



## Cohort and tag-site-specific tag-loss rates in mark–recapture studies: A southern elephant seal cautionary case

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### ABSTRACT

Marker-loss is a common feature of mark–recapture studies and important as it may bias parameter estimation. A slight alteration in tag-site of double tagged southern elephant seals (*Mirounga leonina*), marked at Marion Island from 1983 to 2005 in an ongoing mark–recapture program, had important consequences for tag-loss. We calculated age-specific tag-retention rates and cumulative tag-retention probabilities using a maximum likelihood model selection approach in the software application TAG\_LOSS 3.2.0. Under the tag-loss independence assumption, double tag-loss of inner interdigital webbing tags (IIT; 17 cohorts) remained below 1% in the first 5 yr and increased monotonically as seals aged, with higher tag-loss in males. Lifetime cumulative IIT tag-loss was 11.9% for females and 18.4% for males, and equivalent for all cohorts. Changing the tag-site to the outer interdigital webbing (OIT; 6 cohorts) resulted in increased and cohort-dependent tag-loss, although the variation (mean  $\pm$  95% CI) in cumulative tag-loss probabilities never exceeded 5.3% between cohorts at similar age. Although different studies may homogenize techniques, we advocate the importance of data set-specific assessment of tag-loss rates to ensure greatest confidence in population parameters obtained from mark–recapture experiments. Permanent marking should be implemented where feasible.

Key words: cohort heterogeneity, double tagging, mark–resight, marker-loss, *Mirounga leonina*, Marion Island, phocids, tag shedding, tag placement.

Mark–recapture studies are frequently used by ecologists and wildlife managers to estimate demographic parameters of wildlife populations. These parameters provide insight into population processes and allow implementation of appropriate management policies. Mark–recapture data analyses have largely been based on Cormack–Jolly–Seber (CJS) parameterizations (Lebreton *et al.* 1992). However, violations of the assumptions of the CJS model can severely bias parameter estimates (Arnason and Mills 1981, McDonald *et al.* 2003). Fundamental assumptions are that marks do not affect future survival, are not lost or missed during resights (Seber 1982), and are correctly identified (Stevick *et al.* 2001). However, these assumptions are potentially violated by many marking techniques and may be inherent to all long-term tagging regimes. Marker-loss and marker-induced mortality result in population size overestimates through negatively biased survival rates, since individuals that have lost their marks cannot be identified anymore and appear “dead” to the observer (Arnason and Mills 1981, Pollock *et al.* 1990, McDonald *et al.* 2003). Additionally, if recaptured, such individuals appear to be immigrants, biasing recruitment rates upward (Cowen and Schwarz 2006). Time or group-dependent marker-loss may additionally result in nonuniform biases in survival estimates through heterogeneous recapture probabilities among groups or over time (Pollock *et al.* 2001). Therefore, knowledge of violations of fundamental assumptions such as marker-loss is crucial to obtain robust information of life-history data that allows informed decision making (McMahon and White 2009).

The extensive use of nonpermanent markers to identify individuals in mark–recapture studies for investigations of life-history, demographics, dispersal, growth, and behavior makes estimation of marker-loss rates widely applicable to numerous ecological research disciplines and wildlife authorities across a wide range of species. An increasing number of studies incorporate quantitative estimates of marker-loss rates in conjunction with analytical advances in this field (Barrowman and Myers 1996, Conn *et al.* 2004, Cowen and Schwarz 2006). These include tag-loss in invertebrates (Kneib and Huggler 2001), terrestrial, and marine vertebrates, (Stobo and Horne 1994, Diefenbach and Alt 1998, Adam and Kirkwood 2001, Casale *et al.* 2007) and neckband failure (Johnson *et al.* 1995) and band loss in birds (Spendelov *et al.* 1994). Marker-loss is usually estimated by double marking individuals and approximating marker-loss by following subjects through time and noting whether one or two marks are retained. In the absence of a permanent mark (in addition to the two temporary markers), marker-loss independence is assumed, where the probability of losing the second marker is independent of the probability of losing the first marker. This assumption is difficult to test because permanent marking is not easily accomplished. However, in cases where permanent marks facilitated assessment of the assumption, assuming independence has been shown to underestimate tag-loss (*e.g.*, Diefenbach and Alt 1998, Bradshaw *et al.* 2000, McMahon and White 2009). However, aside from the potential errors associated with the independence assumption, researchers should attempt to quantify inconsistent marker-loss over time or variation therein between groups of marked animals (Spendelov *et al.* 1994). Failure to account for marker-loss differences between juveniles and adults, for example, may lead to erroneous conclusions about the importance of juvenile and adult survival as population growth determinants. Similarly, a false indication of processes such as density-dependent survival may be indicated when marker-loss differs according to the population density, physical environment, or tagger proficiency at specific colonies or study sites.

Many pinniped species are ideal mark-recapture study subjects due to their ubiquitous terrestrial phases, generally high site fidelity and thus their temporal and spatial accessibility to researchers. Individuals are usually marked by double tagging in the connective tissue of the interdigital webbing of each hind flipper in true seals (Phocidae) or in the trailing edge of both front flippers in fur seals and sea lions (Otariidae) (Erickson *et al.* 1993). However, in contrast to permanent markings such as branding or tattoos, tag-loss can be substantial (*e.g.*, Stobo and Horne 1994, McMahon and White 2009) and if left uncorrected may severely bias survival estimates. On sub-Antarctic Marion Island (46°54'S, 37°45'E), southern elephant seals *Mirounga leonina* L. have been subject to a 25-yr (1983–2008) ongoing mark-recapture study. The mark-recapture program forms the foundation of investigations into life-history, demography, dispersal, and philopatry of southern elephant seals at Marion Island (*e.g.*, Bester 1989; Pistorius *et al.* 1999, 2004; Kirkman *et al.* 2003, 2004; McMahon *et al.* 2005). Two previous studies have estimated tag-loss for this population, to incorporate tag-loss adjustments into demographic data. Wilkinson and Bester (1997) used a ratio method to calculate tag-loss over the period 1983–1990 and Pistorius *et al.* (2000) improved on this method, estimating linear tag-loss (1983–1993) based on the time at liberty of tagged seals in a maximum likelihood framework. Age- and sex-specific tag-loss rates from Pistorius *et al.* (2000) were subsequently used to correct mark-recapture survival estimates of southern elephant seals at Marion Island.

