

# Estimating Tag-Shedding Rates for Experiments with Multiple Tag Types

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## SUMMARY

In estimating the size and dynamics of populations in tagging studies, estimates of tag loss due to shedding are required. We extend existing double-tagging methods to include a general formulation for multiple tag types. We show how the inclusion of single-tagged subjects released simultaneously with the double-tagged subjects allows us to improve the precision of estimates, and to test hypotheses previously thought untestable. An example is given involving cod in the Northwest Atlantic.

## 1. Introduction

The estimation of the parameters from mark-recapture studies of wildlife and fish require tags or marks that allow individuals or groups to be identified. If the tags are not permanent, shedding rates of tags must be estimated. Tag-loss rates have traditionally been estimated using double-tagging experiments in which two identical tags are placed upon the same subject, e.g., fish. There are several difficulties with double-tagging experiments: double tags may be more visible than single tags, double tags may be shed at a different rate than single tags, and it may not be possible to place two tags of a single type or use two marks of the same type on a single subject. We address these problems and demonstrate how more precise estimates can often be obtained by using information that is usually ignored.

We demonstrate how the information on double-tagging experiments can be combined with the simultaneous release of single-tagged subjects. Myhre (1966) used simultaneous single-tagging experiments to test for "dependency" of tags, i.e., reporting rates dependent on the presence of other tags on the subject. Here we adopt a more general approach by incorporating the information from simultaneous single-tagging experiments into an overall likelihood. When only data from double-tagging experiments are available, two alternate likelihood functions are available, depending on the assumption of simultaneous release. The inclusion of single-tagging releases is advantageous, however. It can reduce estimation error and, furthermore, the return patterns of single- and double-tagged subjects can be directly compared; this allows us to test hypotheses that were previously thought untestable, e.g., that single- and double-tagged subjects shed tags at the same rate (Kirkwood and Walker, 1984) and are equally visible. Additionally, we extend existing methods to allow for multiple tag types. This extension is needed because it may be impossible to place two identical tags or to use two identical natural marks on a single subject, e.g., in tagging ducks, only one neck band may be possible, whereas two leg bands may be attached. The visibility of neck and leg bands may be quite different, however.

## 2. Models

We extend the methods developed by Kirkwood and Walker (1984) and Hampton and Kirkwood (1990) that use exact time at liberty from double-tagging experiments to obtain estimates of tag-shedding rates. Our method can be applied to any number of tag types. To illustrate the method,

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we consider two tag types, denoted A and B. The tag combinations, reporting rates, and numbers released are summarized below.

Tag combination	Reporting rate	Number released
A	$\lambda_A$	$N_A$
B	$\lambda_B$	$N_B$
AA	$\lambda_{AA}$	$N_{AA}$
BB	$\lambda_{BB}$	$N_{BB}$
AB	$\lambda_{AB}$	$N_{AB}$

A subject with tag combination A has a single A tag, a subject with tag combination AB has both A and B tags, and so on. We assume that if both tags of a pair are retained then either both tags will be reported or neither tag will be reported. This is reasonable because tag returns are usually rewarded on a per-tag basis, so that returning both tags would double the reward with no additional effort.

Let  $Q_A(t)$  be the probability of a tag of type A being retained at time  $t$  after release. For example, if there is an initial tag shedding followed by a constant shedding rate over time,

$$Q_A(t) = \rho_A e^{-\phi_A t}, \tag{1}$$

where  $\rho_A$  is the probability of retention immediately after tagging and  $\phi_A$  is the instantaneous rate of shedding (Beverton and Holt, 1957; Hampton and Kirkwood, 1990). Shedding of B tags is similarly represented.

Let  $p_y^x(t)$  represent the probability of observing tag combination  $y$  given the recapture at time  $t$  of a subject originally marked with tag combination  $x$ . Then, for a subject originally marked with an A tag and recaptured at time  $t$ ,

$$p_A^A(t) = \lambda_A Q_A(t). \tag{2}$$

B tags can be similarly represented.

