Appendices

As the authors pointed out in the Preface, the mathematical models and associated analysis procedures presented in this handbook are new. The first such modern model for analysis of banding data was published by Seber (1970); indeed this work spurred the developments presented here (also see Seber 1962). Robson and Youngs (1971) independently developed the model examined by Seber and extended the analysis procedures. We have referred to the Seber-Robson-Youngs model in Chapter 2 as Model 1. With the exception of Model 1, the extensive models, analyses, and testing procedures presented herein are new to the published literature. The purpose of these appendices is to document the basic references for the technical mathematical development of the models and analysis procedures presented in this handbook.

Appendices A and B are intended for the mathematical statistician who wishes to understand the theory behind the methods presented in the handbook. This theory exists in only a few published sources, the most important one being the doctoral thesis of Brownie (1973) (cf. Brownie and Robson 1976). Appendix A presents, by chapter and model, where the background theory may be found. In those instances where no literature exists on the theory, it is so stated and we sketch the underlying theory. We hope that the mathematically trained reader will be able to fill in the gaps. Appendix B presents information on several points of general methodology useful in these models and methods of analysis. For example, there is a convenient method of deriving the ML estimators of survival and recovery rates for all full-rank models which is much easier than the standard approach of taking partial derivatives of the log-likelihood. We assume the reader has read and understands Section 1.5, as well as any chapters for which greater detail is sought.

Appendix C presents 10 papers specifically related to the subject of this *Handbook* that have appeared since the first edition. They have been reprinted in an effort to allow the second edition to be up-to-date.

Appendix A: Basic Mathematical Background and References for the Specific Models Presented

Chapter 2

Models

Four models for the analysis of recovery data from individuals banded as adults are presented in Chapter 2. They are referred to here as Models 0, 1, 2, and 3 in decreasing order of generality. These models are nested in the sense that if Θ_i is the parameter space for model i, then Θ_{i+1} is a proper subspace of Θ_i, $i=0, 1, 2$.

For k years of bandings and $\ell = k+s$ years of recovery data, the cell probabilities for Model 0 are

$$\pi_{ij}=\begin{cases} f_i^* & ,i=j \\ S_i\cdots S_{j-1}f_j & ,i<j\,, \end{cases}$$

for $i=1,\ldots,k, j=i,\ldots,k+s$. The parameter space is

$$\Theta_0=\{f_1^*,\ldots,f_k^*,f_2,\ldots,f_{k+s},S_1,\ldots,S_{k+s-1}\}\,,$$

with dimensionality $3k+2s-2$. Model 1 is obtained from Model 0 by making the assumption (restriction) that $f_i^*=f_i, i=1,\ldots,k$ Thus the parameter space for Model 1 is

$$\Theta_1=\{f_1,\ldots,f_{k+s},S_1,\ldots,S_{k+s-1}\}\,,$$

giving $2k+2s-1$ parameters. To derive Model 2 from Model 1, assume equality of annual survival rates: $S_i=S$, $i=1,\ldots,k+s-1$.
Thus

$$\Theta_2=\{f_1,\ldots,f_{k+s},S\}\,,$$

has $k+s+1$ parameters. Model 3 is the most restrictive possible as it assumes the restriction $f_i\equiv f, i=1,\ldots,k+s$ on Model 2. Hence, the parameter space for Model 3 is

$$\Theta_3=\{f,S\}\,,$$

with only 2 parameters.

It is seen that the parameter spaces are nested as

$$\Theta_3\subset\Theta_2\subset\Theta_1\subset\Theta_0\,.$$

Statistical inference under Model 1 is well documented by Seber (1970) and Robson and Youngs (1971). The latter reference (available from Cornell University, Biometrics Unit) covers the goodness of fit test for Model 1 and presents additional covariance estimators not given in Seber's paper.

Model 0 is developed in Brownie (1974b). This reference, also available from Cornell University, is the only reference to the mathematical developments of Model 0. It is comprehensive, however, covering parameter estimation, confidence intervals, and the goodness of fit for Model 0. This reference also covers the test of Model 1 vs. Model 0. As indicated above, this is a test of the null hypothesis that $f_i^*=f_i$, $i=2,\ldots,k$. Finally, Brownie (1974b) gives the relationships of the three tests: goodness of fit tests of Models 1 and 0 and the test of Model 1 vs. Model 0.

Model 2 was developed in the course of work by the authors. There is no reference to its development. Model 3 is not exactly new in that numerous authors have dealt with this case (model) of constant annual recovery and survival rates. For a review, see Seber (1973:245-246). However, no one has previously derived the exact ML estimators for this model, nor tested any of the assumptions it makes (e.g., a goodness of fit test or the test against Models 2 and 1).

The ML estimators under Models 2 and 3 do not exist in closed form. The equations to be solved are easily found in the usual manner by taking partial derivatives of the log-likelihood. For Model 2 the likelihood is (using $\underline{f}=[f_1,\ldots,f_\ell]$)

$$\mathcal{L}_2(\underline{f},S)=\left[\prod_{i=1}^{\ell}(f_i^{C_i})\right]S^Q\prod_{i=1}^{k}(\pi_{i,\ell+1})^{N_i-R_i}\,,$$

where

$$R_i = \sum_{j=i}^{\ell} R_{ij} \qquad , i=1,\ldots,k \text{ (row total)}$$

$$C_i = \sum_{h=1}^{\min\{i,\,k\}} R_{hi} \qquad , i=1,\ldots,\ell \text{ (column total)}$$

$$Q = \sum_{i=1}^{k} \sum_{j=i}^{\ell} (j-i)\, R_{ij} \ ,$$

and

$$1-\pi_{i,\ell+1} = \sum_{j=i}^{\ell} \pi_{ij} = f_i + Sf_{i+1} + S^2 f_{i+2} + \cdots + S^{\ell-i} f_\ell \ .$$