The physical placement of markers can be central to the accuracy of estimates gained from mark-recapture experiments. Incorrect tag placement can result in increased mortality (Kneib and Huggler 2001) or reduced apparent survival as a consequence of increased tag-loss. Tag placement has nonetheless received limited attention in studies beyond fisheries management (*e.g.*, Brennan *et al.* 2007). Limpus (1992), however, evaluated tag placement in turtles, where tag-loss was higher in the more distal tagging positions on the front flipper. The hind flipper tag-site used to mark elephant seals at Marion Island changed in 2000 from the inner interdigital webbing (between digits two and three or three and four; 1983–1999) to the upper, outer interdigital webbing of the hind flippers (between digits one and two; 2000–2008). The tag-site adjustment aimed at improving tag visibility for resighting, because the tags placed in the inner interdigital webbing are often obscured by the flipper digits when animals are hauled out on land. The effect of tag-site on tag-loss has not been quantified here or directly for other pinnipeds and such an adjustment may have important consequences for demographic analyses.

We estimate and compare tag-loss rates for 17 cohorts of southern elephant seals double tagged in the inner interdigital webbing (inner interdigital tags: IIT), and six cohorts double tagged in the upper, outer interdigital webbing (outer interdigital tags: OIT). Variation in tag-loss due to seal age and sex, tagging protocol (tag-site, *i.e.*, IIT and OIT) and tagging proficiency by different personnel (resulting in cohort-specific tag-loss rates) are considered.

## METHODS

### *Mark-Resight Framework*

Data from cohorts of southern elephant seals born on Marion Island from 1983 to 2005 and resighted up to April 2008 were used. During each breeding season, virtually all recently weaned southern elephant seal pups born on Marion Island

were sexed and double tagged in the interdigital webbing of the hind flippers with identical, uniquely numbered, color-coded plastic Dal 008 Jumbotags (Dalton Supplies Ltd., Henley-on-Thames, U.K.). These two-piece self-piercing tags are applied with an applicator, and have favorable retention rates as compared to other tag types (Testa and Rothery 1992). The male component of all tags was positioned on the outer surface of the flipper (*i.e.*, the point of this component protrudes from the inner surface). From 1983 to 1999 tags were applied to the center of either of the two inner sections of interdigital webbing of the hind flipper (webbing between digits two and three or three and four; IIT). From 2000 to 2005, tags were applied to the center of the upper interdigital webbing of the hind flipper (between the first and second digit; OIT). At tagging, one-third of the tag extended past the trailing edge of the interdigital webbing. During all years tags were applied by two dedicated field personnel, all of whom were trained by one of the authors Marthán N. Bester (MNB) (except from 1986 to 1988 when up to six pairs of trained field personnel tagged pups). Further details regarding the tagging procedure appear in Wilkinson and Bester (1997) and de Bruyn *et al.* (2008).

During the entire study period (1983–2008), the resighting effort remained constant and included all beaches along a 51.9 km coastline where southern elephant seals can haul out, except during the early period (1983–1988) when no resights were made during winter (mid-April–mid-August). During the molting and winter periods (mid-November–mid-August), all beaches were searched for tagged seals every 10 d, but in the breeding season (mid-August–mid-November) this was done on a 7-d cycle to allow for increased seal numbers and harem density. For every tagged seal that was resighted, the date and locality of the sighting, tag color combination and three-digit number, number of tags remaining (one or two), and the sex of the seal (if identified) were recorded. We assume similar and accurate resight rates of single and double tags owing to the high and constant resight effort by trained personnel on Marion Island, where both flippers of each animal were always inspected for the presence of tags. This was done to prevent different reporting rates for single or double tags that may bias estimates (Adam and Kirkwood 2001). The haul-out pattern of elephant seals (Kirkman *et al.* 2003, 2004) allowed for confirmation of recorded tag data with subsequent resights, often several times over a season. Shed tags were not replaced.

#### *Estimation of Tag-Loss*

We estimated tag-loss using a maximum likelihood method for individually identifiable mark–resight study subjects in the software application TAG\_LOSS (Version 3.2.0; [http://www.ese.u-psud.fr/epc/conservation/Tag\\_Loss/Tag\\_Loss.html](http://www.ese.u-psud.fr/epc/conservation/Tag_Loss/Tag_Loss.html)) as presented by Rivalan *et al.* (2005). This program provides quasi-continuous tag-loss probabilities and incorporates assessment of different trends in tag-loss rates over time. Quasi-continuous tag-loss probabilities based on exact time at liberty remove bias associated with pooled observations (Xiao 1996, Diefenbach and Alt 1998). Model functions described the time-dependent daily probability of tag-loss  $P(t)$  (see Rivalan *et al.* 2005). Model selection was based on Akaike's Information Criterion (AIC), where the model with the smallest AIC value provided the most parsimonious fit (Burnham and Anderson 1998). AIC weights ( $w_i$ ) provided the relative support for each model. Pups initially tagged with only one tag, seals of unknown sex and pups double tagged, but never resighted, were excluded from analyses. Tagged seals that were not resighted most likely died during their first pelagic foraging trip

(60%–65% first year mortality; McMahon *et al.* 1999, Pistorius and Bester 2002) or emigrated from the study area (Bester 1989; MNB, unpublished data). Double tag-loss within the first year is suggested to be minimal (see Results and Discussion).

The annual haul-out cycle of elephant seals, combined with the continuous high resight effort in this study permits calculation of reliable estimates of tag time at liberty, in contrast to studies where few resights are possible (*e.g.*, leatherback sea turtles, *Dermochelys coriacea*, Rivalan *et al.* (2005) and loggerhead sea turtles, *Caretta caretta*, Casale *et al.* (2007)). We constructed individual capture histories for all individuals tagged on day 0 (at weaning), and subsequently resighted ( $n = 7,849$ , cohort range  $n = 228$ –479). Three sets of capture histories were considered, following Rivalan *et al.* (2005): (1) The individual was resighted with two tags intact for the duration of its presence in the study, to estimate the minimum number of days without tag-loss ( $N_{22}$ ;  $n = 6,786$ ). (2) We initially observed the individual with two remaining tags ( $N_{22}$ ), but subsequently with only one tag intact ( $N_{21}$ ). This capture history calculates both the minimum number of days without tag-loss ( $N_{22}$ ) and the interval length (mean = 212 d) during which one tag was lost ( $N_{21}$ ;  $n = 952$ ). (3) Subsequent to double tagging, we only observed the individual with one tag intact for the duration of its presence in the study ( $N_{21}$ ;  $n = 111$ ). Because permanent marks were absent, we could not reliably identify animals that had lost both tags ( $N_{20}$  or  $N_{10}$ ; known  $n = 10$ ), and therefore did not consider such cases. This necessitated the assumption of tag-loss independence, where the probability of losing one tag did not affect the probability of losing the second tag.

