While S1 confounds permanent emigration and mortality, S2 is more likely to reflect true survival.

Goodness of fit was assessed using U-CARE (Choquet et al., 2005). Model selection was based on the lowest $qAIC_c$ value (corrected quasi-likelihood Akaike information criterion). Parameters were estimated using the Markov chain Monte Carlo method and were based on posterior distributions. 95% highest posterior density credibility intervals were reported (see supplementary material for further details).

2.5. Tag loss

Tag returns were ascribed to five types of tag histories (TH), using days as the unit, and were defined as follows: females released/resighted with two tags and resighted with both tags (TH22), with one tag (TH21) or with no tags (TH20); and, females released/resighted with one tag and resighted with one tag (TH11) or no tag (TH10). PIT tag(s) permitted the identification of females having lost both flipper tags and thus the calculation of TH20 and TH10. Tag histories can be combined such that a female released with two tags, resighted with two tags, and resighted again with no tags would have the following tag history: TH22 + TH20.

Tag history probabilities were defined as per Casale et al. (2017), adapted to include TH20 and TH10. Maximum likelihood estimation was performed using the package 'bbml'. The same five models as in Casale et al. (2017, see supplementary material for further details) were compared. Model selection was based on the lowest AIC_c (corrected Akaike Information Criterion) value.

The analysis was conducted separately for each tag type, species and dataset. Both types of plastic flipper tags and PIT tags were grouped due to small sample size. Because new tags were fitted if lost, the datasets included multiple tags per female.

2.6. Other studies

All previously published studies which calculated tag loss using continuous functions were reviewed and presented in Table 1 for comparison. Cumulative tag loss probabilities after 1 and 5 yr were calculated when absent from those original studies (see Table 1 for details).

3. Results

3.1. Population parameters at Alagadi Beach

3.1.1. Female identification

Of the females previously tagged with both flipper and PIT tags at Alagadi Beach, 53% of green turtles ($n = 305$) and 29% of loggerhead

turtles ($n = 132$) were identified in subsequent nesting seasons by PIT tag(s) alone between 2000 and 2017, resulting in the overestimation of neophytes, particularly for green turtles (Fig. 1, Table S1). On average, over that period, without PIT tags, we would have assumed that 74% of green turtles ($n = 671$) and 78% of loggerhead turtles ($n = 492$) nesting were neophyte females, instead of the 44% and 69% respectively using PIT tags (Table S1). Simultaneously, nesting female abundance would have been overestimated by 37% for green turtles (2000–2017, PIT tags: $n = 389$, no PIT tags: $n = 533$) and 9% for loggerhead turtles (PIT tags: $n = 371$, no PIT tags: $n = 405$).

3.1.2. Reproductive periodicity

The median reproductive periodicity was 3.0 yr for both species at this study site, with a mean of 3.5 yr for green turtles and 3.0 yr for loggerhead turtles, and intervals of up to 12 and 10 yr for green and loggerhead turtles respectively (Fig. 2, Table S1). Omitting PIT tags resulted in less accurate estimates of reproductive periodicity, although not significantly, for both species (green turtles: $\chi^2_1 = 1.98$, $P = 0.159$; loggerhead turtles: $\chi^2_1 = 0.15$, $P = 0.701$). For green turtles, the median reproductive periodicity remained unchanged when omitting PIT tags, but the mean was slightly reduced to 3.2 yr, whereas, for loggerhead turtles, it resulted in underestimation of the median (2.0 yr) and the mean (2.8 yr; Fig. 2, Table S1). While PIT tags captured intervals of up to 12 yr, rarely were intervals of > 5 yr captured using flipper tags only at this study site (Fig. 2).

3.1.3. Reproductive longevity

Median and mean reproductive longevity were 6.0 and 8.0 yr for green turtles and 4.0 and 5.5 yr for loggerhead turtles, with females breeding for up to 24 and 25 yr respectively at Alagadi Beach (Fig. 2, Table S1). Estimates of reproductive longevity were significantly improved by PIT tags for green turtles ($F_{1,266} = 15.76$, $P < 0.0001$) but not for loggerhead turtles ($F_{1,182} = 1.25$, $P = 0.265$). Without PIT tags, the median and mean reproductive longevity were reduced by 2.0 and 2.7 yr respectively for green turtles (Table S1). For loggerhead turtles, the median reproductive longevity remained unchanged, whereas the mean was reduced by 1.0 yr without PIT tags (Table S1). While females remained identifiable for up to 25 yr after first nesting at this study site using both flipper and PIT tags, rarely were females of either species still identifiable after 10 yr of breeding using flipper tags only (Fig. 2).

3.1.4. Annual survival

Model results are summarised in Tables S2–5. Without PIT tags, some females would have been misidentified as up to six different females, therefore underestimating annual survival at Alagadi Beach (Table S6). Mean annual survival was 0.48 for the first year after initial capture and 0.84 thereafter for green turtles, instead of 0.66 and 0.97 respectively estimated using PIT tags. For loggerhead turtles, the difference was not as large: 0.36 instead of 0.44 for the first 'age' class and 0.76 instead of 0.83 for the second 'age' class.

3.2. Tag loss

Tag histories, tag retention and model results are summarised in Tables S7–10. Tag retention is illustrated in Fig. S1.

