THE EFFECT OF BAND LOSS ON ESTIMATES OF ANNUAL SURVIVAL

BY LOUIS J. NELSON, DAVID R. ANDERSON, AND KENNETH P. BURNHAM

Banding has proven to be a useful technique in the study of population dynamics of avian species. However, band loss has long been recognized as a potential problem (Hickey, 1952; Ludwig, 1967). Recently, Brownie et al. (1978) presented 14 models based on an array of explicit assumptions for the analysis of band recovery data. Various estimation models (assumption sets) allowed survival and/or recovery rates to be (a) constant, (b) time-specific, or (c) time- and age-specific. Optimal inference methods were employed and statistical tests of critical assumptions were developed and emphasized.

The methods of Brownie et al. (1978), as with all previously published methods of which we are aware, assume no loss of bands during the study. However, some band loss is certain to occur and this potentially biases the estimates of annual survival rates whatever the analysis method. A few empirical studies have estimated band loss rates (a notable exception is Ludwig, 1967); consequently, for almost all band recovery data, the exact rate of band loss is unknown. In this paper we investigate the bias in estimates of annual survival rates due to varying degrees of hypothesized band loss. Our main results are based on perhaps the most useful model, originally developed by Seber (1970), for estimation of annual survival rate. Inferences are made concerning the bias of estimated survival rates in other models because the structure of these estimators is similar.

METHODS

Our specific results are based on Seber's (1970) model (see Model 1 in Brownie et al., 1978:15–20) but with allowance for a general band retention function (Table 1). Model 1 and its assumptions regarding time-specific survival and recovery rates are specified by three sets of parameters:

N_i = Number of adult birds banded in year i,
S_i = Annual survival rate in year i (specifically, the probability that a bird alive at the beginning of year i will survive until year i + 1), and
f_i = Band recovery rate or "sampling rate" in year i (specifically, the probability that a banded bird alive at the beginning of year i will be reported in year i).

For the results presented here, a fourth set of parameters is required:

θ_i = Band retention rate to the end of the i^{th} year after banding (specifically, the probability of a banded bird retaining its band to the end of the i^{th} year following banding). θ_0 is the probability of retaining a band for a short period immediately following banding.

TABLE 1.

Expected numbers of band recoveries under Model 1 allowing for loss of some bands (only four years of banding and recovery are shown).

Year banded	Number banded	Year of recovery			
i	N_i	1	2	3	4
1	N_1	$N_1\theta_0 f_1$	$N_1\theta_1 S_1 f_2$	$N_1\theta_2 S_1 S_2 f_3$	$N_1\theta_3 S_1 S_2 S_3 f_4$
2	N_2		$N_2\theta_0 f_2$	$N_2\theta_1 S_2 f_3$	$N_2\theta_2 S_2 S_3 f_4$
3	N_3			$N_3\theta_0 f_3$	$N_3\theta_1 S_3 f_4$
4	N_4				$N_4\theta_0 f_4$

We conceptualized four functions to express varying degrees of band retention as a function of the number of years after banding (Fig. 1). Functions A, B, and C reflect increasingly severe band loss. We believe many passerine and game species may be represented by functions A or B. The few species in which band loss is very severe are represented by function C and it would seem that this represents an extreme situation. We note that the band retention rates on Ring-billed Gulls (*Larus delawarensis*) in Table 3 of Ludwig (1967) correspond closely to our curve C. Function D is somewhat different and is an attempt to mimic raptorial species in which a proportion $1 - \theta_0$ of the birds may unfasten the band within a very short period following banding (i.e., $\theta_0 < 1$). Function D does allow for a more gradual loss of bands over time from the remaining birds that do not immediately remove their band. The four band retention functions are intended to cover the general range of conditions that seem likely.

Alternatively, we can conceptualize band loss as the band retention rate between any two successive years, given that the band was still in place at the start of year i.

$$\beta_i = \frac{\theta_i}{\theta_{i-1}}, \qquad i = 2, 3, \ldots$$

$$\beta_1 = \theta_1$$

For example, using function C (Fig. 1) we can compute that the band retention rate between the end of year 6 and the end of year 7 is 0.48 ($\beta_7 = \theta_7/\theta_6$ or $\beta_7 = 0.20/0.42$). Both representations of band loss are equivalent and either one can be computed from the other. The band retention functions in Fig. 1 are more convenient expressions for our analysis.