From the above the reader can easily write the likelihood for Model 3 (also note it is given in Section 1.5). We assume the reader can write down the corresponding log-likelihoods and take their partial derivatives. For example, under Model 2:

$$\frac{\partial \ell n \mathscr{L}_2(\underline{\hat{f}},\underline{\hat{S}})}{\partial f_h} = \frac{C_h}{f_h} - \sum_{i=1}^{\min\{h,k\}} \left(\frac{N_i - R_i}{\pi_{i,\ell+1}}\right) S^{h-i} \qquad , h=1,\ldots,\ell \ .$$

There is one general numerical method used in program ESTIMATE to solve the ML equations for Models 2 and 3; we outline this method in Appendix B.

In the cases where closed-form estimators do not exist the variance-covariance matrices of estimators were derived by inverting (numerically, except for Model 3) the Fisher information matrix under the respective models. We assume the reader can derive the elements of these matrices if they so desire.

Test Statistics

The goodness of fit tests for Models 2 and 3 are standard procedures which we feel are satisfactorily explained in the text. The tests between models (i.e., Model 3 vs. Model 2, Model 3 vs. Model 1, and Model 2 vs. Model 1) computed by ESTIMATE are all likelihood ratio tests. The test of the null hypothesis $S_i \equiv S, i=1,\ldots,\ell-1$ is a test of Model 2 vs. Model 1. The test statistic is

$$2\lambda_{12} = 2[\ell n \mathscr{L}_1(\underline{\hat{f}},\underline{\hat{S}}) - \ell n \mathscr{L}_2(\underline{\hat{f}},\underline{\hat{S}})] \ .$$

In this notation $\mathscr{L}_1(\hat{f},\underline{\hat{S}})$ is the log-likelihood function under Model 1 evaluated at the ML estimators under Model 1. Similarly, $\mathscr{L}_2$ is the log-likelihood under Model 2 evaluated at the ML estimators computed under Model 2. If the null hypothesis is true, $-2\lambda_{12}$ is asymptotically distributed as a central chi-square statistic with $(2\ell-1)-(\ell+1) = \ell-2$ degrees of freedom. The other test statistics are representable as

$$2\lambda_{23} = 2[\ell n \mathscr{L}_2(\underline{\hat{f}},\hat{S}) - \ell n \mathscr{L}_3(\hat{f},\hat{S})] \ ,$$

and $2\lambda_{13} = (2\lambda_{12} + 2\lambda_{23})$, where $2\lambda_{23}$ tests Model 2 vs. Model 3 (i.e., H_0: $f_i = f$) and $2\lambda_{13}$ tests Model 1 vs. Model 3. The interested reader should be able to write down the explicit form of $\ell n \mathscr{L}_i$.

Mean Life Span

Under all four models of Chapter 2 an estimate of adult mean life span is computed. Though there are references to this parameter in the literature (e.g., Cormack 1964), it is not very well explained. A general derivation is given here. For a bird alive at time t_0 ($\equiv 0$) its expected additional lifetime or mean life span (MLS) depends upon the survival curve for that species from t_0 on. In general this survival curve may depend upon age, sex, and calendar year. Let $S(0,t)$ be the probability of survival until time t. Without loss of generality we can write

$$S(0,t) = e^{-\int_0^t p(\tau)d\tau}$$

where $p(\tau)$ is the instantaneous mortality rate. If T = life time (a random variable), then the cdf of T satisfies

$$1 - F(t) = S(0,t) = e^{-\int_0^t p(\tau)d\tau}$$

Hence, the pdf of T is

$$f(t) = p(t)\, e^{-\int_0^t p(\tau) d\tau} \qquad ,0 < t$$

and

$$\mathbf{E}(T) = \int_0^\infty t\, p(t) e^{-\int_0^t p(\tau) d\tau}\, dt\ . \tag{A1}$$

Without assuming something about $p(\tau)$ we cannot simplify this formula. The simplest case is $p(\tau) \equiv p$ which implies annual survival rate is constant: $S(0,1) = e^{-p} \equiv S$. Though this implies Model 3 or 2, it is not necessary in those models to have constant instantaneous mortality. The above assumption leads to $\mathbf{E}(T) = \text{MLS} = 1/p$, and $p = -\ell n(S)$, or

$$\text{MLS} = -\frac{1}{\ell n(S)}\ . \tag{A2}$$

Formula $(A2)$ is the basis for the estimators of MLS used in program ESTIMATE. These estimators of MLS are properly considered as approximations; we feel they are useful enough to be computed, using either $\hat{S}$ from Models 2 and 3, or $\tilde{\tilde{S}}$ from Models 1 and 0 in place of S.

Another useful concept is "half-life" or the time period from banding of adults until we expect half the birds to be dead. This was mentioned in the example of Section 2.2. Under the assumption of constant instantaneous mortality rate $p(\tau) \equiv p$ (which implies Model 2 or 3), lifetime T is an exponential random variable with cdf

$$F(t) = 1 - e^{-pt}\ .$$

Hence, the time $t_{1/2}$ such that half the birds are dead and half alive, is given by

$$0.5 = 1 - \exp(-p t_{1/2}).$$

This equation is easily solved for

$$t_{1/2} = \frac{-\ell n(0.5)}{p} = (0.69)\ \text{MLS}.$$

Thus the adult half-life is conveniently computed as 0.69 times the mean life span.