We tested three different trends in daily tag-loss over time: constant rate, monotonic increase/decrease, and a two-step function (*e.g.*, rapid initial tag-loss, followed by a decreased continuous loss pattern and then a further increase or decrease with varying slope; this function can adjust to many different daily tag-loss rate modalities over time). Tag-loss patterns were assessed separately for each sex and cohort and also for cohorts and sexes pooled over time. We used the best fitting trend to test for a sex, cohort, and tag-site effect on tag-loss. For the sex and cohort variables, we compared the AIC model fit for separate sex/cohort models, compared to a single model grouping sexes/cohorts. Constructing models that separated IIT and OIT and subsequently evaluating model fit, assessed tag-site variability. TAG\_LOSS 3.2.0 converted parameter estimates from the best model to daily tag-loss probabilities, age-specific tag-loss probabilities and cumulative tag-loss rates (Rivalan *et al.* 2005). Age-specific tag-loss is the conditional probability that a tag is lost during one year among the tags that were still present at the beginning of that year. Standard errors of parameters were calculated by the square-root of the inverse of the Fisher information matrix (Abt and Welch 1998). The proportion of animals retaining at least one tag is presented as identification probabilities ( $1 - \text{cumulative tag-loss probability}$ ). Identification probabilities, therefore, represent the proportion of individuals still identifiable (retaining either one or two tags) for each age group.

## RESULTS

Tag-loss was best described by a monotonic increase of tag-loss rate with time for both male and female groups ( $AICw_{i(\text{monotonic})} = 1$ ) (Table 1). Although several cohorts showed support for the constant model or two-step function, few of these cohorts showed substantial support against the monotonic increasing model. Males from cohort 17 deviated most from the monotonic trend ( $\Delta AIC = 17.01$ ), while

Table 1. Model selection results for tests of southern elephant seal tag-loss trend over time, at Marion Island. Akaike information criterion (AIC) values in boldface type refer to the most parsimonious models.

Cohort	Tag-site	Males						Females		
		Model of change of tag-loss rate			Model of change of tag-loss rate			Constant	Direction	
		Constant	Monotonic	Direction	2 steps	Monotonic	Direction		2 steps	
1	IIT	119.52	112.51	+	116.50	169.18	171.85	+	173.17	
2	IIT	120.48	117.53	+	121.41	200.60	200.60	+	205.12	
3	IIT	278.71	273.20	+	277.20	300.49	300.49	+	295.10	
4	IIT	170.28	173.42	-	177.44	257.17	257.17	+	258.50	
5	IIT	227.20	224.72	+	228.70	221.33	221.33	+	219.98	
6	IIT	245.02	237.28	+	240.87	258.25	258.25	+	259.28	
7	IIT	258.11	257.76	+	261.74	247.33	247.33	+	255.26	
8	IIT	239.07	234.04	+	238.04	229.30	229.30	+	234.16	
9	IIT	214.48	213.38	+	217.38	327.08	327.08	+	326.64	
10	IIT	222.12	220.40	-	219.05 <sup>a</sup>	400.89	400.89	=	396.93 <sup>b</sup>	
11	IIT	248.59	248.45	+	252.38	288.61	288.61	+	284.12	
12	IIT	134.55	134.05	+	138.05	277.29	277.29	+	280.93	
13	IIT	153.06	155.56	+	156.82	177.04	177.04	+	179.17	

14	IIT	162.68	158.19	+	156.42 <sup>b</sup>	378.33	367.55	+	371.54
15	IIT	219.67	199.89	+	203.88	215.89	205.05	+	209.05
16	IIT	175.11	178.12	+	181.36	318.64	319.25	+	323.20
17	IIT	167.68	171.69	=	154.68 <sup>a</sup>	210.59	205.46	-	202.98 <sup>c</sup>
18	OIT	224.71	199.69	+	203.69	243.94	218.45	+	221.40
19	OIT	189.52	180.91	+	184.91	305.19	289.70	+	293.70
20	OIT	268.39	265.37	+	269.37	324.18	325.70	+	328.43
21	OIT	345.78	339.70	+	343.70	483.32	486.05	+	490.04
22	OIT	89.64	90.72	+	93.55	167.01	169.35	+	171.97
23	OIT	378.02	378.56	-	381.46	393.78	397.78	-	401.28
Total AIC		4,852.39	4,765.10		4,818.59	6,398.92	6,319.70		6,381.97
$\Delta$ AIC		87.25	0.00		53.45	79.22	0.00		62.27
AIC $w_i$		0.00	1.00		0.00	0.00	1.00		0.00

<sup>a</sup>High rate just after tagging and it becomes null after 1,500 d.

<sup>b</sup>High rate just after tagging.

<sup>c</sup>Rate becomes null after 2,000 d.

Table 2. Model performance based on AIC for cohort-dependent and independent tag-loss rates in southern elephant seals at Marion Island.

Cohort grouping	Males	$\Delta$ AIC	AIC $w_i$
1, ..., 23	4,765.14	25.59	0.00
1-17, 18, ..., 23	4,739.55	0.00	1.00
1, ..., 17, 18-23	4,860.33	120.78	0.00
1-17, 18-23	4,834.75	95.19	0.00
1-23	4,910.24	170.68	0.00
Cohort grouping	Females	$\Delta$ AIC	AIC $w_i$
1, ..., 23	6,319.70	0.00	0.93
1-17, 18, ..., 23	6,324.90	5.19	0.07
1, ..., 17, 18-23	6,421.61	101.91	0.00
1-17, 18-23	6,426.81	107.10	0.00
1-23	6,511.57	191.87	0.00
Cohort grouping	M + F	$\Delta$ AIC	AIC $w_i$
1, ..., 23	11,084.85	12.06	0.00
1-17, 18, ..., 23	11,072.78	0.00	1.00
1, ..., 17, 18-23	11,274.87	202.09	0.00
1-17, 18-23	11,262.81	190.03	0.00
1-23	11,431.83	359.05	0.00

only one other cohort (cohort 10 females) with a  $\Delta$ AIC value  $>4$  ( $\Delta$ AIC = 7.95) indicated some support for an alternate model. Both these groups received support for the two-step function model, indicating initial high tag-loss soon after tagging, but leveling off over time.