3.2.1. Loggerhead turtles at Alagadi Beach

Initial daily tag loss probability rapidly decreased before remaining constant 200 and 126 days after initial tagging for plastic and titanium flipper tags respectively for loggerhead turtles at Alagadi Beach (Table 1, Fig. S2). Projections indicated that over half of double-tagged females (58% and 56% respectively) had retained both of their plastic and titanium flipper tags after 1 remigration interval (3 yr), and over four-fifths of single-tagged females (83% and 81% respectively) had retained their only flipper tag (Fig. 3ab). Half of all tagged females had lost their flipper tag(s) and were no longer identifiable after < 3

Table 1

Summary of published studies for which tag loss was estimated using tagging scenarios. Tag loss estimates are as follow: initial value, asymptotic value, cumulative probability of loss after 1 and 5 yr. If two values are presented in the same cell, these corresponds to estimates for the first and second tag.

Species	Year	Tag type	PIT tags	Location	Shedding scenario and assumption	CH	Tag loss estimates				Reference
							Initial	Asymptote	1 yr	5 yr	
Ocean basin and study area											
<i>Dermochelys coriacea</i>											
Atlantic Ocean, French Guiana	1994–2000	Monel 49	√ (1995)	Nesting beach	Decreasing logistic, n-ind.	1293	0.0037 n.a.	0.00028 0.00060	0.24 0.20	0.67 0.67	Rivalan et al. (2005)
<i>Chelonia mydas</i>											
Pacific Ocean, Malaysia	1993–2014	Inconel 681	×	Nesting beach	Decreasing logistic, n-ind.	742	0.0025 0.0180	0.00028 0.00016	0.23 0.42	0.66 0.63	Nishizawa et al. (2017)
Pacific Ocean, Malaysia	1993–2014	Inconel 681	×	Nesting beach	Decreasing logistic, ind. ^a	742	0.0028	0.00025	0.23	0.62	Nishizawa et al. (2017)
Pacific Ocean, Malaysia	1993–2014	Titanium Stockbrand	×	Nesting beach	Decreasing logistic, n-ind.	46	0.0150 0.1100	0.00016 0.00022	0.42 0.78	0.63 0.88	Nishizawa et al. (2017)
Pacific Ocean, Malaysia	1993–2014	Titanium Stockbrand	×	Nesting beach	Decreasing logistic, ind. ^a	46	0.0155	0.00019	0.40	0.66	Nishizawa et al. (2017)
Mediterranean Sea, N Cyprus	1992–2017	Plastic Jumbo and Supertags	×	Nesting beach	Constant, ind.	94	n.a.	0.00022	0.08	0.33 ^b	Present study
Mediterranean Sea, N Cyprus	1992–2017	Plastic Jumbo and Supertags	√ (1997)	Nesting beach	Increasing logistic, ind.	100	0.0004	0.00092	0.16	0.72 ^b	Present study
Mediterranean Sea, N Cyprus	1999–2017	Titanium Stockbrand	×	Nesting beach	Decreasing and increasing logistic, ind.	393	0.0022	0.00013	0.21	0.35 ^b	Present study
Mediterranean Sea, N Cyprus	1999–2017	Titanium Stockbrand	√ (1997)	Nesting beach	Decreasing logistic, ind.	426	0.0038	0.00057	0.25	0.67 ^b	Present study
Mediterranean Sea, N Cyprus	1997–2017	PIT	n.a.	Nesting beach	Decreasing logistic, ind.	317	0.0035	0.00002	0.07	0.10	Present study
<i>Caretta caretta</i>											
Atlantic Ocean, N Carolina	1989–2010	Inconel 681	√ (1995)	By-caught	Constant n-ind. ^a	618	n.a.	0.00033 0.00060	0.11 0.20	0.45 0.67	McNeill et al. (2013)
Atlantic Ocean, N Carolina	1989–2010	Inconel 681	√ (1995)	By-caught	Constant, ind. ^a	618	n.a.	0.00037	0.13	0.49	McNeill et al. (2013)
Atlantic Ocean, N Carolina	1989–2010	Inconel 681	√ First capture	By-caught	Constant and decreasing logistic, n-ind. ^a	585	n.a. 0.0367	0.00037 0.00044	0.13 0.80	0.49 0.94	McNeill et al. (2013)
Atlantic Ocean, N Carolina (USA)	1989–2010	Inconel 681	√ First capture	By-caught	Decreasing logistic, ind. ^a	585	0.0018	0.00034	0.25	0.72	McNeill et al. (2013)
Atlantic Ocean, Georgia (USA)	2008–2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0070 ^{c,d} 0.1160 ^{c,d}	0.00028 ^{c,d} 0.00009 ^{c,d}	~0.18 (0.22 ^{c,d,f})	0.38 ^{c,d}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008–2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0029 ^c 0.0036 ^e	0.00029 ^e 0.00005 ^e	~0.17 (0.21 ^{c,e,f})	0.40 ^{c,e}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008–2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0060 ^d 0.0900 ^d	0.00028 ^d 0.00011 ^d	~0.17 (0.21 ^{d,f,g})	0.37 ^{d,g}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008–2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0040 ^e 0.0034 ^e	0.00029 ^e 0.00006 ^e	~0.17 (0.21 ^{e,f,g})	0.39 ^{e,g}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008–2016	PIT	n.a.	Nesting beach	Constant initial loss, null long-term loss, ind. ^a	186	0.0010 ^d	~0.0000 ^d	0.06	0.06 ^{c,d}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008–2016	PIT	n.a.	Nesting beach	Constant initial loss, null long-term loss, ind. ^a	186	0.0007 ^c	~0.0000 ^c	0.07	0.07 ^{c,e}	Pfaller et al. (2019)
Mediterranean Sea, Italy	2002–2015	Inconel 681	×	Foraging area	Decreasing logistic, ind.	64	0.0058	0.00014	0.15	0.31	Casale et al. (2017)
Mediterranean Sea, N Cyprus	1992–2017	Plastic Jumbo and Supertags	×	Nesting beach	Decreasing logistic, ind.	84	0.0041	0.00008	0.11	0.21 ^b	Present study
Mediterranean Sea, N Cyprus	1992–2017	Plastic Jumbo and Supertags	√ (1997)	Nesting beach	Decreasing logistic, ind.	92	0.0043	0.00041	0.21	0.57 ^b	Present study
Mediterranean Sea, N Cyprus	1999–2017	Titanium Stockbrand	×	Nesting beach	Decreasing logistic, ind.	177	0.0018	0.00022	0.11	0.36 ^b	Present study
Mediterranean Sea, N Cyprus	1999–2017	Titanium Stockbrand	√ (1997)	Nesting beach	Decreasing logistic, ind.	94	0.0019	0.00050	0.19	0.61 ^b	Present study
Mediterranean Sea, N Cyprus	1997–2017	PIT	n.a.	Nesting beach	Decreasing logistic, ind.	155	0.0066	0.00009	0.16	0.26	Present study

