

## The implications of assuming independent tag loss in southern elephant seals

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**Abstract.** Survival and reproductive rate estimation requires following uniquely identified individuals through time, and many statistical models assume markings used to identify individuals are permanent. However, survival rates are underestimated when single marks are lost, since the models will effectively score those animals as dead. In order to account for mark loss, some researchers use a double-mark approach, assuming the probability of losing one mark is independent of losing the other one. Therefore, mark loss can be estimated using animals that have lost one mark. Using a 17-year dataset of southern elephant seals (*Mirounga leonina*) marked with permanent brands and two cattle tags in their hind flippers, we were able to compare tag loss and survival rate estimates with and without the assumption of independent tag loss with respect to age, sex, and wean mass. We demonstrate the assumption of independent tag loss is not valid, showing it is more likely for an animal to lose both tags than just one or the other. The assumption of independent tag loss leads to an underestimate of survival rates which in turn leads to underestimates of population growth rate. In addition, tag loss rates are different by sex and age, with older males more likely to lose tags. Tag loss is also a quadratic function of wean mass through age two, with smaller and larger animals more likely to lose both tags. Such differences are possibly due to differences in behavior, flipper growth, and immune response. Using a Bayesian approach, we will be able to use our tag loss estimates as priors in future analyses for a subset of marked animals that only have flipper tags. With this population, the independent tag loss models are more likely to incorrectly estimate a declining population (growth rate < 1.0), potentially leading to unwarranted management action. To account for non-independent mark loss in survival rate studies, we recommend researchers use at least two forms of marking on at least a subset of animals. However, neither form of marking need be permanent as long as mark loss is independent between the different forms.

**Key words:** Bayesian; Cormack-Jolly-Seber; Macquarie Island; mark-resight; *Mirounga leonina*; population growth rate.

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### INTRODUCTION

Estimates of population growth are often reliant on following individuals throughout their lives to determine survival and reproductive rates. In order to do so, individuals require

unique identifying marks. In some cases, marks are natural, such as coloration patterns, while in other cases individuals are captured and marked with human-created devices. Metal bands attached around birds' legs and plastic tags punctured through soft tissue, such as an ear,

are two examples of many marking methods. However, not all marks are permanent, often wearing or changing with age. When animals lose all markings, statistical models that do not account for mark loss assume animals that have lost all marks are instead mortality events, and one cannot estimate the probability of mark loss when only one mark is present. To solve the mark-loss estimation problem, many studies mark animals with two marks (Bjornsson et al. 2011), and analysis of double marks most commonly assumes the probability of losing one mark is independent of losing the other mark (Beauplet et al. 2005, Oosthuizen et al. 2010, Juillet et al. 2011).

However, the assumption of independent mark loss may create biases in survival rate estimates. Namely, if the proportion of animals that have lost all marks is underestimated, survival rate is biased low since statistical models will assume such animals are mortalities. If the no-mark proportion is overestimated, survival rate is biased high.

Over the years, both branding and numbered plastic cattle tags attached to flippers (flipper tags) have been used to uniquely identify individuals of many pinniped species. Long-term studies have shown that branding is a permanent form of marking while flipper tags are not (Pistorius et al. 2000, van den Hoff et al. 2004, McMahon et al. 2006, Wilkinson et al. 2011). Because of concerns that the branding process is inhumane, flipper tags have subsequently become a common, and sometimes the only, marking method employed, although the issue of tag loss remains.

For a period of seven years (1993–1999), over 6000 weaned southern elephant seal pups (*Mirounga leonina*) at Macquarie Island were given three marks: a brand on their flanks and two plastic cattle tags in the outer webbing of each hind flipper. Resights of brands and tags have been ongoing. This suite of markings provides a unique opportunity to estimate tag loss while the permanent brands provide a means to identify individuals who have lost all tags. The assumption of non-independent tag loss is of particular importance for this population since demographic analysis of cohorts after 1999 will rely solely on resights of flipper tags. McMahon and White (2009) analyzed the first eight years of this data

and showed that tag loss was not independent between the two flipper tags, leading to an underestimate of survival. In addition, tag loss was related to wean mass, with smaller pups more likely to lose both tags (McMahon and White 2009). We aim to revisit this data for three reasons (1) to quantify tag loss for animals over seven years old now that 17 years of data are available, (2) quantify differences in survival rate estimates and population growth rate when independence is assumed vs. not assumed, and (3) perform the analysis in a Bayesian framework so posterior distributions of tag loss probability may be used as priors in analyses of future cohorts and other populations.