Tag-site had a significant effect on tag-loss rates, with cohort and sex differences in tag-loss also dependent on the tag-site. Tag-loss did not differ between cohorts with IIT, and the model with a general estimate calculated over all 17 cohorts received the most AIC support (Table 2). In contrast, strong support for variable tag-loss rates between cohorts was found for OIT (cohorts grouped,  $\Delta$ AIC<sub>18-23</sub> = 190.03) (Fig. 1). Cohort-dependent OIT tag-loss was not unexpected, as field observations indicated that cohort 23 showed uncharacteristically high initial tag-loss associated with suboptimal (shallow: tag extends more than one-third past the trailing edge of the flipper webbing) tagging. In addition, we suspected that cohorts 19 and 20 might show different tag-loss rates that could lead to intercohort variation as these tags were sometimes tagged too deep (tag not extending by one-third past the trailing edge of the flipper webbing). We subsequently removed cohorts 19, 20, and 23 from the OIT model, to test whether cohort variability existed among the remaining three cohorts. Cohort-specific variability persisted (cohorts grouped  $\Delta$ AIC<sub>18,21,22</sub> = 59.34, cohorts separate  $\Delta$ AIC = 0), and we continued analyses considering all OIT cohorts separately. Separate sex models, with increased tag-loss in males, improved model fit for IIT (Table 3). Conversely, a single model for males and females combined was sufficient to describe tag-loss for OIT cohorts.

Age-specific tag-loss rates (Fig. 1) were derived for cohorts 1-17 (IIT; grouped), and cohorts 18-23 (OIT; separately). IIT showed low initial tag-loss rates that increased monotonically over time. Age-specific tag-loss of adult females followed a slight convex curve, with tag-loss increasing at a low rate for adult females above age

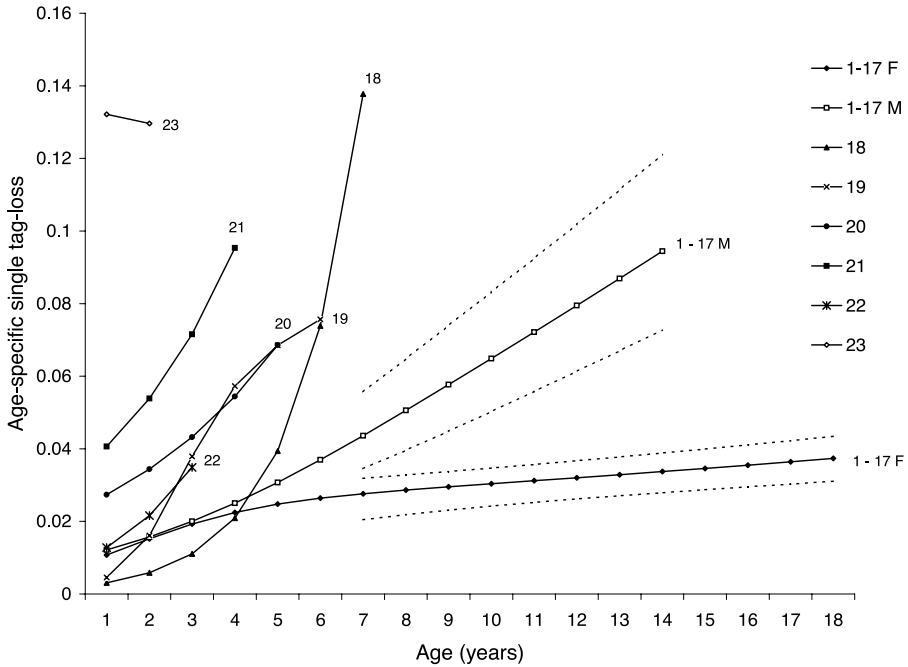


Figure 1. Maximum likelihood functions for age-specific single tag-loss rates over time. Inner interdigital tags (IIT; cohorts 1–17) are represented by two general functions for males and females. Standard errors (tag-loss probability  $\pm 2$  SE) are presented for IIT tags above age 7.

5. Cumulative IIT tag-loss rates (double tag-loss; Fig. 2) were less than 1% up to age 5 for both sexes. Tag-loss in males increased more as they aged when compared with females, although older age classes are represented by fewer males than females (e.g., 13 males and 106 females above age 12), leading to greater confidence in female retention rates to this age. Near the maximum life expectancy, close to 81% of males, and 88% of females were expected to remain identifiable under the tag-loss independence assumption. Age-specific tag-loss rates for OIT were generally higher than those of IIT and predominantly increased over time, apart from cohort 23 in which tag-loss declined after high initial loss. Age-specific cumulative tag-loss rates increased from cohort 18 to 23 (Fig. 2), with the exception of cohort 22 (cumulative tag-loss cohort 18 < 19 < 22 < 20 < 21 < 23), i.e., apart from cohort 22, tag-loss increased as resight time decreased. The variation in cumulative tag-loss rates

Table 3. Model selection for a sex-effect, dependent on tag-site, for southern elephant seal tag-loss from Marion Island. Males in cohorts 1–17 showed higher tag-loss rates than females.