PIT tags: passive integrated transponder tags; CH: number of capture histories; n.a.: not applicable; ind./n-ind: (non)-independence of tag loss between tags. Presence (√) or absence (×) of PIT tags, with start date.

Values in italic were not provided in the original article but were calculated here.

^a Model resulting in better fit to the data.

^b Flipper tag loss estimates calculated for the “no PIT tag” dataset in this study were included in this table to highlight the extent to which flipper tag loss is underestimated when based on one identification method only.

^c Tag loss confirmed using genetic markers.

^d Maximum likelihood parameter estimates.

^e Bayesian parameter estimates.

^f Estimate after 2 years.

^g Tag loss confirmed using PIT tags.

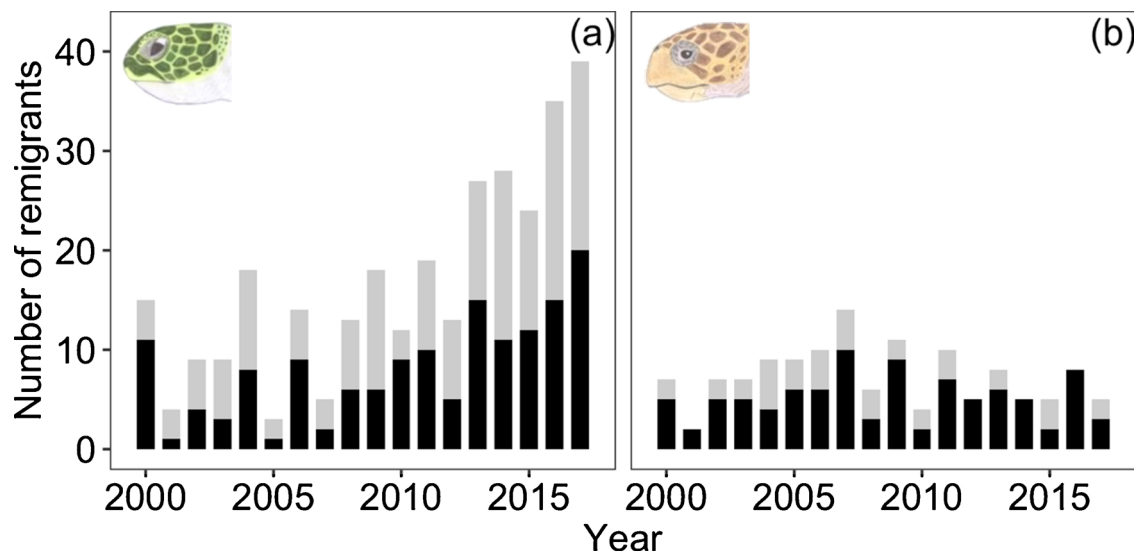


Fig. 1. Misidentification of remigrants. Time series of the number of remigrant green (a) and loggerhead (b) turtles that left Alagadi beach with both flipper and PIT tags and were subsequently identified by PIT tag(s) alone (grey bars) and by PIT and flipper tags or flipper tags alone (black bars). The grey bars show the number of remigrant females that would have been misidentified as neophyte females without the use of PIT tags. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

remigration intervals (~ 8 yr) for plastic flipper tags, and after just over 2 remigration intervals (~ 6.5 yr) for titanium flipper tags (Fig. 3ab). For both flipper tag types, daily tag loss probability was underestimated when PIT tag readings were omitted (Fig. S2), resulting in the overestimation of the proportion of females (single- or double-tagged) having retained their tag(s) over the course of the study period at this study site (Fig. 3ab).

Although initial daily tag loss probability was higher for PIT tags than for both flipper tag types, daily tag loss probability was lower for PIT tags once it plateaued for loggerhead turtles at Alagadi Beach (Fig. S3). Tag retention was higher for PIT tags than for both flipper tag types. After 1 remigration interval, 79% of double-tagged females had retained both PIT tags, and 95% of single-tagged females had retained their only PIT tag (Fig. 3c). Half of double-tagged females still retained both PIT tags 17 yr after initial tagging, and two-thirds of single-tagged females still retained their PIT tag 22 yr after initial tagging (Fig. 3c).