The probabilities of observing the various combinations possible from AA (and similarly for BB) releases are

$$p_{AA}^{AA}(t) = \lambda_{AA} Q_A(t)^2, \tag{3}$$

$$p_A^{AA}(t) = 2\lambda_A Q_A(t)[1 - Q_A(t)]. \tag{4}$$

Finally, the probabilities of observing the various combinations possible from AB releases are

$$p_{AB}^{AB}(t) = \lambda_{AB} Q_A(t) Q_B(t), \tag{5}$$

$$p_A^{AB}(t) = \lambda_A Q_A(t)[1 - Q_B(t)], \tag{6}$$

$$p_B^{AB}(t) = \lambda_B Q_B(t)[1 - Q_A(t)]. \tag{7}$$

In general, suppose there are  $I$  possible outcomes (for now, an outcome is simply a recaptured tag combination), and let  $i$  be an index representing a particular outcome. Suppose there are  $n_i$  occurrences of outcome  $i$ . Let  $t_{ij}$  be the time after release of the  $j$ th occurrence of outcome  $i$  ( $j = 1, \dots, n_i$ ). Let  $p_i(t)$  be the probability of observing an outcome  $i$  at time  $t$ .

### 3. Nonsimultaneous Releases

To analyze the double-tagging releases it is not necessary to assume that the different tag combinations were released simultaneously. For the AB releases we have  $I = 3$  and  $p_1(t) = p_{AB}^{AB}(t)$ ,  $p_2(t) = p_A^{AB}(t)$ , and  $p_3(t) = p_B^{AB}(t)$ . Suppose that a recapture occurs at time  $t$ . The probability that this outcome is of type  $i$  is given by

$$p_i(t) / \sum_{k=1}^I p_k(t). \tag{8}$$

Hence, the log likelihood,  $\ell_{AB}$ , for the data conditional on the observed recapture times is

$$\ell_{AB} = \sum_{i=1}^I \sum_{j=1}^{n_i} \log \left( p_i(t_{ij}) / \sum_{k=1}^I p_k(t_{ij}) \right). \tag{9}$$

Similar expressions apply for the AA and BB releases. The log likelihood,  $\ell$ , for all of the double taggings together conditional on the observed recapture times is obtained by summing the log likelihoods for each tag release conditional on the observed recapture times. In our case,

$$\ell = \ell_{AA} + \ell_{BB} + \ell_{AB}. \quad (10)$$

#### 4. Simultaneous Releases

In order to incorporate information from single-tagging releases, we now suppose that all tags were released simultaneously. In this context, we use the term *outcome* to refer to the pair

(released tag combination, recaptured tag combination).

Let  $N_i$  be the number of subjects marked with the released tag combination corresponding to outcome  $i$ . In our case  $I = 9$  and

$$\begin{aligned} p_1(t) &= p_A^A(t), & N_1 &= N_A, \\ p_2(t) &= p_B^B(t), & N_2 &= N_B, \\ p_3(t) &= p_{AA}^{AA}(t), & N_3 &= N_{AA}, \\ p_4(t) &= p_A^{AA}(t), & N_4 &= N_{AA}, \\ p_5(t) &= p_{BB}^{BB}(t), & N_5 &= N_{BB}, \\ p_6(t) &= p_B^{BB}(t), & N_6 &= N_{BB}, \\ p_7(t) &= p_{AB}^{AB}(t), & N_7 &= N_{AB}, \\ p_8(t) &= p_A^{AB}(t), & N_8 &= N_{AB}, \\ p_9(t) &= p_B^{AB}(t), & N_9 &= N_{AB}. \end{aligned} \quad (11)$$

Because the tags were released simultaneously, if a recapture occurs at time  $t$ , the probability that the outcome is of type  $i$  is given by

$$\frac{N_i p_i(t)}{\sum_{k=1}^I N_k p_k(t)}. \quad (12)$$

Therefore, the log likelihood,  $\ell$ , for the data conditional on the observed recapture times is

$$\ell = \sum_{i=1}^I \sum_{j=1}^{n_i} \log \frac{N_i p_i(t_{ij})}{\sum_{k=1}^I N_k p_k(t_{ij})}. \quad (13)$$

Note that the use of this likelihood assumes that all of the subjects experience the same mortality over time.