Cohorts	Sexes separated	Sexes grouped	$\Delta$ AIC	AIC <sub>wj</sub>
1–17	7,722.49	7,730.82	8.333	0.98
18–23	3,539.07	3,531.99	7.073	0.97

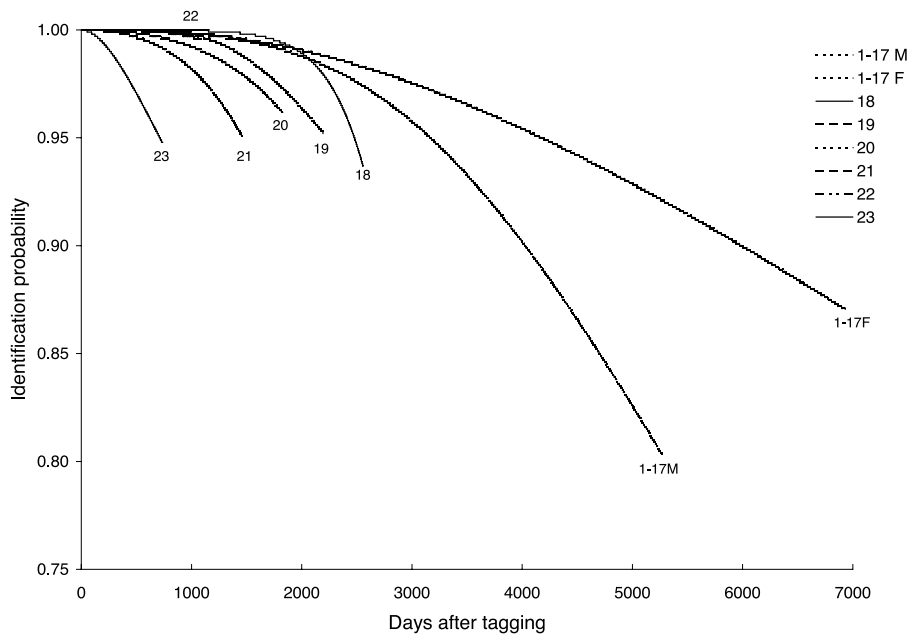


Figure 2. Identification probabilities of double tagged southern elephant seal cohorts at Marion Island. An individual is rendered unidentifiable when both tags are lost.

between individual OIT cohorts and between grouped OIT and grouped IIT cohorts was relatively small, despite model-supported separation. The maximum difference observed between IIT and OIT cohorts was for cohort 23, indicating a 5.2% lower identification probability at age 2 as compared to cohorts with IIT. When cohort 23 was not considered, OIT intercohort variation did not differ by more than  $0.16\% \pm 0.16$  (mean  $\pm$  95% confidence intervals) for ages 0–2. Cohort variation for OIT increased as animals aged (age 3–7), but 95% CI never spanned more than 5.3% for any age (Fig. 3).

## DISCUSSION

Tag-loss for both IIT and OIT cohorts of southern elephant seals is best described by a monotonic increase over time, although the pattern of tag-loss did deviate in some cohorts. Because all tags were applied to recently weaned individuals (~23- to 30-d old; see de Bruyn *et al.* 2008), tag-time and seal age cannot be differentiated. The increase in tag-loss rates over time is assumed to be generally related to an increase in seal—and flipper size and webbing thickness, rather than tag failure due to breakage (Pistorius *et al.* 2000). Extreme sexual dimorphism is present in adult elephant seals and the higher tag-loss rates in males tagged with IIT reflect this. Age-specific IIT tag-loss probabilities of males increased relative to those of females from age 3 to 4 onward. Sexual body size differences become evident at age 3, whereas extreme sexual dimorphism manifests after male elephant seals undergo a secondary growth spurt between ages 4 and 6 (Laws 1984). In contrast, model selection favored a combined male and female model for OIT cohorts. The lack of a sex effect for the

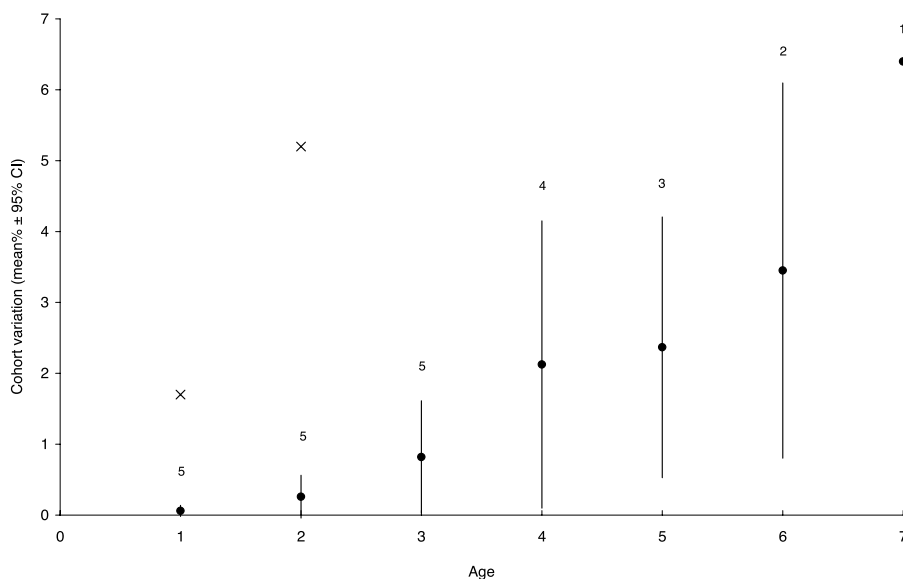


Figure 3. Variation in southern elephant seal tag-loss rates between cohorts 18–23, double tagged in the outer interdigital webbing of the hind flipper (OIT). Points represent the mean tag-loss rate over cohorts 18–22, with numerical values indicating the available sample size (number of cohorts). Cohort 23 (× at ages 1 and 2) is not included in the calculation of mean cohort differences.

OIT cohorts may possibly be explained by a lack of statistical power, due to fewer years post-tagging (maximum = 7 yr) to detect such effects. For IIT, model selected support for different sex models was only present when all cohorts were grouped, and not for individual cohorts (results not shown). Therefore, there may be insufficient statistical power to detect sex differences when using individual cohorts, or only a few combined cohorts (OIT,  $n = 6$ ). However, seals tagged in the outer webbing of the hind flipper at Macquarie Island, similarly did not show sex differences in tag-loss (McMahon and White 2009). This may indicate that the influence of flipper size may be important for IIT-loss, but less so for tags applied to the outer webbing (OIT).

Cumulative tag-loss rates for both IIT and OIT are low in comparison with other phocid studies (*e.g.*, Stobo and Horne 1994, McMahon and White 2009) and with previous assessments for a shorter time-series of this same mark-recapture program (Pistorius *et al.* 2000). Cumulative tag-loss rates from weaning to age 15 computed by Pistorius *et al.* (2000) were 35% and 17% for males and females, respectively, which is higher than those reported here. Pistorius *et al.* (2000) included 11 cohorts (1983–1993), with resighting data up to 1998. Our data included an additional six cohorts with IIT, and a further 10 yr of resighting data. The added cohorts, and more importantly the longer resighting time period, would modify the tag-loss estimation. This may be especially important for the adult age categories (*e.g.*, 13 males over age 12 in this study *vs.* only two males in Pistorius *et al.* 2000). The different analytical approach between this study and Pistorius *et al.* (2000) furthermore resulted in these differences. The Pistorius *et al.* (2000) function constrained tag-loss to be a straight

line, with the younger age categories (the region in the graph that has the more weight in the likelihood output, because more individuals are included) guiding the initial slope of the linear trend line. Age-specific IIT tag-loss (this study) did not fit the linear function exactly, but was rather slightly concave up (males) or convex down (females), leading to lower cumulative loss.