3.2.2. Green turtles at Alagadi Beach

Initial daily tag loss probability increased before remaining stable 9 yr after initial tagging for plastic flipper tags, whereas it rapidly decreased before remaining constant 192 days after initial tagging for titanium flipper tags for green turtles at Alagadi Beach (Table 1, Fig. S4). Whereas daily tag loss probability was higher in green turtles than in loggerhead turtles at this study site for plastic flipper tags, it plateaued around similar values for titanium flipper tags.

Projections indicated that half of double-tagged females (50% for both flipper tag types) had retained both of their plastic and titanium flipper tags after 1 remigration interval (3 yr), and three-quarters of single-tagged females (76% and 75% respectively) had retained their only flipper tag at Alagadi Beach (Fig. 3de). Half of all tagged females had lost their flipper tag(s) and were no longer identifiable after < 2 remigration intervals (~ 5 yr) for plastic flipper tags, and after 2 remigration intervals (6 yr) for titanium flipper tags (Fig. 3de). Similarly to loggerhead turtles at this study site, the omission of PIT tags resulted in the underestimation of daily tag loss probability for green turtles and, therefore, the overestimation of the proportion of females having retained their flipper tags over the course of the study period, irrespective of tag type (Fig. 3de).

Although initial daily tag loss probability for PIT tags and titanium flipper tags were similar for green turtles at Alagadi Beach, daily tag loss probability was lower for PIT tags once it stabilised (Fig. S3). Tag

retention 3 yr after initial tagging was much higher for PIT tags than for both flipper tag types, and was higher in green turtles than in loggerhead turtles at this study site. After 1 remigration interval, 91% of double-tagged females had retained both PIT tags, and 99% of single-tagged females had retained their only PIT tag (Fig. 3f). Only 5% of all tagged females were no longer identifiable using PIT tags 22 yr after initial tagging (Fig. 3f).

3.2.3. All studies

Table 1 compiles all previously published studies which estimate tag loss using continuous functions, including this study. Estimates for both flipper tag types at Alagadi Beach for green turtles were higher than those calculated in Malaysia for Inconel and titanium flipper tags. For loggerhead turtles, estimates at this study site were within the range of those previously reported for Inconel flipper tags in Italy and the USA. In contrast, the asymptotic values and the cumulative tag loss probabilities after 5 yr for PIT tags for the two species at Alagadi Beach were far lower than those corrected by the presence of PIT tags for all flipper tag types. Without accounting for non-independence of tag loss, on average, over a fifth (22%) of tagged individuals will have lost at least one flipper tag after 1 yr and over half (58%) of tagged individuals after 5 yr across green and loggerhead turtle studies. In contrast, on average, 10% of tagged individuals will have lost at least one PIT tag after 1 yr and 14% after 5 yr.

3.3. Combination of annual survival and tag loss

Half of loggerhead turtles tagged at Alagadi Beach will still be identifiable with at least one tag upon recapture 2–3 yr after initial tagging using titanium flipper tags, and 3–4 yr after initial tagging using PIT tags (Fig. S5a). On average, irrespective of tag type, only 50% of loggerhead turtles will be identifiable upon recapture after 1 remigration interval only. In contrast, 50% of green turtles tagged at Alagadi Beach will still be identifiable using at least one tag upon recapture 3–5 yr after initial tagging using titanium flipper tags, and 16–21 yr after initial tagging using PIT tags (Fig. S5b).

4. Discussion

Here, we show the importance of PIT tags for the long-term population monitoring of two different sea turtle species. Combining flipper