## METHODS

### Data collection

Macquarie Island (54°30' S, 158°50' E) is 1500 km southeast of Tasmania and 1300 km north of Antarctica. Although elephant seals travel long distances to forage, the Macquarie Island population is considered an isolated breeding group and is the only major Pacific sector breeding group in the Southern Ocean (McMahon et al. 2006). In addition, females exhibit a high degree of philopatry (giving birth 1–4 km from their birth site) (Nicholls 1970, Hindell and Little 1988), and the island is comparatively small (34 km long by 5 km wide at its widest), making inter-annual resights of individuals possible.

From 1993–1999, approximately 2000 pups per year were tagged with uniquely numbered plastic tags in both hind flippers within 24 hours of birth and subsequently recaptured and branded at weaning (Table 1). Consistent hot-iron branding methods were used, so 98% of brands were readable and permanent after the seals' first molt (van den Hoff et al. 2004, McMahon et al. 2006), and flipper tagging methods were also standardized (McMahon and White 2009). Of the branded animals, about 45% were also weighed at weaning using a sling and pulley system (McMahon and White 2009). In 2000, 1999 pups were given only flipper tags while roughly half of them were also weighed at weaning ( $n = 1029$ ).

Given the philopatric nature of this species, resight efforts were primarily focused in the northern region where seals were initially born (and marked). Between August 1993 and October

Table 1. Number of branded and tagged southern elephant seals by survey season and count for which wean mass was also measured.

Survey season	No wean mass	Wean mass
1993	1021	1079
1994	1448	554
1995	1161	826
1996	1088	909
1997	1136	837
1998	1092	909
1999	1068	933

2006, isthmus beaches were searched daily for tagged and branded animals. The northern third of the island was searched every ten days, while the remaining coastline was searched monthly. Searches were standardized by following the same route on each occasion and were started at the same time each day, week or month depending on the search category. After October 2006 all searches were opportunistic.

As brands can be seen from a distance, resights of brands do not directly disturb the animals. Detecting and reading flipper tags sometimes required spreading the hind flipper, when possible. During many resights, observers were able to read the unique number and determine the color of each tag. When unique numbers could not be read, the number of remaining tags was still recorded. Multiple sightings of a seal within a seal year ( $15 \text{ October}_t - 14 \text{ October}_{t+1}$ ) were treated as a single sighting and used to create annual individual mark-recapture histories.

In summary, we used mark-resight data of branded animals from 1993–2009 to estimate tag loss with and without the assumption of independence. To quantify differences in survival rate estimates with and without independent tag loss, we used mark-resight data from the 2000 tag-only cohort, using tag loss probabilities estimated from the branded data as priors in the analysis.

### Analysis

We created a Bayesian multi-event, multi-state method based on the standard Cormack-Jolly-Seber (CJS) mark-recapture model (Lebreton et al. 2009). The model allowed for several different states depending on the number of tags, detection, and survival. At each time step, an

individual can fall in to several unique categories: (1) alive or dead; (2) brand detected or not detected; (3) number of tags detected or not detected; (4) number of tags: 0, 1, or 2.

Overall, the unique categories lead to 24 theoretical states for a given animal. However, we can make two simplifications based on data collection procedures for this particular southern elephant seal colony. Tags were never detected without the brand also being seen, and dead animals are never detected. Therefore, at each time step southern elephant seals fall in to one of 10 distinct states:

1. Alive, brand detected, tag count detected, 0 tags
2. Alive, brand detected, tag count detected, 1 tags
3. Alive, brand detected, tag count detected, 2 tags
4. Alive, brand detected, tags not detected, 0 tags
5. Alive, brand detected, tags not detected, 1 tags
6. Alive, brand detected, tags not detected, 2 tags
7. Alive, brand not detected, tags not detected, 0 tags
8. Alive, brand not detected, tags not detected, 1 tags
9. Alive, brand not detected, tags not detected, 2 tags
10. Dead

Transition from one state to another state between sample periods involves four basic probabilities that are estimated in the Bayesian model: survival rate ( $s$ ), probability of detecting a brand ( $d_B$ ), probability of detecting tags ( $d_T$ ), probability of losing tags ( $\Psi$ ). The parameters are represented as vectors since they can be separated into further categories depending on assumptions we make about potential differences as a function of time, different state transitions, and many other factors.

Based on previous analyses by McMahon and White (2009), different parameters were estimated as a function of sex, number of tags, year, and wean mass. All parameters were estimated separately by sex. Presence of a tag is easier to detect than absence of a tag, so probability of

detecting tags was estimated separately by the number of tags. Resight effort was annually variable, so brand detection was estimated separately by year. To ensure survival rates did not bias tag loss probabilities, survival was estimated separately by age, cohort, and as a quadratic function of wean mass for ages 1 and 2 yr. Finally, to compare with previous work, tag loss was estimated separately by age and sex and as a quadratic function of wean mass for ages 1 and 2 yr. To make use of the entire dataset, survival rates and tag loss probabilities were also estimated only by age for the subset of data that lacked wean mass measurements.