OIT were shed at a higher rate than IIT. In aquatic mammals, body and fin/flipper undulations pass water posterior along the body with increasing force, creating body-bound vorticity. This vorticity is transmitted along the body to the trailing edge of the fin, or flipper, where it is shed in a thrust jet (Fish *et al.* 2008). In swimming phocids, the center of the flipper is in addition more rigid than the flipper extremities (Fish *et al.* 1988). While swimming, OIT may thus be subjected to increased drag and movement, leading to increased tag-loss. On land, IIT are usually protected from the substrate and environmental variables (*e.g.*, ultraviolet [UV] light) because the tag is typically enclosed in the folds of the resting flipper (between adjacent flipper digits). OIT visibly protrude more, improving tag visibility for resighting and reducing disturbance to seals during tag resighting (the objective of the change in tag-placement in this study program). However, OIT are therefore also more likely to make contact with the substrate, plausibly leading to more abrasion and snagging, and potential loss from the flipper. Additionally, OIT exposed to more UV radiation than the enclosed IIT may become weakened over time and result in increased tag breakage, although we rarely observed such breakage.

McMahon and White (2009) compared tag-loss at Macquarie Island to Marion Island, and suggested that tag placement may affect tag-loss as tag-loss was much greater at Macquarie Island (OIT) than at Marion Island (IIT, from Pistorius *et al.* 2000). Our results support their interpretation. However, the large difference in tag-loss between the OIT from Macquarie Island (McMahon and White 2009) and Marion Island (this study) indicates that other factors are also important. We suggest that the timing of tagging is a critical determinant in life-time retention rates. At Marion Island, pups are always tagged postweaning (age ~23–30 d), while pups on Macquarie Island were tagged at birth. McMahon and White (2009) rejected this hypothesis, as they calculated tag-loss from weaning (when pups were branded) only, and not birth. However, it is probable that flipper damage from tagging at birth may lead to increased tag-loss postweaning and not necessarily only during the preweaning period as assumed by McMahon and White (2009). For example, newborn pups may be more immuno-compromised than weaned pups. Tag-loss due to immune reaction may, however, only occur in a few months time, rather than within the 3–4 wk preweaning age. Weaned pups, in contrast, may be less susceptible to infection of the tag-site than newborn pups, leading to lower tag-loss. We recommend that pups are tagged at weaning only and suggest an alternative method to identify preweaned pups (de Bruyn *et al.* 2008). On Marion Island, preweaned pups are marked with temporary Supersmall<sup>®</sup> tags (Dalton Supplies Ltd.) that are designed to minimize injury to the tag-site on the preweaned pup's delicate hind flipper. These tags are applied to the inner interdigital webbing of the hind flipper. At weaning (when hind flippers are sturdier), pups are tagged in the outer webbing of the hind flipper with the more robust Jumbotags<sup>®</sup>. This tagging protocol allows identification of preweaned pups (de Bruyn *et al.* 2008), while postponing marking with long-lasting tags to a period when; (1) the pup flipper is stronger; (2) the pup is generally in better condition and has greater immunity than at birth; and (3) tagging of weaned pups occurs well outside the harem (without the need to return the pup to the harem) that enable the precise placing of tags, which is required for low loss rates. The correlation

between tag-loss, tag-site and time of tagging between Marion Island and Macquarie Island may further be influenced by different tag types used (Dal 008 Jumbotags [Marion] *vs.* Supertag Size 1 [Macquarie]; Dalton Supplies Ltd.) and possibly the practice of cutting and filing the tag pin on Macquarie Island. If this procedure puts any strain on the tag itself (*e.g.*, holding the tag to file it down, while the pup tries to move the flipper), tag-loss may be increased due to damage/enlargement of the tag-site.

Differences in tagging proficiency of personnel may lead to heterogeneous tag-loss. Tag-loss in South African fur seals *Arctocephalus pusillus pusillus*, for example, varied between 6.8% and 33.8% for different tagging personnel (Shaughnessy 1994). Stobo and Horne (1994) reported cohort variation in tag-loss among year-old gray seals, *Halichoerus grypus*, which varied between 7.2% and 18.8%. In this study, interannual variation in tagging proficiency may result in cohort-specific tag-loss rates, despite stringent efforts to maintain constant tagging technique. Wilkinson and Bester (1997) compared tag-loss of 1-yr-old elephant seals at Marion Island, and found no significant variation amongst eight cohorts. This trend continued for all age groups in the 17 IIT cohorts, and no important variation in tag-loss between cohorts was evident. Conversely, OIT tag-loss varied by cohort. Field observation indicated that tag placement in three of the OIT cohorts were marginally suboptimal. It thus appears as if tag placement for OIT needs to be even more exact ( $\sim 5$  mm) as compared with IIT, as only a slight misplacement of the tags (OIT) at tagging may render tags attached too deep (cohorts 19 and 20) or too shallow (cohort 23). Tags applied too deep in the webbing may increase infection and tissue necrosis of the tag-site as the flippers grow while tags applied too shallow are more likely to tear out of the trailing edge of the flipper. The outer webbing of the hind flipper also provides a smaller surface area in which to place a tag as compared to the neighboring inner webbings between digits two and three and three and four. This may, therefore, explain the cohort dependence observed (and the suggested need for more precise tag placement) for OIT, but not IIT.