The simultaneous formulation can be used even when data from just double-tagging experiments are available, assuming that the assumption of simultaneity is adequate. Note that the likelihoods for the nonsimultaneous and simultaneous cases are not equal.

It may be possible to include two (or more) nonsimultaneous releases by introducing a nuisance parameter that links the two experiments. For example, a parameter  $\theta$  might represent the survival of animals between the tagging periods. This would only be useful if the second tagging could not be analyzed as a separate experiment, e.g., if it were a single-tagging release. An alternative approach is to model the tag loss in the same model as exploitation, as considered by Wetherall (1982).

#### 5. Hypothesis Testing

For a double-tagging experiment with a single tag type, only the parameters  $\rho$  and  $\phi$  of our tag-shedding model can be estimated (more generally, provided sufficient data, estimation for nonlinear tag-shedding models is possible). When multiple tag types with different visibilities are introduced, the situation is more complex. Suppose that A tags are more visible than B tags, and that together

double tags have the visibility of the more visible of the individual tags. Thus,

$$\begin{aligned} \lambda_A &= \lambda_{AA} = \lambda_{AB}, \\ \lambda_B &= \lambda_{BB} \end{aligned} \tag{14}$$

The relative visibilities of the A and B tags may be obtained by fixing  $\lambda_A = 1$  and estimating  $\lambda_B$ . The models are overparameterized so that, in general, it is not possible to estimate all of the  $\lambda$ 's, but rather, as illustrated above, a reasonable subset.

The simultaneous formulation not only leads to more precise estimates, it also makes it possible to test previously untestable hypotheses (Kirkwood and Walker, 1984). For example, hypotheses about the tag loss rates of single- versus double-tagged subjects can be tested (Appendix). We use a model in which single tags have different loss rates than double tags, and compare this to a null model in which single and double tags have identical loss rates.

Hierarchical models and likelihood ratio tests can be used to test for significant differences between selected parameters.

**6. An Example**

In February 1979, a cod tagging experiment was carried out at 52°N, 51°W (Lear, 1984). We shall consider two of the tag types used in this experiment: 13-mm-diameter yellow Petersen discs (denoted A for convenience) and 8.25-cm yellow or orange spaghetti T-bar tags (denoted B; there was no difference in the return rates of the yellow and orange spaghetti tags). The tags were attached in the area of the first and second dorsal fins. Single tags (A or B) were attached to a total of 3018 fish, while double tags (AA, BB, or AB) were attached to a total of 999 fish (Table 1). Over the next 10 years, the tags from a total of 795 fish were returned.

We maximize the log-likelihood using the BFGS positive definite secant update algorithm (Dennis and Schnabel, 1983). Asymptotic standard errors and correlations of the estimates are calculated from the inverse of the Hessian matrix evaluated at the maximum (Cox and Hinkley, 1974).

First, we estimate the tag-shedding rates separately for the AA, BB, and AB releases (Table 2, models (1), (2), (3)). Note that the data from the AB releases permit the estimation of  $\rho_A$ ,  $\phi_A$ ,  $\rho_B$ , and  $\phi_B$ . These estimates are within one standard error of the corresponding parameters estimated using the AA and BB data.