Chapter 3

All the material in Chapter 3 is new, having been developed within the past 4 years; the primary reference is the doctoral thesis by Brownie (1973).

Models

Five models are presented in Chapter 3; in order of decreasing complexity these are H_3, H_2, H_1, H_{02}, and H_{01}. These five models are nested in the same sense as those of Chapter 2. The model structure (there are two arrays, R_{ij} for adults and Q_{ij} for young) for H_3 is representable as

$$\mathbf{E}\left(\frac{R_{ij}}{N_i}\right) = \pi_{ij} = \begin{cases} f_i''' & ,j = i \\ S_i'''\, f_{i+1} & ,j = i+1 \\ S_i'''\, S_{i+1} \cdots S_{j-1} f_j & ,j = i+2, \ldots, \ell \end{cases}$$

$$\mathbf{E}\left(\frac{Q_{ij}}{M_i}\right) = \pi'_{ij} = \begin{cases} f_i' & ,j = i \\ S_i'\, f_{i+1}'' & ,j = i+1 \\ S_i'\, S_{i+1}'' S_{i+2} \cdots S_{j-1} f_j & ,j = i+2, \ldots, \ell \end{cases}$$

(see also Table 3.7). Because H_3 assumes three age classes, it has quite a few parameters, with the exact number difficult to write unless the value of ℓ (i.e., $\ell = k$, $k+1$, or $\ell > k+1$) is specified. For $\ell = k$ the parameter space of Model H_3 is $\theta_3 = \{f_1''', \ldots, f_k''', f_2'', \ldots, f_k'', f_1', \ldots, f_k', f_2, \ldots, f_k, S_1''', \ldots, S_{k-1}''', S_2'', \ldots, S_{k-1}'', S_1', \ldots, S_{k-1}', S_2, \ldots, S_{k-1}\}$, which has $8(k-1)$ parameters.

Model H_2 is derived from H_3 by assuming the null hypothesis $S_i''' = S_i'' = S_i$ and $f_i'' = f_i$, where the range of i depends upon the value of ℓ.

Further restricting Model H_2 by assuming $f_i''' = f_i$ gives Model H_1 with the structure

$$\pi_{ij} = \begin{cases} f_i & ,j = i \\ S_i S_{i+1} \cdots S_{j-1} f_j & ,j > i\ . \end{cases}$$

$$\pi'_{ij} = \begin{cases} f_i' & ,j = i \\ S_i' S_{i+1} \cdots S_{j-1} f_j & ,j > i\ . \end{cases}$$

The parameter space for Model H_2 when $\ell = k$ is $\Theta_2 = \{f_1''', \ldots, f_k''', f_1', \ldots, f_k', f_2, \ldots, f_k, S_1', \ldots, S_{k-1}', S_1, \ldots, S_{k-1}\}$ with $5k-3$ parameters. The parameter space for Model H_1 when $\ell = k$ is $\Theta_1 = \{f_1', \ldots, f_k', f_1, \ldots, f_k, S_1', \ldots, S_{k-1}', S_1, \ldots, S_{k-1}\}$, with $4k-2$ parameters.

Model H_{02} is derived from H_1 by assuming constant annual survival rates: $S_i' = S'$, and $S_i = S$. The model structure of H_{02} is

$$\pi_{ij} = S^{j-i} f_j \qquad ,j = i, \ldots, \ell,\ i = 1, \ldots, k$$

$$\pi_{j} = \begin{cases} f_i' & ,i = j \\ S' S^{j-i-1} f_i & ,j \geqslant i+1 \end{cases}$$

with parameter space $\Theta_{02} = \{f_1', \ldots, f_k', f_1, \ldots, f_\ell\ , S', S\}$.

Finally, restricting H_{02} by assuming time-constant, but age-specific, recovery rates gives Model H_{01}: $f_i \equiv f, f_i' = f'$. This simplest model has the following structure

$$\pi_{ij} = S^{j-i} f$$

$$\pi'_{ij} = \begin{cases} f' & ,j = i \\ S' S^{j-i-1} f & ,j \geqslant i+1\ . \end{cases}$$

The parameter space is simply $\Theta_{01} = \{f', f, S', S\}$.

The parameter spaces of these five models are nested as $\Theta_{01} \subset \Theta_{02} \subset \Theta_1 \subset \Theta_2 \subset \Theta_3$. The best way for the reader to become familiar with these models is to write out the model structures, in detail for specific k and ℓ (e.g., $k = \ell = 4$ and $k = 3$, $\ell = 5$), and determine the exact number of parameters in each model.

There is an analogy between the one-age-class (adult) and two-age-class (adult and young) models with respect to the assumptions made about time specificity of parameters. This is diagramed below (models are presented in the order, restrictive to general):

Adults	*Adults and Young*
Model 3	H_{01}
Model 2	H_{02}
Model 1	H_1
Model 0	H_2
	H_3

Just as Model H_3 represents a three-age-class case, Model M_0 can represent a two-age-class case (see Section 2.5). Note that in program BROWNIE Model M_1 is referred to as Model H_0.

The development of Models H_1, H_2, and H_3, all estimators, covariances, tests between models, and goodness of fit tests are thoroughly dealt with by Brownie (1973) and Brownie and Robson (1976). We therefore make no further reference to these models.