To test for tag loss independence, we ran the model two different ways. First, we estimated tag loss transition probabilities between tag states separately:  $\Psi_{2:0}$ ,  $\Psi_{2:1}$ ,  $\Psi_{1:0}$ . Then, using the same data, we estimated tag loss probability ( $p$ ) assuming independence where

$$\Psi_{2:0} = p^2$$

$$\Psi_{2:1} = 2 \times p \times (1 - p)$$

$$\Psi_{1:0} = p$$

Overall, 182 parameters were estimated in the case of dependent tag loss. One hundred thirty-eight parameters were estimated when assuming independent tag loss.

To determine how the assumption of tag loss independence affects survival rate estimates, we used the resulting tag loss probabilities as priors to estimate survival for the cohort that did not have brands, so survival was based solely on resights of flipper tags while accounting for tag loss. This final analysis incorporated an additional 33 parameters: cohort-specific survival by age and by wean mass for years 1 and 2 and detection probability of tags by year and number of tags. There is one primary reason to limit this last analysis to a tag-only cohort. In the branded cohorts, brands and tag numbers are always resighted together. Consequently, survival estimates of branded animals are based on resights of the permanent brands while the number of tags is simply a characteristic of the animals. If we exclude brand data to estimate tag loss and survival for the branded cohorts, we are limited to sightings of animals with one or two tags. Therefore, we can no longer estimate tag loss as

potentially independent.

Quadratic parameters were given broad, uniform distributions wide enough to prevent truncation of posterior distributions. All other parameters were given uniform priors between zero and one. The Bayesian analysis was done using program MTG (Metropolis within Gibbs) developed by Daniel Goodman of Montana State University (Schwarz 2008). To maximize computer efficiency, simulations were performed on orthogonally transformed parameters when correlation between parameters was high (all quadratic parameters). Simulations were set for a rejection rate near 0.7, a sub-sampling (thinning) of 1 in 50 and a burn-in period of 50, continuing for a subsample size of 10,000 for each inference (see Cowles and Carlin 1995). The resulting lag-1 autocorrelations were  $< 0.1$ , and independent chains with different parameter starting values gave indistinguishable results. To verify convergence and stationarity within the final chains, we used the Heidelberger and Welch convergence diagnostic available from the CODA package in R using standard 10% increments and  $p \leq 0.05$  (Heidelberger and Welch 1983, Plummer et al. 2006).

Lastly, to understand the influence of the independent tag-loss assumption on population growth rate estimates, we created a simple Leslie matrix with the oldest age classes as a single state (Fig. 1). We assumed an equal pup sex ratio, constant survival after age 9, and constant reproductive rate starting at age 3. The last two assumptions represent a best-case scenario with no senescence and maximum reproduction starting at the youngest observed reproductive age (Hindell 1991, McMahon et al. 2003). We utilized posterior samples of survival rates from the non-branded cohort with and without the assumption of tag loss independence. We allowed reproductive rate to range between 0.2 and 1.0. Sensitivity analysis shows the population growth rate is most sensitive to variation in adult survival rates. Therefore, survival rate after age nine ( $s_A$ ) was either the highest adult survival rate (best-case scenario) or the lowest adult survival rate (worst-case scenario) estimated for the non-branded cohort. We then calculated population growth rate as the dominant eigenvalue of the Leslie matrix.



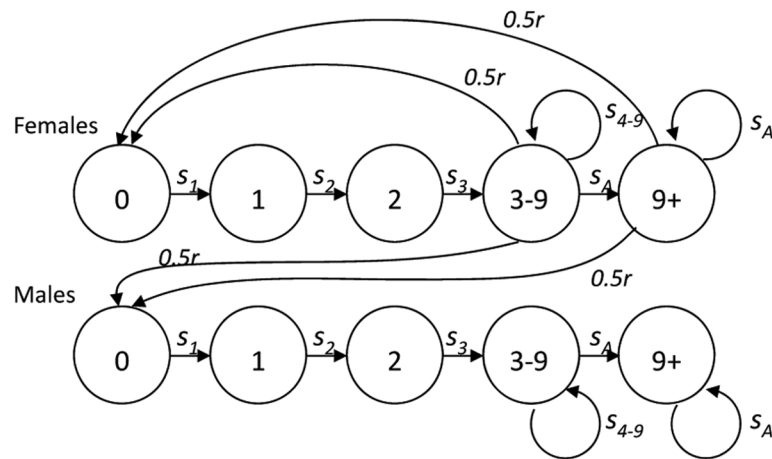


Fig. 1. Life history diagram of stage-based model. Circles with numbers represent age classes, while arrows represent transitions between age classes based on survival ( $s$ ) and reproductive ( $r$ ) probabilities.