Next, estimates are obtained using the nonsimultaneous model for the AA, BB, and AB data together. This time an additional parameter, representing the relative visibilities of A and B tags, is estimated. Using the model of equation (14), we fix  $\lambda_A = 1$  and estimate  $\lambda_B$  along with the other parameters (model (4)). A likelihood ratio test rejects the hypothesis that the reporting rates for A and B tags are different (model (4) vs. model (5),  $p = 0.61$ ); hence, we reduce the model by setting all  $\lambda$ 's to 1. The probability of immediate retention is not different for A and B tags (model (5) vs. model (6),  $p = 0.27$ ); hence, we adopt a reduced model in which  $\rho = \rho_A = \rho_B$  (model (6)). Finally, the shedding rate for B does not appear to be greater than that for A (model (6) vs. model (7),  $p = 0.14$ ). We repeated the analysis with the same data (i.e., the AA, BB, and AB data together) but using the simultaneous releases model. The estimates were nearly identical, except for the esti-

**Table 1**

*Tag releases and tag returns grouped by year. Note that exact return times are used in the subsequent parameter estimates.*

Released		Returned										
Tag combination	Tag number	Combination	Year									
			1	2	3	4	5	6	7	8	9	10
A	1014	A	109	50	16	19	11	11	4	1	0	0
B	2004	B	157	84	29	39	18	8	6	2	0	0
AA	200	AA	23	3	4	0	0	1	1	0	0	0
		A	7	1	1	1	0	0	0	0	0	1
BB	400	BB	30	23	7	6	5	1	3	0	0	0
		B	3	5	6	11	3	1	0	0	0	0
AB	399	AB	31	18	4	2	2	1	1	0	0	0
		A	5	5	1	1	2	0	0	0	0	2
		B	5	2	0	1	1	0	0	0	0	0

**Table 2**

Parameter estimates, with asymptotic standard errors in parentheses, and log likelihoods for selected models. Brackets [ ] in the data span indicate simultaneity. An empty cell indicates that the corresponding parameter was not estimated in the model. In the models where the parameter  $\lambda_B$  is estimated, we assume that  $\lambda_A = \lambda_{AA} = \lambda_{AB} = 1$  and  $\lambda_B = \lambda_{BB}$ . In models (6), (7), (9), (10), and (11),  $\rho = \rho_A = \rho_B$ . In models (7) and (11),  $\phi = \phi_A = \phi_B$ .

Model	Data	Estimates					Log-likelihood
		$\rho_A$	$\phi_A$	$\rho_B$	$\phi_B$	$\lambda_B$	
1	AA	0.88 (0.05)	0.03 (0.04)				-24.0
2	BB			0.95 (0.03)	0.07 (0.03)		-56.8
3	AB	0.87 (0.05)	0.01 (0.04)	0.89 (0.06)	0.09 (0.05)		-64.9
4	AA BB AB	0.87 (0.04)	0.02 (0.03)	0.93 (0.03)	0.08 (0.02)	0.81 (0.39)	-147.0
5	AA BB AB	0.88 (0.03)	0.02 (0.03)	0.93 (0.03)	0.08 (0.03)		-147.1
6	AA BB AB	0.90 (0.02)	0.02 (0.02)		0.07 (0.02)		-147.7
7	AA BB AB	0.91 (0.02)	0.05 (0.02)				-148.8
8	[A B AA BB AB]	0.89 (0.03)	0.03 (0.03)	0.91 (0.03)	0.07 (0.02)	0.90 (0.08)	-1247.3
9	[A B AA BB AB]	0.90 (0.02)	0.03 (0.03)		0.06 (0.02)	0.92 (0.08)	-1248.4
10	[A B AA BB AB]	0.90 (0.02)	0.02 (0.02)		0.07 (0.02)		-1249.0
11	[A B AA BB AB]	0.90 (0.02)	0.06 (0.02)				-1250.9

mate of  $\lambda_B$ , which was 1.22 (SE = 0.17) compared to 0.81 (SE = 0.39) for the nonsimultaneous releases model.