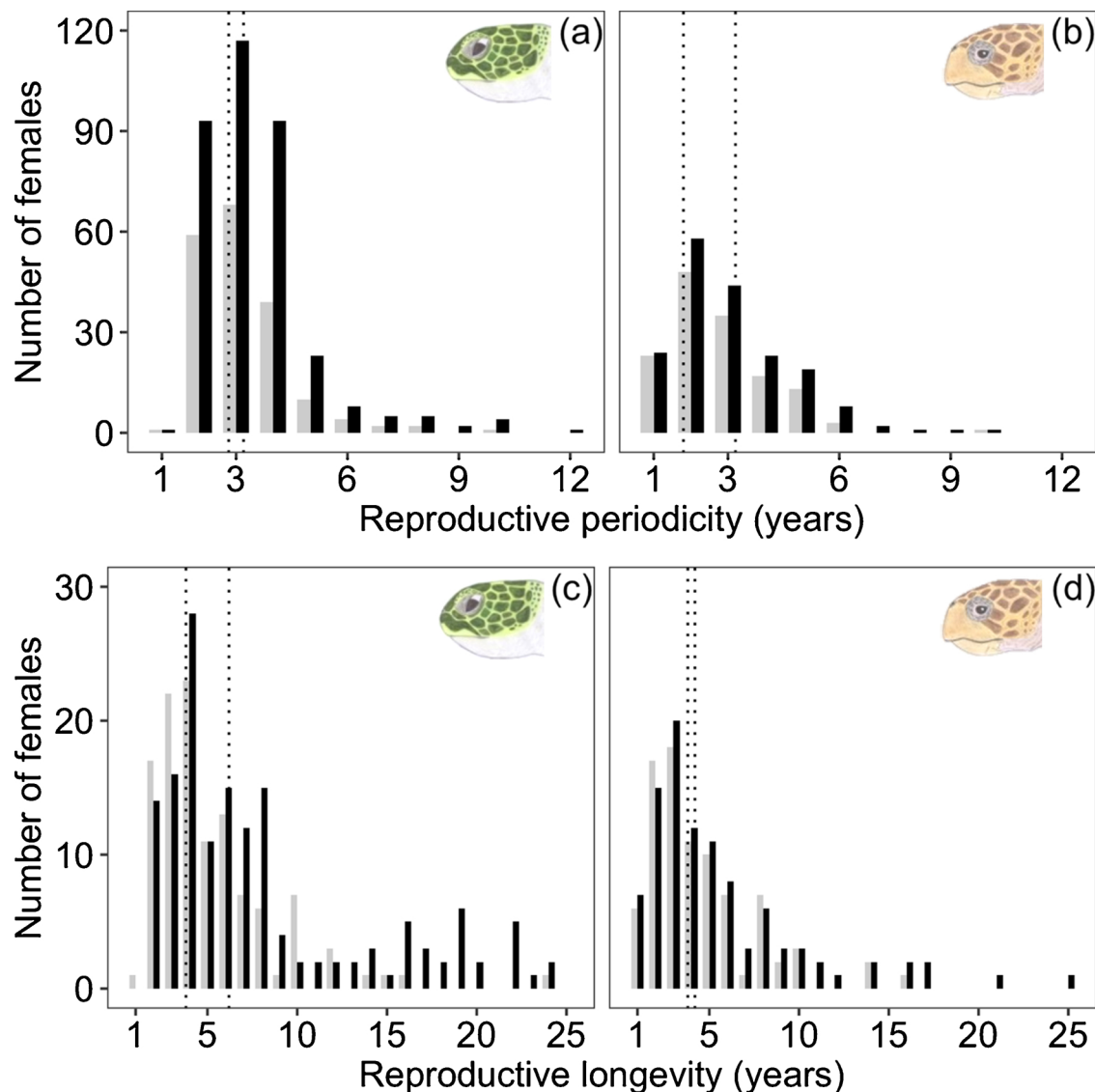


Fig. 2. Accuracy of reproductive parameter estimates. Frequency distribution of reproductive periodicity (a–b) and longevity (c–d) for green (a, c) and loggerhead (b, d) turtles, as a function of female identification method. Identification based on flipper and PIT tag readings is shown in black and based on flipper tags only is shown in grey. Dotted lines are median values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and PIT tagging at this study site allowed for greater female identification and thus more accurate estimates of tag loss, life-history traits and population parameters, in particular for green turtles.

4.1. Flipper tag loss

Variation in flipper tag loss can be observed across species, life stages, sex, tag types and geographical locations (e.g. Bradshaw et al., 2000; Chambers et al., 2015; Hastings et al., 2018; Oosthuizen et al., 2010). For sea turtles, a pattern appears to be emerging, whereby flipper tag loss is best described by a decreasing logistic curve with a lower asymptote (Table 1). While flipper tag loss was found to increase with age due to individual growth in elephant seals for example (Oosthuizen et al., 2010), this was not observed in sea turtles, potentially because estimates were mainly from adults, which have negligible growth (Omeier et al., 2017, 2018). The increase in tag loss found for plastic flipper tags in green turtles here is likely due to the writing on the tag fading rather than loss per se. In contrast, the constant tag loss for loggerhead turtles in McNeill et al. (2013) likely resulted from the lack of short-term recaptures, preventing the detection of high initial loss. Additionally, while tag loss may be influenced by interspecific

behavioural differences and habitat effects, as observed in fur seals (Bradshaw et al., 2000) and previously described in sea turtles (Limpus, 1992), this was not apparent from Table 1, likely due to small sample size. Initial and asymptotic flipper tag loss across sea turtle studies remained within the same order of magnitude (Table 1), although care should be taken when drawing conclusions from such comparisons because of the inherent differences among studies (Casale et al., 2017; McNeill et al., 2013; Nishizawa et al., 2017; Pfaller et al., 2019; Rivalan et al., 2005).

Evidence is increasingly suggesting that loss is not independent between flipper tag pairs (Stellar sea lions: Hastings et al., 2018; elephant seals: McMahon and White, 2009; Schwarz et al., 2012; sea turtles: McNeill et al., 2013; Nishizawa et al., 2017; Pfaller et al., 2019; Rivalan et al., 2005). Not accounting for non-independence of tag loss overestimates loss for the first tag and largely underestimates loss for the second tag. Unfortunately, investigating this at Alagadi Beach was not possible because of the large number of researchers with varying tagging abilities involved over the course of the study period, the inclusion of multiple tags per female and the relatively small cohort size. It has, nevertheless, been documented for leatherback (Rivalan et al., 2005), loggerhead (McNeill et al., 2013; Pfaller et al., 2019) and green