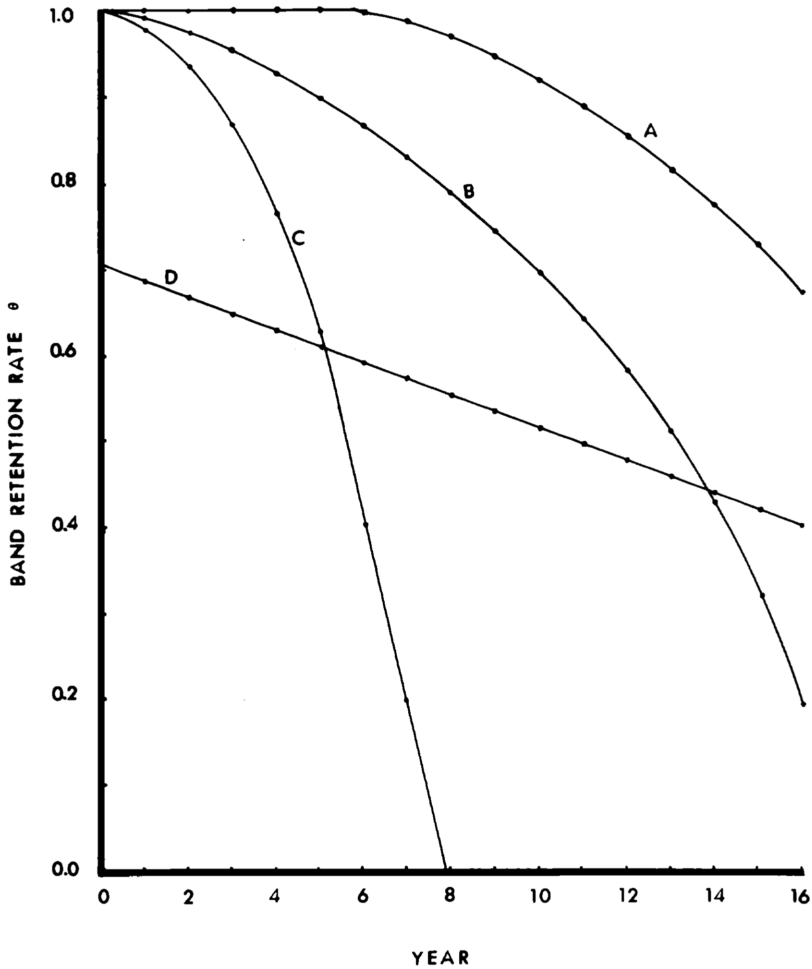

FIGURE 1. Band retention rate as a function of the number of years after banding.

The magnitude of the bias will be influenced by the true survival rate. We use the following sets of survival and recovery rate parameters to examine the effect of band loss $(1 - \theta)$ on the estimators of annual survival:

Case I	$S_i = 0.35$	$f_i = 0.10$,
Case II	$S_i = 0.60$	$f_i = 0.10$,
Case III	$S_i = 0.85$	$f_i = 0.10$,

where i = year.

TABLE 2.
Actual confidence interval coverage as a function of bias/se($\hat{S}_i$).

$\lvert\delta\rvert$ = b/se($\hat{S}_i$)	Coverage
0	0.950
0.1	0.949
0.2	0.945
0.25	0.943
0.3	0.939
0.4	0.932
0.5	0.921
0.6	0.908
0.7	0.892
0.75	0.884
0.8	0.874
0.9	0.853
1.0	0.830
1.5	0.677
2.0	0.484

In all cases we used N_i = 1,500 and examined bias for data sets having 16 years of banding and recovery (i.e., i = 1, 2, . . . , 16). The four band retention functions (A–D) were used for each of the three cases (I–III), giving a total of 12 situations. The quantities N_i, S_i, f_i, and θ_i specify the 12 sets of expected band recovery data under the model specified in Table 1. For each of the 12 sets (where S_i is a known parameter) we computed the expected value of $\hat{S}_i$, $E(\hat{S}_i)$ using the maximum likelihood estimator for Model 1 (see Brownie et al., 1978:16). Because the estimator of S_i under Model 1 is unbiased assuming all $\theta_i = 1$ (no band loss), we can assess the bias of the estimator due to band loss by using the model structure in Table 1 which allows for band loss.

Two remaining quantities were employed in our evaluation and are defined:

$$\text{Bias} = E(\hat{S}_i) - S_i$$

$$\text{Percent relative bias (PRB)} = \frac{E(\hat{S}_i) - S_i}{S_i} \times 100,$$

where $E(\hat{S}_i)$ is computed using the maximum likelihood estimator of the parameter S_i.

The significance of the magnitude of the bias can be evaluated by comparing the bias to the standard error of the estimated annual survival rate. The maximum likelihood estimates of survival under Model 1 (i.e., $\theta_i \equiv 1$) are approximately normally distributed so a 95% confi-

TABLE 3.

Estimated annual survival rates and percent relative bias with $S_i = 0.35$ and $f_i = 0.10$ (Case I) with Model 1. The $\hat{S}_i$ are given as a percentage (i.e., $\hat{S}_i \times 100$).