Next, in order to include the single-tagging data, the simultaneous formulation is used (model (8)). The probability of immediate retention is not different for A and B tags (model (8) vs. model (9),  $p = 0.14$ ); hence, we adopt a reduced model in which  $\rho = \rho_A = \rho_B$  (model (9)). The reporting rates for the A and B tags are not different (model (9) vs. model (10),  $p = 0.27$ ); hence, we further reduce the model by setting all  $\lambda$ 's to 1. This time there is stronger evidence that the shedding rate for B is greater than the shedding rate for A (model (10) vs. model (11),  $p = 0.05$ ). The inclusion of the single-tagging data thus improves power.

To test whether single and double tags are shed differently we used the two models of the Appendix. Model (A1), in which different shedding rates are assumed for fish that were originally double-tagged and fish that were originally single-tagged, did not provide a significantly better fit than model (A0), in which the rates are assumed equal ( $p = 0.60$ ). Likewise, model (A2), in which tags on a fish with two tags are assumed to have one shedding rate and tags on a fish with one tag are assumed to have another shedding rate, did not provide a significantly better fit than model (A0) ( $p = 0.62$ ). We conclude that the tag-shedding rates for single- and double-tagged fish are not different.

## 7. Discussion

We have shown that by including all the data available, improved estimates may be obtained from tag-shedding experiments. In the example, the inclusion of single-tagging data gave a more precise estimate of relative visibility and improved the power to determine differences in tag-shedding rate. The issue of experimental design—how should the different tag combinations be allocated?—has not been addressed here. Often the particular characteristics of an application will constrain the allocation of tags; e.g., for ducks the AA tag combination (a tag on each leg) is possible, but the BB tag combination (two neck bands) may not be.

## 8. Conclusion

In this paper we have extended the theory and methods of estimating tag-shedding rates using exact recapture times to cases where more than one tag type is used, and have allowed for the cases of double taggings and the simultaneous release of single- and double-tagged subjects. We have constructed likelihoods incorporating not only information from double-tagging releases, but also information from simultaneous single-tagging releases. We know of no other case where this information has been incorporated into the estimation of tag-shedding rates, although this type of information is often available (e.g., Kirkwood and Walker, 1984). We have also been able to estimate the relative visibility of different tag types and the relative tag-loss rates of single and double tags.

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## RÉSUMÉ

Lors de l'estimation de la taille et de l'évolution de populations dans des études de marquage, les estimations des marques perdues à cause de chutes sont nécessaires. Nous généralisons les méthodes de double-marquages existantes de façon à inclure une formulation générale pour des types de marquages multiples. Nous montrons comment l'inclusion de sujets avec marquage simple libérés simultanément avec des sujets à marquage double nous permet d'accroître la précision des estimations et de tester des hypothèses que l'on considérait jusqu'à présent non testables. Un exemple est fourni, concernant la morue dans l'Atlantique-Nord.

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## APPENDIX

*Tag Shedding for Single- and Double-Tagged Fish*

Using the simultaneous model presented in this paper, hypotheses concerning tag-loss rates for single- versus double-tagged subjects may be tested and parameters estimated. A number of different models have been proposed (e.g., Beverton and Holt, 1957). Here we consider three simple models. We assume that the immediate tag retention rate is always  $\rho$ .

- A0. (Null model.) The shedding rate for all tags is  $\phi$ .
- A1. Tags on subjects that were originally double-tagged have instantaneous shedding rate  $\phi_2$ , while tags on subjects that were originally single-tagged have instantaneous shedding rate  $\phi_1$ .
- A2. When a subject has two tags, each tag has instantaneous shedding rate  $\phi_2$ . When a subject has one tag, each tag has instantaneous shedding rate  $\phi_1$ .