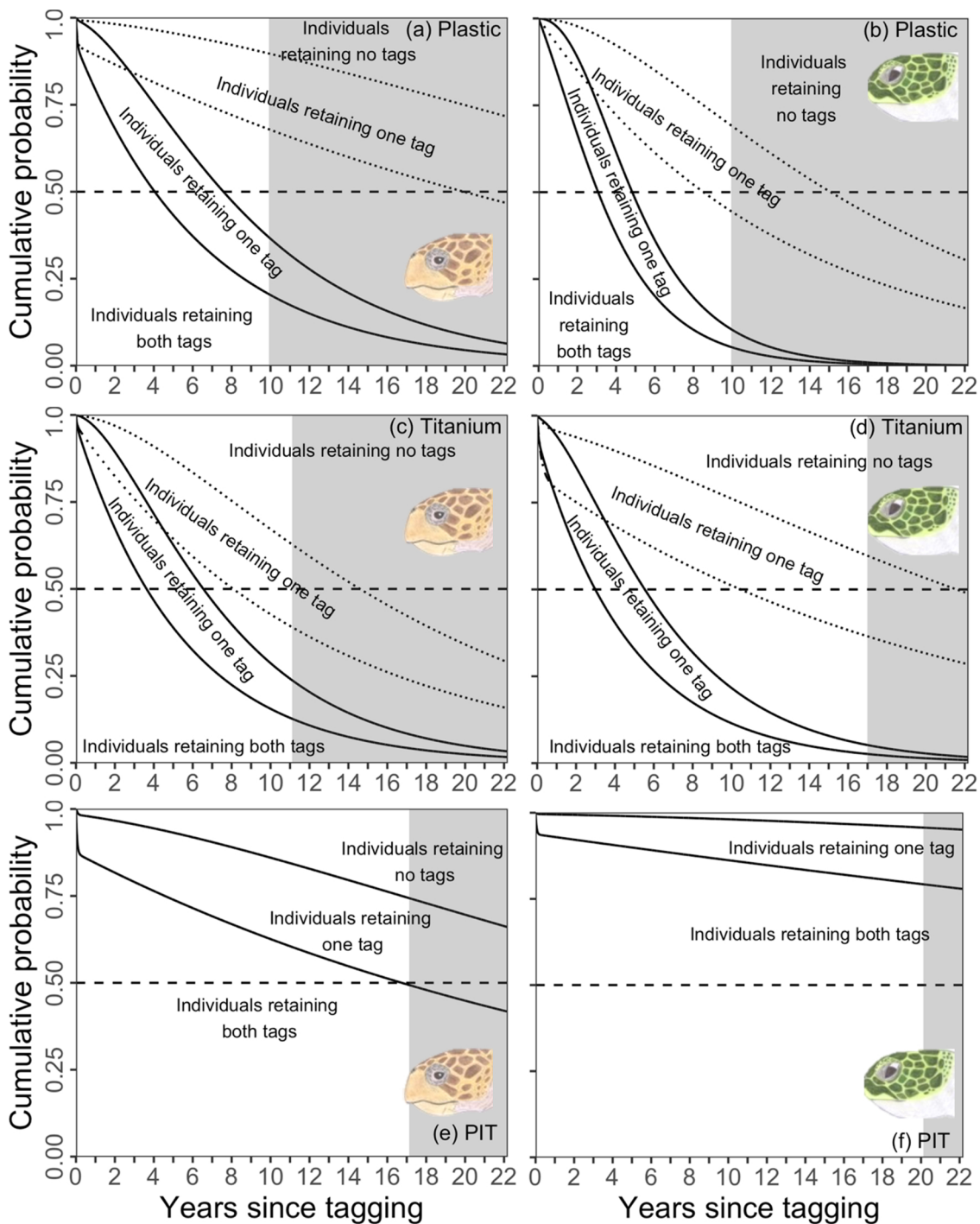


Fig. 3. Tag loss. Estimated cumulative probabilities of individuals retaining two, one or no plastic (a,b), titanium (c,d) and PIT (e,f) tags, predicted by the models with the lowest AICc values, for loggerhead (a,c,e) and green (b,d,f) turtles, as a function of identification method ('PIT tag' dataset: solid curves; 'no PIT tag' dataset: dashed curves). The upper curve of each pair represents the probability that a single-tagged individual retains its tag, whereas the lower curve represents the probability that a double-tagged individual retains at least one tag. The horizontal dashed line represents 50% probability. The grey area shows extrapolation outside the range of the observed data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Nishizawa et al., 2017) turtles. While tissue necrosis was proposed to be the cause for leatherback turtles, it was suggested for the other two species to result from human error, also thought to be the cause of the high initial flipper tag loss in sea turtles (Table 1). Such a tagger effect on tag loss estimates has also been documented in fur seals (Bradshaw et al., 2000) and bluefin tuna (Chambers et al., 2015). Both of these emerging patterns – high initial loss and non-independence of flipper tag loss – suggest that thorough training of the tagging research staff is key to

increasing long-term flipper tag retention across sea turtle studies (McNeill et al., 2013; Pfaller et al., 2019).

4.2. PIT tags

PIT tags have been proposed as permanent tags (Gibbons and Andrews, 2004), despite also being subject to loss (lemon sharks: Feldheim et al., 2002; salmon: Foldvik and Kvingedal, 2018; sea turtles:

McNeill et al., 2013; Pfaller et al., 2019; spiny lobsters: O'Malley, 2008). In this study, for both species, PIT tag loss was found to be best described by a decreasing logistic curve with a lower asymptote, similarly to flipper tags (Table 1). The high initial loss is likely to be the result of faulty application or ejection from the body before wound healing, such as in lemon sharks (Feldheim et al., 2002) and loggerhead turtles (Pfaller et al., 2019). As opposed to fish (e.g. Onders et al., 2004) and moulting species (e.g. Frusher et al., 2009; González-Vicente et al., 2012), physical loss is highly unlikely in sea turtles once the insertion wound has healed (Pfaller et al., 2019). Once improperly applied tags have been shed, detection failure is more likely due to human error, although mechanical failure (i.e. failure in tag transmission or reader failure) and tag migration may also influence PIT tag detection (McNeill et al., 2013; Pfaller et al., 2019; Van Dam and Diez, 1999; Wyneken et al., 2010). Indeed, this can be seen in our data where PIT tags previously thought to be lost are recorded at future recapture events. This phenomenon is bound to be exacerbated in females with multiple PIT tags in the same shoulder at this study site, in particular, if the research staff does not consistently search for the presence of more than one PIT tag. Similarly to flipper tags, short-term within-season PIT tag retention could be improved by providing adequate training to the tagging research staff (McNeill et al., 2013; Pfaller et al., 2019). Pfaller et al. (2019) also suggest the use of a temporary, fast-drying adhesive or patch at the tagging site as a method to reduce the likelihood of PIT tag expulsion before wound healing. While this suggestion could improve long-term PIT tag retention, it should not be seen as an alternative method to reducing high initial loss, but rather should be used in conjunction with thorough training of the tagging research staff. This additional step to the tagging procedure will require further training and will reduce within-season PIT tag loss only if performed correctly.