	Band retention function A		Band retention function B		Band retention function C		Band retention function D	
Year (i)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)
1	34.8	-0.6	34.5	-1.4	33.6	-3.9	33.6	-3.9
5	34.4	-1.8	34.3	-2.0	32.9	-5.9	32.5	-7.2
10	34.3	-2.0	34.2	-2.3	32.9	-5.9	32.5	-7.2
15	34.9	-0.4	34.5	-1.5	33.7	-3.8	33.6	-3.9

dence interval can be computed as $\hat{S}_i \pm 1.96\ \mathrm{se}(\hat{S}_i)$. This procedure is not valid if $E(\hat{S}_i)$ is biased (e.g., by band loss). In this case $E(\hat{S}_i) = S_i + b$, where b is the bias. We can assess the coverage (the proportion of the time that this interval would include the true parameter S_i) of the usual 95% confidence interval procedure, $\hat{S}_i \pm 1.96\ \mathrm{se}(\hat{S}_i)$, by calculating the bias relative to the standard error. Therefore, let

$$\begin{aligned}\delta &= \text{bias/standard error}\\ &= b/\mathrm{se}(\hat{S}_i).\end{aligned}$$

Actual coverage can then be computed from knowledge of the absolute value of δ, $|\delta|$ (see Cochran, 1977:12–15). Of course, if $|\delta| = 0$, the coverage is 0.95. Confidence interval coverage for selected values of $|\delta|$ is given in Table 2.

The four band retention functions presented here are intended to cover the range of likely situations. Many other choices exist for band retention functions, numbers banded, survival rates, and recovery rates that may be of special concern in a given situation. These specific cases can be analyzed for the effects of band loss by the same procedures used in this paper. First, specify the parameters that define the problem (i.e., specify values for N_i, S_i, f_i, and θ_i). Second, calculate the expected recoveries using the specified parameters and the model given in Table 1. Third, compute the expected values of the maximum likelihood estimators of annual survival rates from the generated recoveries (i.e., treat it as a data set and use the formulas given by Brownie et al., 1978:16). Fourth, compute the bias, percent relative bias, and the ratio of bias to standard error with the formulas given above.

Some results on bias will be discussed for other models for adult birds (i.e., Models 2 and 3) as well as several models for young birds where

TABLE 4.

Estimated annual survival rates and percent relative bias with $S_i = 0.60$ and $f_i = 0.10$ (Case II) with Model 1. The $\hat{S}_i$ are given as a percentage (i.e., $\hat{S}_i \times 100$).

	Band retention function A		Band retention function B		Band retention function C		Band retention function D	
Year (i)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)
1	59.7	-0.5	58.8	-2.0	56.1	- 6.4	58.2	-3.0
5	59.4	-1.0	58.2	-3.0	53.9	-10.2	57.6	-4.1
10	59.4	-0.8	58.3	-2.8	53.8	-10.3	57.6	-4.0
15	59.6	-0.6	58.8	-1.9	56.9	- 5.2	58.3	-2.8

S and f are allowed to be time-specific as well as age-specific (i.e., Model H_1) (see Brownie et al., 1978 for details on these estimation models).

RESULTS

The expected annual survival rate $E(\hat{S}_i)$ and the percent relative bias (PRB) for all four band retention functions are given in Table 3 (Case I), Table 4 (Case II) and Table 5 (Case III). The PRB is small in band retention functions A and B and is larger in band retention functions C and D. However, the absolute bias is less than the standard error in nearly all instances (Table 6). The standard error of the estimate depends on the number of birds banded, the recovery rate, and the survival rate. A smaller number of birds banded or a lower recovery rate would result in a larger estimated standard error. This would indicate an even smaller ratio of bias to standard error of the estimate.

Tables 3–5 were computed with 1,500 birds banded each year and a recovery rate of 0.10. In general, fewer than 1,500 birds of a given age, sex, and species are banded each year in a particular study. Furthermore, most species have a band recovery rate considerably less than 0.10. This would suggest strongly that values of $|\delta|$ for most studies would be less than those shown in Table 6 and, therefore, the confidence interval coverage for most real data would be closer to 95% than are our examples.

We found that the bias of the estimator of annual survival rate is virtually independent of our choices of N_i, f_i, and the numbers of years of banding and recovery. Therefore, our results are much more general than the 12 specific examples reported.

The expected values of the maximum likelihood estimators for other models of banded adults (Models 0, 2, and 3; see Brownie et al., 1978) were also computed using the 12 data sets and we found them to be

TABLE 5.

Estimated annual survival rates and percent relative bias with $S_i = 0.85$ and $f_i = 0.10$ (Case III) with Model 1. The $\hat{S}_i$ are given as a percentage (i.e., $\hat{S}_i \times 100$).