Models H_{01} and H_{02} Likelihood Functions

The development of Models H_{01} and H_{02}, and associated inference procedures, is not documented anywhere. Consequently, we give the likelihood under each model (denoted $\mathscr{L}_{01}$ and $\mathscr{L}_{02}$):

$$\mathscr{L}_{01}(f', f, S', S) = (f')^{A} (S')^{(TQ-A)} f^{\,(TR+TQ-A)} S^{B} \prod_{i=1}^{k} (\pi_{i,\ell+1})^{N_i - R_{i\cdot}} \prod_{i=1}^{k} (\pi'_{i,\ell+1})^{M_i - Q_{i\cdot}}$$

where

$$A = \sum_{i=1}^{k} Q_{ii}$$

$$TQ = \sum_{i=1}^{k} \sum_{j=i}^{\ell} Q_{ij}$$

$$TR = \sum_{i=1}^{k} \sum_{j=i}^{\ell} R_{ij}$$

$$B = \sum_{i=1}^{k} \sum_{j=i+1}^{k} (j-i)R_{ij} + \sum_{i=1}^{k} \sum_{j=i+2}^{\ell} (j-i-1)Q_{ij}$$

$$\pi_{i,\ell+1} = 1 - f\left(\frac{1-S^{\ell-i+1}}{1-S}\right)$$

$$\pi'_{i,\ell+1} = \begin{cases} 1-f' & ,i=k=\ell \\ 1-f'-S'f\left(\frac{1-S^{\ell-i}}{1-S}\right) & ,\text{otherwise.} \end{cases}$$

Given the above, the reader can determine the log-likelihood function and its derivatives (specifically the likelihood equations). For example

$$\frac{\partial \ell n \mathscr{L}_{01}}{\partial f'} = \frac{A}{f'} - \sum_{i=1}^{k} \left(\frac{M_i - Q_{i.}}{\pi'_{i,\ell+1}}\right).$$

The likelihood under Model H_{02} is

$$\mathscr{L}_{02}(f'_1,\ldots,f'_k,f_1,\ldots,f_\ell,S',S) = \prod_{i=1}^{k} (f'_i)^{Q_{ii}} (S')^{(TQ-A)} \; f_1^{R_{11}} \prod_{j=2}^{k} (f_j)^{(R_{.j}+Q_{.j}-Q_{jj})} \prod_{j=k+1}^{\ell} (f_j)^{(R_{.j}+Q_{.j})} S^B$$
$$\prod_{i=1}^{k} (\pi_{i,\ell+1})^{N_i - R_{i.}} \prod_{i=1}^{k} (\pi'_{i,\ell+1})^{M_i - Q_{i.}}$$

In the above

$$\pi_{i,\ell+1} = 1 - (f_i + Sf_{i+1} + S^2 f_{i+2} + \cdots + S^{\ell-i} f_\ell)$$

$$\pi'_{i,\ell+1} = \begin{cases} 1 - f'_k & ,\, i=k=\ell \\ 1-(f_i + S'f_{i+1} + S'Sf_{i+2} + \cdots + S'S^{\ell-i-1} f_\ell) & ,\,\text{otherwise.} \end{cases}$$

From $\mathscr{L}_{02}$ we can derive the likelihood equations (and the information matrix), for example

$$\frac{\partial \ell n \mathscr{L}_{02}}{\partial f'_h} = \frac{Q_{hh}}{f'_h} - \sum_{i=1}^{\min(h,k)} \left(\frac{M_i - Q_{i.}}{\pi'_{i,\ell+1}}\right) \qquad ,\, h=1,\ldots,k.$$

For Models H_{01} and H_{02}, the log-likelihood equations are solved for the ML estimators by program BROWNIE, using the method of scoring (see Appendix B). The tests among Models H_{01}, H_{02}, and H_1 are all likelihood ratio tests. For example, the test statistic

$$\lambda_{01,02} = -2(\ell n \mathscr{L}_{01} - \ell n \mathscr{L}_{02}) \;,$$

with the likelihoods evaluated at the respective ML estimates, tests Model H_{01} vs. the alternative of Model H_{02}. The null hypothesis for this test is $f'_i \equiv f'$, $i=1,\ldots,k$, and $f_i \equiv f$, $i=1,\ldots,\ell$. The test statistic

$$\lambda_{02,1} = -2(\ell n \mathscr{L}_{02} - \ell n \mathscr{L}_1)$$

tests Model H_{02} vs. the alternative of Model H_1 (the reader should be able to write down the likelihood function for Model H_1). Finally, the test of the H_{01} vs. H_1 model is based on the statistic

$$\lambda_{01,1} = (\lambda_{01,02} + \lambda_{02,1}) \;.$$

Under the null hypothesis, each test statistic is asymptotically distributed as a chi-square random variable with degrees of freedom equal to the difference in the number of parameters between the more general and less general model. For example, there are $(2k+s+2)-4 = 2k+s-2$ degrees of freedom for $\lambda_{01,02}$, and $(4k+2s-2)-(2k+s+2) = 2k+s-4$ degrees of freedom for $\lambda_{02,1}$.

The material presented in Section 3.9 is new to the literature; there are no other similar references.