Nevertheless, PIT tag loss is substantially less than that of flipper tags for sea turtles (Table 1; Pfaller et al., 2019; Groom et al., 2017; Schäuble et al., 2006; Parmenter, 2003, 1993). While PIT tags are also subject to loss, Pfaller et al. (2019) tested the assumption that PIT tags can be used as permanent markers in nesting loggerhead turtles in the USA. Using genetic markers, they showed that flipper tag loss estimates were not substantially biased by PIT tag loss, although this should be tested at other locations. Such high retention has also been observed in salmon (Foldvik and Kvingedal, 2018) and sea lions (Chilvers and MacKenzie, 2010). PIT tag retention is, however, highly variable between species, ranging from 100% in lobsters (Frusher et al., 2009) to as low as 3% in paddlefish (Onders et al., 2004), and is likely to be impacted by species-specific life-history traits and behaviours. The interspecific differences in PIT tag retention at this study site are likely to be due to a combination of different factors. Indeed, the accuracy of PIT tag loss estimates for loggerhead turtles is likely to have been influenced by the lower return rates of this species linked to lower nest site fidelity compared to green turtles (Snape et al., 2018, 2016) thus, reducing sample size, as well as associated length of capture histories (Tables S7–S8, Fig. S1; Omeyer et al., 2019, 2018). Increasing PIT tag reporting rates at a basin-wide scale would improve, and likely reduce, long-term PIT tag loss estimates for loggerhead turtles but is dependent on the availability of PIT tag readers at other monitoring sites.

The rate at which flipper tags and other external tags are being lost in sea turtles, sea lions (Hastings et al., 2018) and spiny lobsters (González-Vicente et al., 2012) for example, is of concern for long-term individual-based population monitoring relying solely on one set of identification markers. The estimation of life-history traits and population parameters may, however, be improved by the use of additional identification methods, such as those making use of natural patterns (e.g. Smout et al., 2011), human-made marks (e.g. branding, Smout et al., 2011) or genetic markers (Pfaller et al., 2019). Here, results highlighted that the typical method used to estimate tag loss by quantifying the loss of one of the two tags in double-tagged individuals largely underestimated tag loss in the absence of PIT tags. As such, tag loss estimates which are not corrected for using at least one other

identification method should be interpreted with caution.

PIT tags allowed for a larger number of individual females to be identified after a longer period of time compared to flipper tags, increasing the accuracy of life-history traits and population parameters, as also demonstrated in sea lions (Chilvers and MacKenzie, 2010; Hastings et al., 2018). As such, the use of PIT tags over flipper tags is far preferable for the long-term individual monitoring of sea turtles (Pfaller et al., 2019), and particularly for green turtles at this study site. Nevertheless, both types of tags are still being used at Alagadi Beach as the presence of flipper tags may encourage researchers to look more thoroughly for PIT tags. Flipper tags should also improve short-term identification of individual females at recapture opportunities elsewhere when PIT tag readers are not available, such as when individuals are bycaught. The difference in the efficacy of PIT tags was likely influenced by interspecific differences in nest site fidelity at this study site (Snape et al., 2018). Indeed, considering the high flipper tag loss observed at Alagadi Beach, the proportion of loggerhead turtle females identified by PIT tags alone, as well as the accuracy of parameter estimates for this species, would likely increase should return rates be higher.

4.3. Annual survival

The 'time-since-marking' modelling approach allowed the decoupling of annual survival estimates for sea turtles. Survival was lower the first year after initial tagging (S1) than in subsequent years (S2) and was likely underestimated as mortality and permanent emigration were confounded. However, there is currently no way to assess permanent emigration given the coverage of CMR programmes in North Cyprus and in the Mediterranean. Although imperfect fidelity to our study site was accounted for by the modelling approach, the misclassification of remigrant nesters having nested undetected elsewhere as neophytes could have further influenced estimates.

While S1 estimates are low, S2 estimates are more likely to reflect true survival of remigrant females. Estimates calculated here highlight yet again the consistently lower estimates for loggerhead turtles globally compared to those of green turtles (Pfaller et al., 2018), which is thought to be the result of interspecific differences in foraging behaviour (Broderick et al., 2006). Apparent annual survival estimates for loggerhead turtles (0.83, CI: 0.78–0.87) are comparable to those of Casale et al. (2015, 2007) for large juveniles and adults in the Mediterranean, to those of adults from subset groups at this study site (Omeyer et al., 2019; Snape et al., 2016), and fall within the predictions for loggerhead turtles globally (0.82, 0.79–0.85; Pfaller et al., 2018). For green turtles, S2 estimates (0.97, CI: 0.95–0.99) are also comparable to those from subset groups at Alagadi Beach (Omeyer et al., 2019) and exceed the global predictions for green turtles (0.88, CI: 0.80–0.93; Pfaller et al., 2018). The difference in PIT tag loss estimates, combined with interspecific differences in annual survival, resulted in large differences in the proportion of individuals still alive and identifiable using PIT tags over time between the two species at this study site. It is, however, likely that the values presented here for loggerhead turtles are an underestimate due to low nest site fidelity (Snape et al., 2018, 2016).