Although tag location on the outer interdigital webbing may lead to a lower retention rate, it is assumed that loss of tags should occur randomly among cohorts when they are similarly tagged. Yet, even when we removed cohorts that we *a priori* believed might have been responsible for the observed bias, the remaining three cohorts still could not be grouped. The estimates of OIT are hampered by a lower sample size (six cohorts) for a maximum time at liberty of 7 yr, compared to 17 cohorts at a maximum time at liberty of over 24 yr for IIT cohorts. As such, OIT resight data exists for only five cohorts of adult females, and two cohorts of adult males (based on the age at maturity for this species at Marion Island; Kirkman *et al.* 2003). Tag-loss probabilities are based on the time at liberty of tags: the time from application of the tag, to the last occasion that the individual was seen with two tags ( $N_{22}$ ) or first seen with one tag ( $N_{21}$ ). However, cohorts have different maximum times at liberty (maximum resight time decreases by 1 yr for successive cohorts) which could influence parameter estimates, especially when the time at liberty is relatively short. This potential bias is apparent in this study, significantly more so for OIT with shorter time at liberty and few sexually mature cohorts. For example, cohort 23 tags have a maximum time at liberty of around 900 d, in comparison with the first OIT cohort (18) at liberty for more than 2,700 d. Intercohort variation should be more pronounced when these data are sparse, and a few random cases of tag-loss could potentially help to drive cohort-specific differences. For five of the six OIT cohorts (cohort 22 being the exception), tag-loss estimates increased as absolute

cohort age was younger. Therefore, we attribute at least part of the cohort-specific tag-loss rates observed for OIT as an effect of fewer days to maximum time at liberty (specifically the time-span of  $N_{22}$ ). We suspect that as more data becomes available, tag-loss of OIT should become more homogenous among cohorts, although at higher rates than the IIT cohorts.

The cohort effect observed for OIT necessitates caution when deriving life-history parameter estimates (such as age-specific survival rates) from these cohorts. Because animals from separate OIT cohorts lose tags at different rates, the proportion of marked animals in the population at any period will differ between cohorts, and not represent a homogenous group with respect to tag-loss. An increase in tag-loss rate between IIT and OIT *per se* does not present considerable analytical drawbacks as survival rate corrections may simply be structured to represent the two different tag-sites. Extreme cohort variability, however, would negate the implementation of survival models structured at a population level (rather than a cohort level) as population level survival trends might be influenced by cohort-specific tag-loss rates.

To demonstrate the differences in tag-loss rates between OIT cohorts, we considered an arbitrary cohort of 500 double tagged pups, a good approximation of the number of pups born annually on Marion Island in recent years (MNB, unpublished data). On average, at age 2, cumulative tag-loss will render all individuals identifiable for three of the OIT cohorts (and all of the IIT cohorts). Tag-loss in cohort 20 and 21 will result in double tag-loss in two and four pups, respectively, while tag-loss in cohort 23 rendered 26 pups unidentifiable. Therefore, in a mark-recapture framework, within the first 2 yr of life, only cohort 23 had biologically meaningful variation in tag-loss rates—which may lead to a decrease of 5% in apparent survival rate [ $1 - (26/500) = 0.948$ ]. The maximum variance in OIT loss was present at age 4, where one (cohort 18) or 25 (cohort 21) pups out of 500 are expected to lose both tags, leading to a 4.8% decrease in apparent survival rate of cohort 21 at this age. Survivorship is chiefly responsible for population regulation at Marion Island (see Pistorius *et al.* 1999, 2004), and indeed in many mammal populations where immigration and emigration is limited; accurate estimates of these rates are therefore invaluable. In this case, apparent survival rates for juveniles should not be biased by tag-loss even if IIT and OIT cohorts were combined in survival analysis (excluding cohort 23). However, variation in tag-loss between cohorts can negatively bias estimates for subadult male and adult age classes if such cohorts are pooled.

#### *Assumption of Independent Tag-Loss*

The results presented assume tag-loss independence. Violations of the independence assumption will result in a greater proportion of animals retaining two or losing two tags, with few animals retaining only one tag. This would result in an overestimate in tag retention rates, and negative bias in survival rates. Testing for dependence in tag-loss requires the permanent marking of study subjects. Permanent marking of southern elephant seals at Marion Island is not possible to facilitate testing of this assumption. Tattoos, for example (Diefenbach and Alt 1998) although useful in a mark-recapture framework, are not realistic in our mark-resight design. Southern elephant seals have been successfully branded on Macquarie Island with no long-term influence on survival or condition (McMahon *et al.* 2006a). This protocol has allowed testing of the independence assumption for the period where flipper

tagging and branding overlapped (McMahon and White 2009). However, branding is logistically impractical at Marion Island and this technique incorporates animal welfare concerns (Jabour Green and Bradshaw 2004) that resulted in the termination of the Macquarie Island southern elephant seal monitoring program (McMahon *et al.* 2006b, 2007). Passive integrated transponder (PIT) tags have been used successfully to mark numerous species (Gibbons and Andrews 2004) including southern elephant seals (Galimberti *et al.* 2000). PIT tags facilitate reliable long-term identification of elephant seals up to adult age-classes for both sexes.<sup>1</sup> However, in contrast to external hind flipper tags that can be sighted from a distance, PIT tags require scanning each seal from a close distance (<20 cm) with an electronic reader. This is often impossible to achieve, in particular for breeding females within harems, and aggregations of seals during the molt haul out.<sup>1</sup> PIT tags are additionally more invasive than external tags, may itself incur tag-loss (Gibbons and Andrews 2004) and are expensive. Therefore, by comparison, double tagging with plastic tags remains the preferred choice of marking in elephant seals. Still, where PIT tags can be used in combination with double-tagging to provide an additional mark, this method will be useful to improve tag-loss estimates. Previously tagged animals can in some cases be identified through scarring, and Bradshaw *et al.* (2000) used flipper scarring in New Zealand fur seal, *Arctocephalus forsteri*, pups to address dependence in tag-loss estimates. Such scarring (tag punctures in the flipper) is sometimes visible in elephant seals, but it is virtually impossible to regularly and accurately distinguish seals that have lost both tags from untagged seals (*e.g.*, transients/immigrants).