Mean Life Span

No mean life span statistics are computed by program BROWNIE. Anderson (1975) gives a formula for MLS of young and applies it to mallard data. Again the formula is derived by assuming constant instantaneous mortality for adults and young, but the two age classes have different rates. It is assumed a bird is "young" for the 1 year from time of banding until the first banding anniversary. Hence

$$p(t) = \begin{cases} p' & , 0 \leq t < 1 \\ p & , 1 \leq t \end{cases} ,$$

with

$$S' = e^{-p'},$$

$$S = e^{-p}.$$

Making these substitutions in formula *(A1)* gives, for young, a MLS formula analogous to that developed for adults:

$$\mathbf{E}(T) = \int_0^1 (t\, p'\, e^{-tp'})\mathrm{d}t + \int_1^\infty (t\, p\, e^{-(p' + (t-1)p)})\mathrm{d}t = \frac{1}{-\ell n(S')} + \frac{S'}{-\ell n(S)} + \frac{S'}{\ell n(S')} \; .$$

Chapters 4, 5 and 7

All the material in Chapters 4 and 7, and the test of male vs. female parameters of Chapter 5, is developed in Brownie (1973). There is no other reference for any of this material. The interested reader who comprehends the material of Chapters 2 and 3 should have no trouble understanding the mathematical background of Models H_4, H_5 and H_6 (Chapter 4 of this handbook) and Models H_7 and H_8 (Chapter 7) from Brownie (1973).

The material of Chapter 5 is largely new and only the test of adult males vs. adult females appears in Brownie (1973). The other tests (males vs. females for young and adults, and extension of both these "sex" tests to r areas) were developed explicitly for this handbook. Consequently, the relevant derivations are sketched in Section 5.3. There are no other references dealing with these tests.

Chapters 8 and 9

The materials of Chapters 8 and 9 were also developed entirely in the course of this handbook; consequently, there are no references elaborating on any of this material with the one exception of Section 8.6. In recognition of this, the authors have given enough of the background for mathematical statisticians to understand these sections. Specifically, this is true of Sections 8.2, 8.3, 9.3, and 9.4. While there is no particular mathematical background to Section 8.4, the interested reader should refer to Anderson and Burnham (1976) for more elaboration on the proper interpretation of sampling correlations.

Section 8.6 deals with making direct tests of the equality of survival rates (the same sort of tests can be made for equality of recovery rates). The basic concepts are quite familiar to statisticians in terms of "contrasts" in the context of general linear hypothesis theory (cf. Seber 1966:29).

From the general theory of maximum likelihood estimation we have the parameter estimator vector $\underline{\hat{\theta}}$ is asymptotically distributed as a multivariate normal random variable. Moreover we have an estimator, $\hat{\Sigma}$ of the dispersion matrix of $\underline{\hat{\theta}}$. Consequently for any vector of constants $\underline{c}$, we have $\underline{c}'\,\underline{\hat{\theta}} = \hat{\delta}$ is asymptotically normal with mean $\underline{c}'\,\underline{\theta} = \delta$, and variance estimator

$$\mathrm{var}(\hat{\delta}) = \underline{c}'\,\hat{\Sigma}\,\underline{c} \; .$$

A test of the null hypothesis H_0: $\underline{c}'\,\underline{\theta} = \delta_o$, is thus derived from

$$z = \frac{\underline{c}'\,\underline{\hat{\theta}} - \delta_o}{\sqrt{\underline{c}'\,\hat{\Sigma}\,\underline{c}}} \; ,$$

where under this null hypothesis z is asymptotically normal (0,1). Both two-sided and one-sided alternatives can be tested.

For testing equality of annual survival rates, as from Model 1, we have $\underline{\hat{\theta}}' = (\tilde{S}_1, \ldots, \tilde{S}_{k-1})$, the elements of $\hat{\Sigma}$ are easily obtained from the computer printout, and the specific hypothesis of interest will dictate the constants $\underline{c}$.

For example, if $k-1=7$, and we know the first 3 years were ones of restrictive hunting while the last 4 were liberal regulation years, we might test the null hypothesis of equal average survival rates in these two groups of years:

$$\frac{S_1+S_2+S_3}{3}=\frac{S_4+S_5+S_6+S_7}{4}\ .$$

Hence

$$\underline{c}'=(1/3,\ 1/3,\ 1/3,-1/4,-1/4,-1/4,-1/4).$$

Such tests can be used in all the models and across data sets as well as within data sets. For example, if $\bar{\bar{S}}_f$ and $\bar{\bar{S}}_m$ are estimated average male and female survival rates, respectively, from the same population over the same period of years, then to test H_0: $\bar{S}_f \geq \bar{S}_m$ vs. H_a: $\bar{S}_f < \bar{S}_m$ we use

$$z=\frac{(\bar{\bar{S}}_m-\bar{\bar{S}}_f)}{\sqrt{\operatorname{var}(\bar{\bar{S}}_m)+\operatorname{var}(\bar{\bar{S}}_f)}},$$

and reject H_0 if z exceeds 1.645, for a 5% level test. When the estimators derive from different data sets, which they would in the above example, they are uncorrelated; hence, no covariance terms enter.

The only reference to this type of test for equality of survival rates using banding data is Brownie and Robson (1974b); their paper deals mainly with the optimality and power of these tests under Model 1.

Appendix B: Some General Methodology Underlying Analysis Methods Presented

All of the statistical theory applied to the various models presented here is standard (i.e., Maximum Likelihood estimation, likelihood ratio tests, chi-square goodness of fit tests). There are, however, a few general points of methodology that we wish to point out to the reader interested in the statistical theory behind these applications. These points concern primarily derivation of estimators and their sampling variances.

As was stated in Section 1.5, all models presented here are products of multinomial distributions. Moreover, all 14 models are in the exponential family of probability distributions. Two distinct situations arise with respect to estimation: the full-rank case and the less-than-full-rank case. In the full-rank case the dimensionality of the minimal sufficient statistic (MSS) is the same as that of the parameter space. The alternative is a parameter space of lower dimensionality than the MSS; in this case closed-form estimators usually do not exist. In the full-rank case there is a very useful shortcut to deriving both point estimators and their large sample variance covariance matrix (i.e., the inverse of the information matrix).