## RESULTS

The probability an animal has survived but lost all its tags (i.e., the probability an animal has transitioned to the zero-tag state) is the key to determining the importance of non-independent tag loss on survival rate estimates. Overall, our results show the assumption of independent tag loss underestimated the probabilities of moving to a zero-tag state ( $\Psi_{2:0}$  and  $\Psi_{1:0}$ ) while overestimating the probability of moving to or staying in a higher-tag state ( $\Psi_{2:2}$ ,  $\Psi_{2:1}$ , and  $\Psi_{1:1}$ ) regardless of wean mass (Figs. 2–4). The one exception is the probability of going from a one-tag state to a zero-tag state in the first year (Fig. 2). In that case, independent tag loss overestimated the probability of moving to a zero-tag state. However, the sample size for this analysis was comparatively small since only one cohort was tagged with single tags. Since analysis with independent tag loss uses all tag loss data to estimate one rate, results with independent tag loss are driven by the other tag loss probability estimates.

We also investigated tag loss as a function of wean mass for the first two years. With the exception of Age Class 1  $\Psi_{2:1}$ , tag loss is a quadratic function of wean mass, and there are no strong differences between males and females (Figs. 2 and 3). In general, both smaller and larger weaned pups had a higher probability of transitioning to a zero-tag state (going from two

or one to no tags) compared to pups between 100 and 150 kg wean mass (Figs. 2 and 3). However, during the first year, the probability an animal with two tags will lose both of them is at its lowest around 175 kg wean mass (Fig. 2).

For ages three and older, there is not strong evidence for differences in tag loss between males and females (Fig. 4). However, when using posterior distributions of tag loss probabilities to estimate the proportion of animals without tags, the proportions remain similar by sex for only the first eight years. At nine years and older, tag loss is higher for males (Fig. 5). Within the data, all re-sighted males greater than 13 years old had lost all their tags.

The assumption of independent tag loss leads to an underestimate of the proportion of animals still alive that have lost all their tags (Fig. 5). In general, the difference between proportions increases until age eight. For females, the bias remains relatively constant after age 8, while the bias for males declines as the proportion of animals with zero tags approaches one.

The underestimate of the proportion alive without tags then produced an underestimate of survival for the tag-only cohort (Fig. 6). The difference is higher and relatively constant for females after age two. Since the underestimate of the proportion alive without tags diminishes for males after age nine, the bias in male survival rate also declines at age nine.

Underestimates in survival rate created a

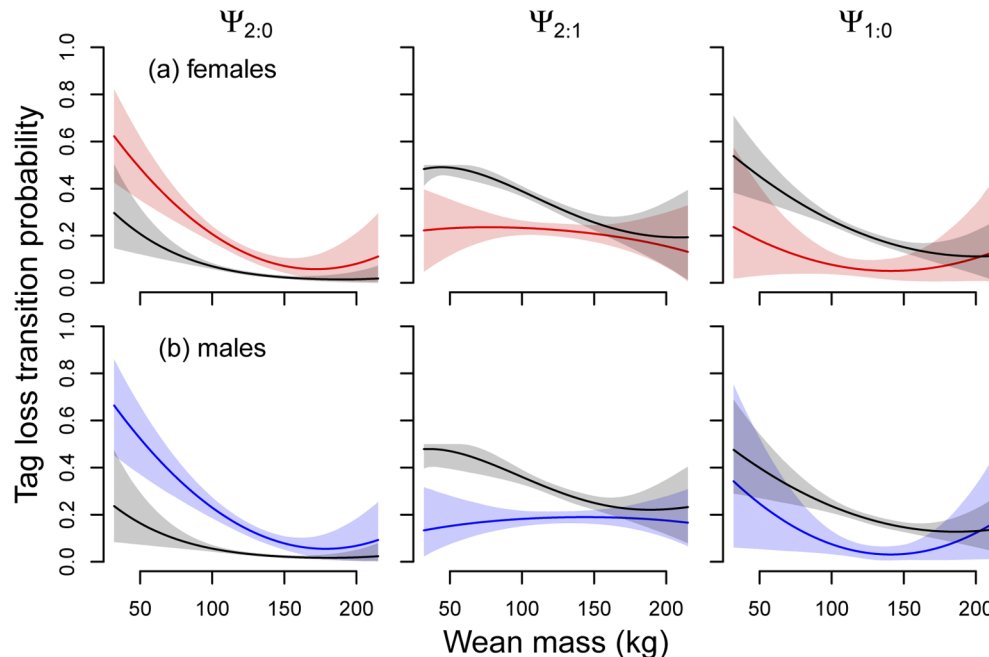


Fig. 2. Posterior distributions of tag loss transition probabilities as a function of wean mass and number of tags from birth to age 1 yr.  $\Psi_{x:y}$  is the probability of transitioning from an  $x$ -tag state to a  $y$ -tag state. For example,  $\Psi_{2:0}$  is the probability of going from two to no tags by the time the animal reaches one year old. Females are red, and males are blue assuming tag loss is dependent on the number of tags. Black lines represent expected tag loss assuming independence. Shaded areas are 95% posterior intervals.