Excluding PIT tags resulted in the underestimation of both S1 and S2 survival estimates for both species. As Wilkinson et al. (2011) highlighted for sea lions using branding marks, the presence of PIT tags allowed for more robust estimates of annual survival to be calculated at this study site. Because life-history data are often not available, sea turtle population assessments have been based on temporal changes in nest counts rather than individual counts. Therefore, providing new or improved estimates of life-history traits and population parameters, such as those calculated here, will be key in generating population models for IUCN Red List assessments for both species in the Mediterranean, which will contribute to the conservation of these threatened species. Indeed, such population models will inform our understanding of population demography and dynamics and can be used to identify

life-history parameters at which to target conservation actions (sea turtles: Casale and Heppell, 2016; Crouse et al., 1987; Crowder et al., 1994; Mazaris et al., 2005; spotted turtles: Enneson and Litzgus, 2008). However, these models are dependent on high-quality, long-term data on all life stages to be accurately parametrised, yet they are necessary to avoid erroneous or detrimental management decisions from being made (Hernández-Camacho et al., 2015; Winker and Sherley, 2019; Yokoi et al., 2017).

4.4. Future recommendations

Life-history data can be acquired using multiple techniques, however, the accuracy of parameter estimates is dependent on the inherent biases of each method as highlighted in this study. Therefore, data used for IUCN Red List assessments should systematically be updated for each species and sub-populations when tag loss estimates become available. While we have shown how PIT tags have improved the accuracy of female identification and life-history and population parameter estimates at this study site, there is still scope in improving these estimates further. Indeed, for example, satellite tracking, which has been used extensively across marine megafauna to provide information on animal behaviour, distribution and movement (e.g. Hart et al., 2019; Heerah et al., 2019; Snape et al., 2018), could be used to refine estimates of clutch frequency at this study site without relying on tag returns. This would be particularly relevant for loggerhead turtles as they have been shown to nest in multiple countries within the same nesting season (Snape et al., 2018, 2016). Tracking devices, however, are costly, have a shorter lifespan compared to PIT tags especially (e.g. $\max < 2$ yr in Hart et al., 2019; and in Stokes et al., 2015), and therefore cannot be used to obtain individual-based long-term life-history data for the species.

While CMR programmes rarely set out to quantify tag loss, less invasive monitoring techniques, such as natural marks (sea turtles: Araujo et al., 2016; whale sharks: McCoy et al., 2018), human-made marks (hawkbill turtles: Richardson et al., 2006) or genetic markers (lemon sharks: Feldheim et al., 2002; sea turtles: Pfaller et al., 2019; giant salamanders: Unger et al., 2012), will be useful in further improving tag loss estimates and determining biological and physical factors driving this loss. Indeed, an improved understanding of flipper and PIT tag loss in sea turtles will help to determine better tagging practices. Although photo-identification and genetic tagging can be used to track individuals through time without being subject to tag loss (bottlenose dolphins: Diaz-Aguirre et al., 2018; short-finned pilot whales: Hill et al., 2018; whale sharks: McCoy et al., 2018), physical tags will currently remain necessary in the wild for sea turtles when individual-specific procedures are required as neither method allow for near real-time individual identification. The CMR programme at Alagadi Beach currently lacks a photo-identification library, however, genetic samples of both species have been collected for almost two decades. Therefore, genetic tagging at this study site could be used to assess the accuracy of our PIT tag loss estimates, as per Pfaller et al. (2019), as well as estimates of life-history parameters (e.g. Shamblin et al., 2017).

5. Conclusion

In conclusion, we showed the importance of PIT tags for long-term individual-based population monitoring for two different sea turtle species. Permanent marks or long-lasting tags, such as PIT tags, are invaluable to provide more accurate estimates of tag loss and life-history parameters. Not accounting for tag loss has large implications for the interpretation of population demography, such as population abundance and recruitment. Thus, estimates where tag loss has not been corrected for should be interpreted with caution and could bias IUCN Red List assessments. Long-term population monitoring programmes should aim to estimate tag loss using continuous functions and multiple identification methods and assess its impact on life-history

traits, in order to provide robust parameter estimates without which population models and stock assessments cannot be derived accurately.

Role of funding source

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Ethics

All applicable international, national and/or institutional guidelines of the care and use of animals were followed. Fieldwork was approved by the University of Exeter Ethics Committee.

Declaration of competing interest

No conflict to declare.

Acknowledgements

We thank the reviewers and the editor, whose input greatly improved the manuscript. We also thank all volunteers who assisted with the data collection of the Marine Turtle Conservation Project from 1992 to 2017, a collaboration between the Marine Turtle Research Group, the North Cyprus Department for Environmental Protection and the North Cyprus Society for the Protection of Turtles. We thank Alexander Saliveros for the illustrations. Fieldwork was supported by the British Associate of Tortoise Keepers, British Chelonia Group, British High Commission in North Cyprus, British Residents Society, Carnegie Trust for the Universities of Scotland, Darwin Initiative, Erwin Warth Foundation, Karşıyaka Turtle Watch, Angela Wadsworth, Glasgow University Court, Kuzey Kıbrıs Turkcell, MEDASSET UK, and Natural Environment Research Council (NE/J012319/1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108248>.

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