The Full-rank Case

Point Estimation

Models M_1, M_0 and H_1 through H_8 of this handbook are full rank. For these models the ML estimators may be derived by equating the observed MSS to its (vector valued) expectation and solving for the unknown parameters. By an appropriate choice of an MSS, this approach can achieve great simplicity over the "usual" approach of deriving and solving the likelihood equations (the partial derivatives of the log-likelihood). This procedure is proven by Davidson and Solomon (1974).

Symbolically, if $Z_1,\ldots,Z_r$ is the MSS from an exponential family with expectations $\mathbf{E}(Z_i)=g_i(\underline{\theta})$, where $\underline{\theta}=(\theta_1,\ldots,\theta_r)'$, then the ML estimator is that value $\underline{\hat{\theta}}$ which satisfies

$$Z_i=g_i(\underline{\hat{\theta}}) \qquad ,i=1,\ldots,r.$$

For all the applicable (full-rank) models of this handbook both the MSS and its expectation are relatively easy to find. For example, for the case of adults only, under Model M_1 (see Appendix A and Section 2.2), with $k=\ell$, a MSS is $\{R_1,\ldots,R_k,C_1,\ldots,C_{k-1}\}$. Its dimensionality is $2k-1$. The parameter space is $\{f_1,\ldots,f_k,S_1,\ldots,S_{k-1}\}$.

In terms of previously used notation we have

$$\mathbf{E}(R_i)=N_i\,[f_i+S_if_{i+1}+\cdots+S_iS_{i+1}\cdots S_{k-1}f_k]=N_i\rho_i$$
$$\mathbf{E}(C_i)=N_1S_1\cdots S_{i-1}f_i+N_2S_2\cdots S_{i-1}f_i+\cdots+N_if_i=\xi_if_i.$$

One could equate R_i and C_i to their expectations and solve for the ML estimators. A little cleverness will, however, make matters easier to the point of being simple. Note that given the above MSS we can compute the quantities $T_1,\ldots,T_k$ because $T_1\equiv R_1$, and

$$T_i=T_{i-1}-C_{i-1}+R_i \qquad ,i=2,\ldots,k.$$

Thus, not only do the ML estimators satisfy $R_i=\mathbf{E}(R_i)=N_i\rho_i$, and $C_i=\mathbf{E}(C_i)=\xi_if_i$, but they also must satisfy $T_i=\mathbf{E}(T_i)$. With minimum difficulty we can find

$$\mathbf{E}(T_i)=\xi_i\rho_i.$$

Now, using this "method of expectation," we can quickly find

$$\hat{\rho}_i=\frac{R_i}{N_i}$$

$$\hat{f}_i=\frac{C_i}{T_i}\frac{R_i}{N_i}.$$

Then noting that $\rho_i = f_i + S_i \rho_{i+1}$, $i = 1, \ldots, k-1$, we can solve for $\hat{S}_i$:

$$\hat{S}_i = \frac{R_i}{N_i}\left(1 - \frac{C_i}{T_i}\right) \Big/ \frac{R_{i+1}}{N_{i+1}}.$$

This approach is much easier than attempting to determine the $2k-1$ likelihood equations by brute force partial differentiation of the Model M_1 log-likelihood function. Admittedly it takes some trial and error to find the simplest MSS to use, but once the reader develops a familiarity with the full-rank models presented here, there should be no great difficulty deriving the ML estimators.

Because of the obvious importance of the point estimators, we will give a second example using the two-age-class model H_1 with $k = \ell$. The elements of the MSS are (see Section 3.1) $R_{i\cdot}$, $R_{\cdot i}$, $Q_{i\cdot}$, $Q_{\cdot i}$, Q_{ii} as well as derived values $T_i + U_i - Q_{i\cdot}$. Relevant expectations are

$$\left.\begin{aligned} \mathbf{E}(R_{i\cdot}) &= N_i \rho_i \\ \mathbf{E}(R_{\cdot i}) &= \xi_i f_i \\ \mathbf{E}(Q_{i\cdot}) &= M_i(f_i' + S_i' \rho_{i+1}) \\ \mathbf{E}(Q_{\cdot i}) &= \xi_i' f_i + M_i f_i' \\ \mathbf{E}(Q_{ii}) &= M_i f_i' \\ \mathbf{E}(T_i + U_i - Q_{i\cdot}) &= \xi_i \rho_i + \xi_i' \rho_i \end{aligned}\right. \qquad , i = 1, \ldots, k-1$$

It is also useful to define $W_i = R_{\cdot i} + Q_{\cdot i} - Q_{ii}$, then

$$\mathbf{E}(W_i) = \xi_i f_i + \xi_i' f_i \quad .$$

Using these various equations, it is not difficult to derive, by the method of expectation, the ML estimators:

$$\begin{aligned} \hat{f}_i' &= \frac{Q_{ii}}{M_{ii}} \ , \\ \hat{f}_i &= \frac{R_{i\cdot}}{N_i}\left(\frac{W_i}{T_i + U_i - Q_{i\cdot}}\right) \ , \\ \hat{S}_i' &= \frac{Q_{i\cdot} - Q_{ii}}{M_i}\left(\frac{N_{i+1}}{R_{i+1\cdot}}\right) \\ \hat{S}_i &= \frac{R_{i\cdot}}{N_i}\left(\frac{T_i + U_i - Q_{i\cdot} - W_i}{T_i + U_i - Q_{i\cdot}}\right)\frac{N_{i+1}}{R_{i+1\cdot}} \quad . \end{aligned}$$

This approach to deriving the ML estimators in the full-rank models is *much* easier than the standard approach of solving the likelihood equations (which are even hard to write down due to their complexity). It does require determining the MSS (cf. Kendall and Stuart 1961, Vol. 2: 193-195) and then for ease of solution some examination of alternative versions of the MSS is recommended.