Model (A1) represents the case where the act of tagging permanently modifies the tag-shedding rate for a particular subject. This would be the case, for example, when tagging fish, if nearby tags were more prone to shedding because of damage to the skin. Model (A2) represents the case where tag loss is more likely when multiple tags are present. This would be the case, for example, if the tags tend to get snagged in vegetation, etc., and, once snagged, the resulting struggle might dislodge any one of the tags. For each of models (A1) and (A2), we wish to test the hypothesis that  $\phi_2 \neq \phi_1$ . To do this we use a likelihood ratio test, i.e., we compare the log-likelihood for model (A0) with that for model (A1) (and likewise for model (A2)).

For these models there are three outcomes. If a subject, originally single-tagged, is recaptured at time  $t$ , the probability that it retains its tag is denoted  $S_1(t)$ . If a subject, originally double-tagged, is recaptured at time  $t$ , the probability that it retains both tags is denoted  $D_2(t)$ , and the probability that it retains just one tag is denoted  $D_1(t)$ . Let  $N_S$  be the number of subjects marked with single tags and let  $N_D$  be the number marked with double tags. Hence,  $I = 3$  and

$$\begin{aligned} p_1(t) &= S_1(t), & N_1 &= N_S, \\ p_2(t) &= D_2(t), & N_2 &= N_D, \\ p_3(t) &= D_1(t), & N_3 &= N_D, \end{aligned} \tag{15}$$

and the log likelihood is given by equation (13). We now obtain expressions for  $S_1(t)$ ,  $D_2(t)$ , and  $D_1(t)$  under model (A1) and under model (A2).

**Model (A1)**

Model (A1) is easily formulated. Let

$$Q_2(t) = \rho e^{-\phi_2 t}, \tag{16}$$

$$Q_1(t) = \rho e^{-\phi_1 t}. \tag{17}$$

For double-tagged subjects,

$$D_2(t) = Q_2(t)^2 \tag{18}$$

$$D_1(t) = 2Q_2(t)[1 - Q_2(t)]. \tag{19}$$

And for single-tagged subjects,

$$S_1(t) = Q_1(t). \tag{20}$$

**Model A2**

For a single-tagged subject recaptured at time  $t$ , the probability of observing a single tag is

$$S_1(t) = \rho e^{-\phi_1 t}. \tag{21}$$

For double-tagged subjects, things are more complicated. We use a compartmental model to obtain expressions for  $D_2(t)$  and  $D_1(t)$ . For subjects with two tags, the instantaneous tag-shedding rate is  $\phi_2$ . Because each subject has two tags, the instantaneous change in  $D_2(t)$  is

$$\frac{dD_2}{dt} = -2\phi_2 D_2. \tag{22}$$

For subjects with one tag, the instantaneous tag-shedding rate is  $\phi_1$ . The instantaneous rate of change in  $D_1(t)$  is given by the proportion of double-tagged subjects losing a tag at time  $t$  minus the proportion of single-tagged subjects losing a tag at time  $t$ , i.e.,

$$\frac{dD_1}{dt} = 2\phi_2 D_2 - \phi_1 D_1. \tag{23}$$

This is a system of linear differential equations. Assuming that  $\phi_1 \neq 2\phi_2$ , the solution is

$$D_2(t) = D_2(0)e^{-2\phi_2 t}, \tag{24}$$

$$D_1(t) = \frac{2\phi_2}{\phi_1 - 2\phi_2} \left( D_2(0)e^{-2\phi_2 t} + \left[ D_1(0)\frac{\phi_1 - 2\phi_2}{2\phi_2} - D_2(0) \right] e^{-\phi_1 t} \right), \tag{25}$$

where  $D_2(0)$  and  $D_1(0)$  are the initial proportions of subjects with two tags and one tag, respectively. Here  $D_2(0) = \rho^2$  and  $D_1(0) = 2\rho(1 - \rho)$ . If  $\phi_1 = 2\phi_2 = \phi$ , then

$$D_1(t) = D_1(0)e^{-\phi t} + D_2(0)\phi t e^{-\phi t}. \tag{26}$$