negative bias in population growth rate (Fig. 7). The mean population growth rate with independent tag loss was 0.025–0.064 lower. The bias is more pronounced when adult survival is low and reproductive rates are high. In addition to tag loss probabilities, we estimated detection probabilities of brands by year and tags by number of tags. Resight probability was relatively stable from 1994 through 2001 with equal brand detection by sex, but resight probabilities post-2001 were variable, different by sex, and comparatively lower (Table 2). The probability of determining tag status was lowest when no tags were present and highest when both tags were present. Overall, tag status was determined more often in males than females (Table 3).

## DISCUSSION

Although an increasing number of mark-recapture analyses account for tag loss, our analysis emphasizes the importance of testing and accounting for the assumption of indepen-

dent tag loss. Analyzing the first eight years of this data series, McMahon and White (2009) showed the assumption of independent tag loss led to an underestimate of age-specific survival rates. Our updated analysis of the longer 17 year time series concurred with those of McMahon and White (2009) and showed that assuming independent rates of loss continued to produce inaccurately low survival rate estimates at older ages. In turn, population growth rate estimates were biased down and were consequently more likely to fall below 1, potentially incorrectly implying a declining population.

The incorrect assumption of independent tag loss could be of particular concern when policy-makers rely on such results to make species management decisions. When survival rates are biased low, erroneous results could trigger unwarranted, costly management action. For example, if listing of this population under the IUCN's red list criteria was based solely on this analysis, the population would have more than a 50% probability of falling in to at least the

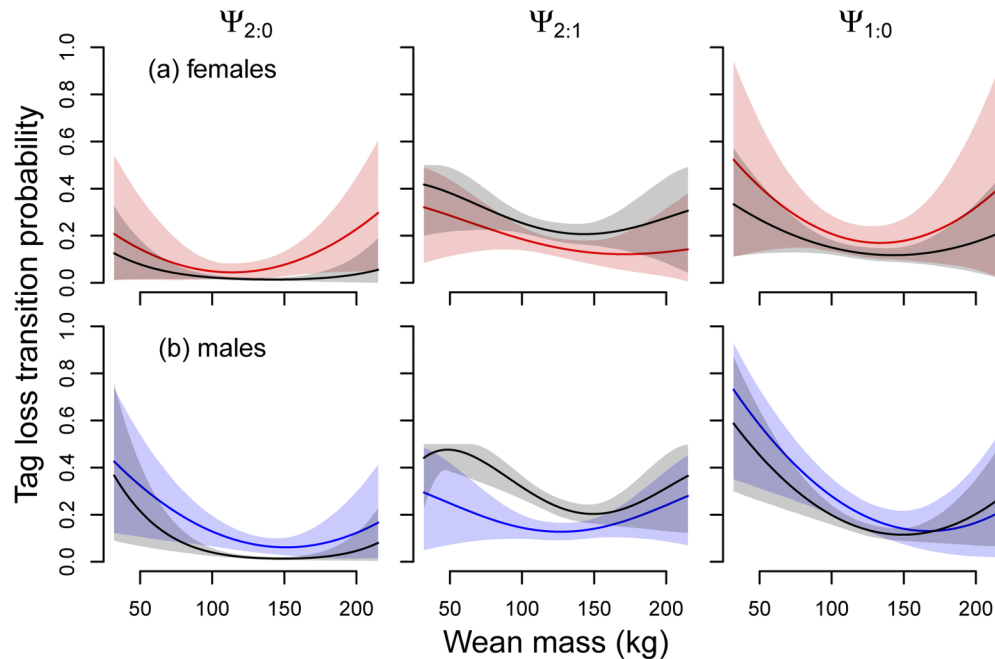


Fig. 3. Posterior distributions of tag loss transition probabilities as a function of wean mass and number of tags from age 1 yr to 2 yr.  $\Psi_{x:y}$  is the probability of transitioning from an  $x$ -tag state to a  $y$ -tag state. For example,  $\Psi_{2:0}$  is the probability of going from two to no tags between the ages of one and two years old. Females are red, and males are blue assuming tag loss is dependent on the number of tags. Black lines represent expected tag loss assuming independence. Shaded areas are 95% posterior intervals.

vulnerable category ( $\geq 30\%$  decline over 10 years) with a reproductive rate of 0.77, a high adult survival rate, and the incorrect assumption of independent tag loss (IUCN 2011.). With dependent tag loss, the reproductive rate would need to be much lower at 0.44.