Variance Estimation

Under Maximum Likelihood theory one usually derives the (asymptotic) variance-covariance matrix as the inverse of the Fisher information matrix. However, direct computation of that matrix requires computing mixed second partial derivatives of the log-likelihood function. Clearly this is not feasible if first partials are not even available. Seber (1970) and Brownie (1973) used the alternative Taylor series approach (or delta method—cf. Seber 1973). In the somewhat general terms used above, let the estimator be derived from the equations

$$\underline{Z} = \mathbf{E}(\underline{Z}) = \underline{g}(\underline{\theta}),$$

where $\underline{Z} = (Z_1, \ldots, Z_r)'$ and $\underline{g}(\underline{\theta}) = (g_1(\underline{\theta}), \ldots, g_r(\underline{\theta}))'$. Assuming a unique solution then we can write

$$\underline{\hat{\theta}} = \underline{g}^{-1}(\underline{Z})$$

and the asymptotic variance-covariance matrix of $\underline{\hat{\theta}}$ is given by

$$V(\underline{\hat{\theta}}) = A \Sigma A'$$

where Σ is the r by r variance covariance matrix of $\underline{Z}$ and

$$A = \left[\frac{\partial \underline{g}^{-1}(\underline{Z})}{\partial \underline{Z}}\bigg|_{\underline{Z} = \mathbf{E}(\underline{Z})}\right].$$

Because this method produces an asymptotically valid result, one would think it ought to be the same as, or similar to, the variance-covariance matrix of $\hat{\underline{\theta}}$ generated as the inverse of the information matrix. In fact, $V(\hat{\underline{\theta}})$ computed this way is *identical* to the inverse of the information matrix in this full-rank exponential family case (we do not know of a published proof of this, but we have such proof on file). It follows that not only are ML estimators given in this handbook, but their variances and covariances are identical to what would be derived by the information matrix approach.

Bias of estimators

Given closed-form formula for parameter estimators, it was possible to evaluate their expectations, hence bias. For example, under Model M_1 the ML estimator of S_i is biased:

$$\begin{aligned}\mathbf{E}(\hat{S}_i) &= \mathbf{E}\left\{\frac{R_i}{N_i}\left(1-\frac{T_i}{C_i}\right)\left(\frac{N_{i+1}}{R_{i+1}}\right)\right\}\\ &= \left\{\mathbf{E}\left(\frac{R_i}{N_i}\right)-\mathbf{E}(\hat{f}_i)\right\}\mathbf{E}\left(\frac{N_{i+1}}{R_{i+1}}\right)\\ &= S_i\rho_{i+1}\mathbf{E}\left(\frac{N_{i+1}}{R_{i+1}}\right),\end{aligned}$$

(from Robson and Youngs (1971), $\hat{f}_i$ is unbiased).

Note that $\rho_{i+1}=\mathbf{E}\left(\frac{R_{i+1}}{N_{i+1}}\right)$, hence we can write

$$\mathbf{E}(\hat{S}_i)=S_i\mathbf{E}(R_{i+1})\mathbf{E}\left(\frac{1}{R_{i+1}}\right)>S_i\ .$$

Strictly speaking $\mathbf{E}(1/R_{i+1})$ is infinite, so we interpreted it as the conditional expectation given R_{i+1} greater than zero. Because R_{i+1} is binomial (N_{i+1}, ρ_{i+1}) it is easy to investigate the bias of $\hat{S}_i$. We did so and found relative bias will run around 1% to 5% for many realistic values of N_{i+1} and ρ_{i+1}. Moreover, asymptotically the bias is of order $1/N_{i+1}$. Specifically, in the limit as $N_{i+1}\rightarrow\infty$

$$\left\{N_{i+1}\left(\frac{\mathbf{E}(\hat{S}_i)}{S_i}-1\right)\right\}\rightarrow\left(\frac{1-\rho_{i+1}}{\rho_{i+1}}\right)\ .$$

A simple modification of the ML estimator produces what we call an essentially unbiased estimator:

$$\tilde{S}_i=\frac{R_i}{N_i}\left(1-\frac{C_i}{T_i}\right)\left(\frac{N_{i+1}+1}{R_{i+1}+1}\right)\ .$$

The exact expectation of $\tilde{S}_i$ is

$$\mathbf{E}(\tilde{S}_i)=S_i[1-(1-\rho_{i+1})^{N_{i+1}+1}]\ .$$

It is seen the bias of $\tilde{S}_i$ decreases exponentially; hence, it will be zero for all practical purposes for samples of banded birds that are large enough to merit analysis $(N_i \geqslant 300)$. It is for this reason we say $\tilde{S}_i$ is essentially unbiased.

The same approach was used to derive essentially unbiased estimators of survival rates (and recovery rates for some models) for the other full-rank models. For example, under Model H_1

$$\tilde{S}_i=\frac{R_{i\cdot}}{N_i}\left(\frac{T_i+U_i-Q_{i\cdot}-W_i}{T_i+U_i-Q_{i\cdot}}\right)\frac{N_{i+1}+1}{R_{i+1\cdot}+1}\ ,$$

$$\tilde{S}_i'=\left(\frac{Q_{i\cdot}-Q_{ii}}{M_i}\right)\frac{N_{i+1}+1}{R_{i+1\cdot}+1}$$

The Less-than-full-rank Case

Four of the 14 models presented here are not full-rank: M_3, M_2, H_{02}, H_{01} (the first two are for adults, the second two for bandings of adults and young). For these models the ML estimators do not exist in closed form; rather they must be found by numerical procedures. Programs ESTIMATE and BROWNIE find these estimators by the method of scoring (cf. Rao 1965:302; Kale 1962). An outline of the method of scoring is given below.