	Band retention function A		Band retention function B		Band retention function C		Band retention function D	
Year (i)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)	Annual survival rate ($\hat{S}_i$)	Percent relative bias (PRB)
1	84.4	-0.8	82.1	-3.4	74.6	-12.2	82.7	-2.8
5	84.3	-0.8	81.9	-3.6	69.7	-18.0	82.3	-3.2
10	84.6	-0.5	82.2	-3.3	70.3	-17.3	82.3	-3.2
15	84.6	-0.5	82.7	-2.7	77.8	- 8.4	82.8	-2.6

generally insensitive to band loss. Bias and PRB were minimal except in severe cases with long-lived species. We did note that bias was slightly worse for the estimates of survival under Model 0. In addition, the estimators of annual survival for birds banded separately as young and adults, or young, subadults and adults (Brownie et al., 1978, Chapters 3 and 4, respectively) are also relatively insensitive to bias caused by band loss. The estimators for these models are functions of row totals of the recovery matrix and their structure is quite similar to the estimation models for adults (Models 0, 1, 2, and 3).

The effect of band loss on estimates of annual survival is quite marked in the dynamic and composite dynamic life table methods that allow *only* age-specific survival. In these models, θ_j and S_j are seriously confounded for j = age of bird or band. For example, the life table methods give

TABLE 6.

Ratio of bias to standard error (δ = bias/se($\hat{S}_i$)) for Cases I–III and band retention functions A–D. Refer to Table 2 for the actual coverages of 95% confidence intervals for these ratios.

	Band retention function A			Band retention function B			Band retention function C			Band retention function D		
Year (i)	Case I	Case II	Case III	Case I	Case II	Case III	Case I	Case II	Case III	Case I	Case II	Case III
1	0.1	0.1	0.2	0.1	0.3	1.0	0.3	0.8	2.7	0.3	0.3	0.6
5	0.2	0.1	0.2	0.2	0.4	1.0	0.5	1.5	4.6	0.6	0.5	0.6
10	0.2	0.1	0.1	0.2	0.4	0.8	0.5	1.5	4.2	0.6	0.5	0.6
15	0.1	0.1	0.1	0.1	0.2	0.3	0.3	0.5	0.9	0.2	0.2	0.2

the following estimates of age-specific mortality rates for Case II, function C: 43.9, 45.8, 48.1, 51.9, 57.7, 63.6, 75.0, 100.0, 100.0, etc. Because the true parameter for each age is 40%, we see that not only are the estimators quite biased, but one could easily draw the incorrect conclusion that the population exhibits a markedly age-specific mortality process. The life table methods are affected badly by band loss and have other serious deficiencies (Burnham and Anderson, 1979). We do not recommend making inference from life table analyses nor can we offer advice on how to interpret the present literature based on life table analyses. The new methods derived by Brownie et al. (1978) represent a substantial advance in the analysis of bird banding data.

The goodness of fit tests presented by Brownie et al. (1978) will detect band loss if it is substantial and if sample sizes are large. However, no such test of band loss is possible for the life table models because θ_j and S_j (j = age of bird or band) are confounded (unless a separate, specific study is made of band loss, such as Ludwig, 1967).

CONCLUSIONS

The principal conclusion from these results is that the estimates of adult annual survival rates with Model 1 are only slightly negatively biased by band loss. The effects of band loss on the estimates of annual survival are especially small for species with high mortality rates and are a significant problem only with long-lived species experiencing especially severe band loss. We again emphasize that the bias of the estimated annual survival rate is not affected by our choices of numbers banded (N_i) or recovery rates (f_i). The standard errors of $\hat{S}_i$ will be strongly affected by N_i and f_i (se($\hat{S}_i$) will decrease as either N_i and f_i increases). Most real data will have fewer birds banded than 1,500 per year and smaller recovery rates than 10%. As a result, the applicable standard error of $\hat{S}_i$ for real data will be larger (possibly much so) than we obtained here. It follows that the confidence interval coverage for S_i with real data will be closer to 95% than the results we indicate in Table 6.

The estimated recovery rates ($\hat{f}_i$) are affected primarily by θ_0 and to a much lesser degree by subsequent annual band loss rates. If the first-year band retention is 1.00, then the recovery rate estimate will be slightly inflated (generally less than 1%). If the first-year band retention is less than 1.00, then the recovery rates will be defaulted by this proportion.

SUMMARY

The effect of band loss on the estimators of annual survival rates given in Brownie et al. (1978) was examined. We examined a series of band retention functions and sets of survival rates which cover the range of real-world situations likely to be encountered. Estimates of annual survival rates were found to be only slightly negatively biased in most cases. The bias would be significant only for species with low mortality rates and severe band loss. In contrast, the bias of age-specific survival rates from the life table-type methods is quite marked.

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Utah State University, Department of Wildlife Science, Logan, UT 84322. (Present address of L.J.N.: College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID 83843.) Received 19 October 1978, accepted 29 June 1979.