It is unclear why animals would preferentially lose both tags instead of just one. One potential explanation is an immune system response related to condition, which can be demonstrated with tag loss in young animals as a function of wean mass. Our extension of the McMahon and White (2009) analysis verified a difference in tag loss as a function of wean mass during the first year and also showed evidence for differences in tag loss as a function of wean mass through year 2. In year 1, double-tag loss declined with wean mass, reaching its lowest around 175 kg, then increasing again at higher wean masses. In year 2, double-tag loss is at its lowest near 110 kg for females and 150 kg for males. The pattern is also seen in animals with only one tag, with the smallest and largest pups preferentially losing

tags. Inversely, survival rate is a function of wean mass during the first two years, with survival rates peaking around 140 kg in year 1 and 180 kg in year 2 (McMahon et al. 2003). Other research has suggested an elevated immune response in animals of poor condition, leading to a higher likelihood of dependent tag loss in smaller animals (Rivalan et al. 2005). Our results, combined with survival rate estimates, could imply that the heaviest weaned pups are also not of best condition. Behavioral variability and physical growth of the flipper may explain tag loss differences between males and females as they age. Flipper growth may explain why tag loss levels off in females around eight years old, when their growth slows, and why male tag loss continues to be high as they continue to grow. Male flippers become so large, the tags may either slide out or break. In addition, males exhibit different foraging strategies and compete for females as they age, which may cause tags to fall out or affect immune responses.

In general, these new analyses show lower and

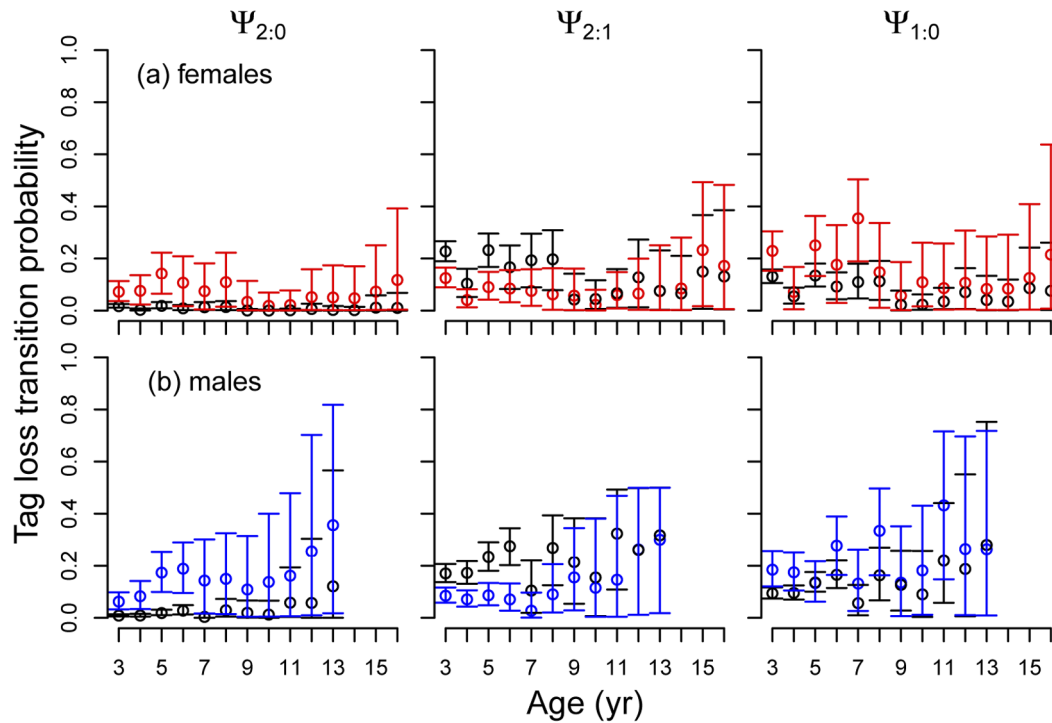


Fig. 4. Posterior distributions of tag loss transition probabilities as a function of age and number of tags.  $\Psi_{x:y}$  is the probability of transitioning from an  $x$ -tag state to a  $y$ -tag state. For example,  $\Psi_{2:0}$  is the probability of going from two to no tags within a year. Females are red, and males are blue assuming tag loss is dependent on the number of tags. Tag loss assuming independence is shown in black. Points are means and bars are 95% credible intervals.