Several studies have provided evidence of dependent tag-loss, and the assumption of independence appears to be biologically unrealistic. Double ear tag-loss in sea otters, *Enhydra lutris*, (Siniff and Ralls 1991) and black bears, *Ursus americanus*, (Diefenbach and Alt 1998), and flipper tag-loss in fur seal pups (Bradshaw *et al.* 2000) and leatherback sea turtles (Rivalan *et al.* 2005) were all greater than expected under the independence assumption. Similar results for elephant seals from Macquarie Island have been shown (McMahon and White 2009), and the expectation is therefore that tag-loss at Marion Island would also be dependent. Dependent tag-loss varies according to individual attributes, leading to heterogeneous tag-loss probabilities (McMahon and White 2009). In black bears, individual behavior such as fighting, mother-pup grooming or playing probably influences tag-loss (Diefenbach and Alt 1998). In fur seal pups, mechanical abrasion is thought to induce tag-loss, which is likely influenced by substrate, pup behavior and condition (Bradshaw *et al.* 2000). Dependent tag-loss in leatherback sea turtles is probably related to individual immunity, as the majority of tags are lost as a result of tissue necrosis. Individuals prone to infection may, therefore, be more likely to lose the second tag if the first tag was already lost (Rivalan *et al.* 2005). Tag-loss in elephant seals at Macquarie Island seems to be more dependent on pup wean mass. Lower wean mass concurrent with lowered immuno-competence is suggested to result in a greater incidence of dependent tag-loss, while larger pups generally exhibit independent tag-loss (McMahon and White 2009). To what extent observations from different species or different marking protocols can be used to infer dependent tag-loss in individual elephant seals at Marion Island is unsure. Even species-specific comparison is intricate due to the large difference in age-specific single tag-loss rates between Marion Island (0.0–0.14, this study) and Macquarie Island (0.0–0.364, McMahon and White 2009). Ideally,

<sup>1</sup> Personal communication from F. Galimberti, Elephant Seal Research Group, Sea Lion Island, Falkland Islands, 15 April 2009.

because the degree of tag-loss heterogeneity varies among study species, physical environment and tagging protocol, with the bias associated with assuming tag-loss independence reliant on the magnitude of tag-loss, data set-specific assessment of this assumption will be of greatest value.

Pistorius *et al.* (2000) expected a low degree of bias caused by dependent tag-loss for the Marion Island tagging regime owing to; (1) an observed increase in tag-loss rate over time instead of an apparent decline (see Xiao *et al.* 1999), (2) low absolute tag-loss rates resulting in a modest bias, (3) high resight frequency, where most animals are seen multiple times per year, reducing the probability of missing tag transition from  $N_{22}$  to  $N_{20}$  (*i.e.*, not seeing the seal changing tag status from two to one tag), and (4) the relatively high proportion of resightings of seals with one tag remaining for extended periods. Diefenbach and Alt (1998) predicted from observations of permanently marked animals that low tag-loss and frequent resightings should result in little bias from dependent tag-loss. Therefore, as the rate of tag-loss from two tags to one tag ( $N_{21}$ ) is markedly lower at Marion Island than at Macquarie Island (Fig. 4), dependence of tag-loss should result in a smaller bias of survival rate at Marion Island, and results should be fairly robust in dealing with these violations, especially for IIT. However, we acknowledge the potential bias in our results and agree that the tag-loss estimates provided here will be underestimated due to partial dependence of tag-loss in individuals. In cohorts with relatively high tag-loss (cohort 23, for example), the bias in survival rates will be higher.

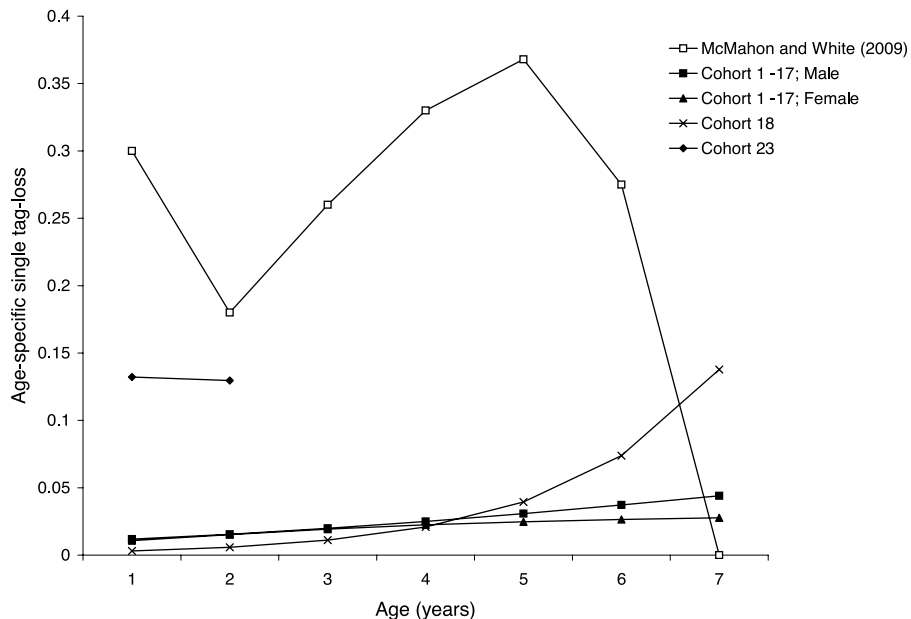


Figure 4. Age-specific single tag-loss ( $N_{21}$ ) in southern elephant seals from Macquarie Island (McMahon and White 2009) and Marion Island (data shown for IIT [cohort 1–17 males and females] and OIT cohorts 18 [longest OIT time-series] and 23 [cohort with greatest tag-loss measured]). Tag-transition from two to one tag is accurately measured at both locations, and not influenced by the independence of tag-loss assumption.

### Conclusion

Generally, small shifts in demographic rates of large-mammal populations, especially adult female survival, are able to produce a change in population growth (Eberhardt and Siniff 1977, Pistorius *et al.* 1999, McMahon *et al.* 2005). This illustrates the importance of accurate estimation of survival rates in mark-recapture studies, as biased estimates of demographic rates may result in erroneous conclusions and implementation of inappropriate management strategies leading to failure in management objectives (Brook *et al.* 1997, McMahon and White 2009). Tag-loss corrections in mark-recapture studies improve accuracy by adjusting survival estimates upward. Double tagging with high retention tags, in conjunction with permanent marking (where possible) should be used, while frequent resight/recapture occasions should improve life-history estimates (McDonald *et al.* 2003). Fluctuation in tag-loss rates between years, tag-site, and other variables (*e.g.*, colony and habitat differences) must be considered. We illustrate that small changes in tagging methodology can have potentially serious consequences for life-history estimates of a population if such changes are not investigated and, ideally, quantified. While homogenizing techniques for extensive use across study locations are appropriate for comparative purposes, we advocate the importance of data set-specific assessment of tag-loss rates to ensure greatest confidence in population parameters obtained from mark-recapture experiments.

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