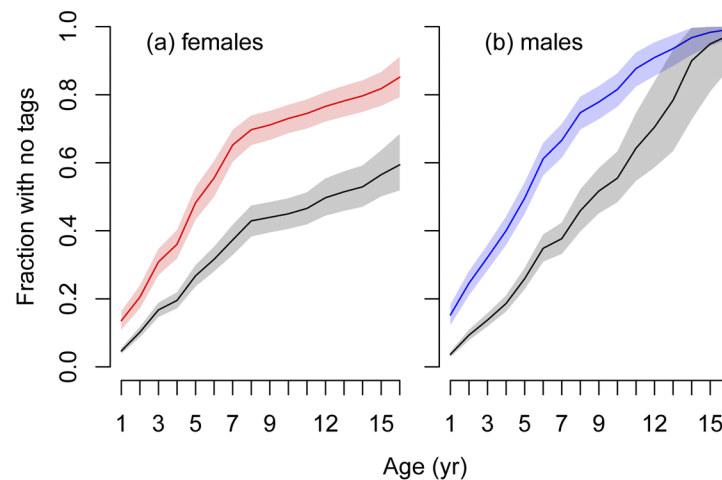


Fig. 5. Posterior distributions of the fraction of individuals with no tags given age assuming all animals start with two tags. Black lines represent expected tag loss assuming independent tag loss. Females are red, and males are blue assuming tag loss is dependent on the number of tags. Shaded areas are 95% posterior intervals.



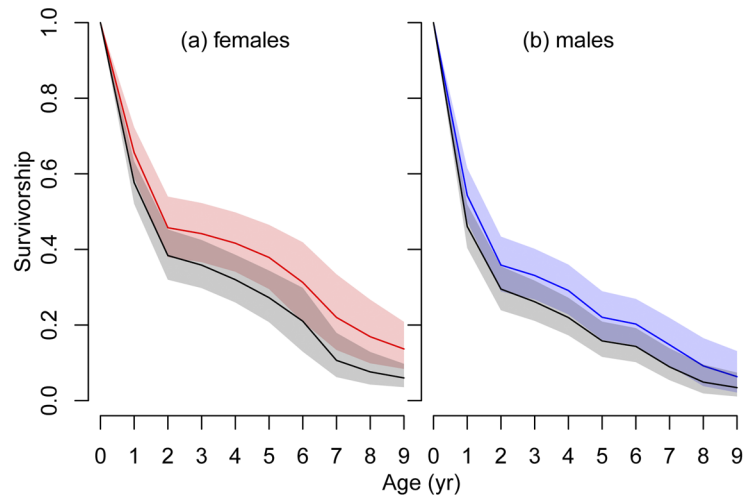


Fig. 6. Posterior distributions of survivorship to age  $x$ . Females are red, and males are blue assuming tag loss is dependent on the number of tags. Black lines represent expected survivorship assuming tag loss is not dependent on number of tags. Shaded areas are 95% posterior intervals.

less variable age-specific tag loss compared to McMahon and White (2009), most likely due to a larger sample size by age class. It is important to note, however, that the remaining high level of uncertainty in tag loss, survivorship, and population growth rates is not due to small sample sizes. Rather, relatively low and variable annual resight probabilities contribute substantially to posterior variability in parameter estimates.

In addition, our estimates of  $\Psi_{2:1}$  as a function of wean mass were substantially lower than those reported in McMahon and White (2009). Since the parameter is only represented in their analysis as the probability of losing one or the other of two tags ( $2 \times p \times (1 - p)$ ), the distribution is inherently bimodal. Because of the bimodal characteristic, their results show, correctly, a value of 0.5. By simply defining the probability

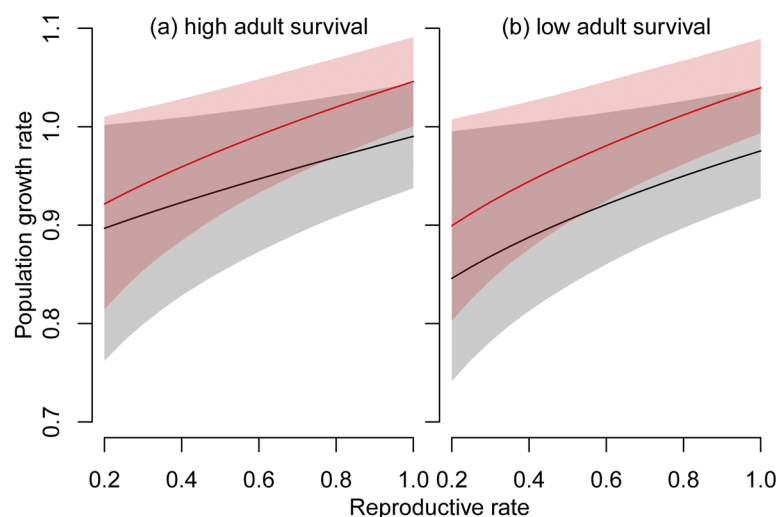


Fig. 7. Population growth rate as a function of reproductive rate, tag loss assumptions, and high or low adult survival. Red lines are mean growth rate when tag loss is dependent on number of tags. Black lines represent mean growth rate assuming independent tag loss. Shaded areas are 95% posterior intervals.

Table 2. Probability of detecting a brand by survey year and sex. Marginal means with 95% credible intervals in parentheses.

Year	Females	Males
1994	0.62 (0.58, 0.66)	0.63 (0.59, 0.67)
1995	0.54 (0.51, 0.57)	0.54 (0.50, 0.57)
1996	0.46 (0.43, 0.49)	0.50 (0.47, 0.53)
1997	0.56 (0.54, 0.58)	0.56 (0.54, 0.58)
1998	0.51 (0.49, 0.53)	0.56 (0.53, 0.58)
1999	0.64 (0.62, 0.66)	0.65 (0.63, 0.67)
2000	0.63 (0.61, 0.65)	0.62 (0.60, 0.64)
2001	0.64 (0.62, 0.66)	0.59 (0.57, 0.62)
2002	0.20 (0.18, 0.22)	0.31 (0.29, 0.34)
2003	0.55 (0.52, 0.57)	0.55 (0.52, 0.58)
2004	0.46 (0.43, 0.49)	0.44 (0.40, 0.47)
2005	0.61 (0.58, 0.65)	0.46 (0.42, 0.51)
2006	0.29 (0.26, 0.32)	0.40 (0.35, 0.45)
2007	0.44 (0.40, 0.48)	0.52 (0.46, 0.59)
2008	0.20 (0.17, 0.24)	0.44 (0.34, 0.55)
2009	0.90 (0.73, 1.00)	0.64 (0.41, 0.95)

as a transition from a two-tag state to a one-tag state, the data quickly show this probability falls below 0.5. In either case,  $\Psi_{2,1}$  did not show a strong correlation with wean mass for age class 1.

The results of this analysis may only be valid for flipper tags attached in the outer webbing, as results from other populations imply inner webbing tags last longer (Oosthuizen et al. 2010). Our results also show higher outer-webbing tag loss compared to the Marion Island population of southern elephant seals (Oosthuizen et al. 2010). The dissimilarity may be due to differences in timing of tagging. Marion Island pups are tagged at weaning while Macquarie Island pups are tagged as newborns. Although only animals that retained their two tags until weaning were used in this analysis, early development of the flipper and mechanical abrasion in those first few weeks may play a role in later tag loss. Differences in the placement of the tags (distance from the edge of the flipper) may also play a role. Behavioral and environmental differences as well as variability in immune response could also explain the differences between populations.

Tag loss studies at Marion Island have also found higher tag loss rates for males than females, particularly at older ages (Pistorius et al. 2000, Oosthuizen et al. 2010). Although our results did not support a strong case for estimating tag loss separately by sex, one may want to consider doing so, particularly when the probable age at which all males have lost all tags

Table 3. Probability of detecting tag status by number of tags and sex for branded animals. Marginal means with 95% credible intervals in parentheses.

Number of tags	Females	Males
0	0.28 (0.27, 0.29)	0.39 (0.38, 0.40)
1	0.64 (0.60, 0.68)	0.76 (0.73, 0.79)
2	0.71 (0.69, 0.73)	0.79 (0.77, 0.81)

falls below the maximum age of survival. Such a distinction has important implications not only in demographic rate estimates but also for studies comparing sex differences in behavior and life history traits as a function of age.

## CONCLUSIONS

Other studies have shown that the assumption of independent tag loss is incorrect for black bears (*Ursus americanus*) (Diefenbach and Alt 1998), New Zealand fur seals (*Arctocephalus forsteri*) (Bradshaw et al. 2000), and grey seals (*Halichoerus grypus*) (Smout et al. 2011b). In all cases, including this one, the assumption of independent tag loss produced an underestimate in the proportion of animals with zero tags which led to underestimates in survival. This study takes those analyses one step further and shows such underestimates can be large enough to trigger unwarranted management actions. In addition, analyses should not assume mark loss is constant over all ages or by sex. If double tags are to be the primary method for identifying individuals, it is important to test the assumption of independent tag loss by employing at least two forms of unique identification on at least a subset of the sampled population (Juillet et al. 2011, Smout et al. 2011a). No mark types need to be permanent as long as the different types are lost independently of each other. Such an approach allows us to estimate potentially dependent tag loss which can be used on the data subset with only one mark type.

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