Let the likelihood function be $\mathscr{L}(\underline{\theta})$, where $\underline{\theta}=(\theta_1,\ldots,\theta_r)'$ is the vector-valued parameter. The likelihood equations are

$$g_i(\underline{\theta})=\frac{\partial \ell n \mathscr{L}(\underline{\theta})}{\partial\theta_i} \qquad ,i=1,\ldots,r.$$

The information matrix is $I(\underline{\theta})$ with elements

$$I_{hm}=\mathbf{E}\left[-\frac{\partial^2 \ell n\mathscr{L}(\underline{\theta})}{\partial\theta_h\partial\theta_m}\right] \qquad h,m=1,\ldots,r.$$

Let $\underline{g}(\underline{\theta})=(g_1(\underline{\theta}),\ldots,g_r(\underline{\theta}))'$, and let $\underline{\hat{\theta}}_0$ be an initial guess at the ML estimator $\underline{\hat{\theta}}$. The method of scoring is the iterative procedure defined by

$$\underline{\hat{\theta}}_{i+1}=\underline{\hat{\theta}}_i+\mathrm{I}^{-1}(\underline{\hat{\theta}}_i)g(\underline{\hat{\theta}}_i) \qquad ,i=0,1,2,\ldots$$

Under suitable conditions (as shown by Kale 1962) the sequence $\underline{\hat{\theta}}_i$ converges to the ML estimator of $\underline{\theta}$.

In practice one uses some stopping rule, generally based on convergence of the $\underline{\hat{\theta}}_i$. If the initial "estimate" is good, the number of iterations will be few. For use in ESTIMATE and BROWNIE, the initial estimates of parameters were obtained from an appropriate full-rank model. For example Model M_2, for $k=\ell$, has parameters, $f_1,\ldots,f_k$ and S. From Model M_1, closed-form estimates exist of the parameters $f_1,\ldots,f_k$ and $S_1,\ldots,S_{k-1}$. The only difference between the two models is that M_1 has year-specific survival rates while M_2 has a constant yearly survival. Initial estimates to start the iteration to find ML estimates under M_2 are $\hat{f}_1,\ldots,\hat{f}_k$ from Model M_1 and

$$\hat{\hat{S}}=\frac{1}{k-1}\sum_{i=1}^{k-1}\hat{S}_i\ ,$$

where each $\hat{S}_i$ derives from M_1. Similarly, for the two-age-class models H_{01}, H_{02}, the initial estimators are derived from the closed-form formulae of Model H_1. Because these give excellent starting values, convergence typically requires only 3-5 iterations. In fact we had no convergence problems, except with absolutely horrible data sets (i.e., those with almost no recoveries).

Both point estimation and variance-covariance matrix estimation are taken care of simultaneously by this iterative method because $\mathrm{I}^{-1}(\underline{\hat{\theta}})$ is also computed. When convergence occurs, one has both the ML estimator $\underline{\hat{\theta}}$ and the inverse of the information matrix available.

We leave it to the interested reader to pursue the subject in more depth, for instance by computing the likelihood equations and information matrix under some or all of the models M_3, M_2, H_{02} and H_{01}.

Appendix C: Ten Important Papers Since the First Edition.

Anderson, D.R., and K.P. Burnham. 1980. Effect of delayed reporting of band recoveries on survival estimates. J. Field Ornithol. 51(3):244-247.

Anderson, D.R., A.P. Wywialowski, and K.P. Burnham. 1981. Tests of the assumptions underlying life table methods for estimating parameters from cohort data. Ecology 62(4):1121-1124.

Anderson, D.R., K.P. Burnham, and G.C. White. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. J. Anim. Ecol. 54:89-98.

Burnham, K.P., and D.R. Anderson. 1979. The composite dynamic method as evidence for age-specific waterfowl mortality. J. Wildl. Manage. 43(2):356-366.

Conroy, M.J., and B.K. Williams. 1984. A general methodology for maximum likelihood inference from band-recovery data. Biometrics 40(3):739-748.

Mardekian, S.Z., and L. McDonald. 1981. Simultaneous analysis of band-recovery and live-capture data. J. Wildl. Manage. 45(2):484-488.

Nelson, L.J., D.R. Anderson, and K.P. Burnham. 1980. The effect of band loss on estimates of annual survival. J. Field Ornithol. 51(1):30-38.

Nichols, J.D., S.L. Stokes, J.E. Hines, and M.J. Conroy. 1982. Additional comments on the assumptions of homogeneous survival rates in modern bird banding estimation models. J. Wildl. Manage. 46(4):953-962.

Pollock, K.H., and D.G. Raveling. 1982. Assumptions of modern band-recovery models, with emphasis on heterogeneous survival rates. J. Wildl. Manage. 46(1):88-98.

White, G.C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. J. Wildl. Manage. 47(3):716-728.

J. Field Ornithol., 51(3): 244–247

EFFECT OF DELAYED REPORTING OF BAND RECOVERIES ON SURVIVAL ESTIMATES

BY DAVID R. ANDERSON AND KENNETH P. BURNHAM

Brownie et al. (U.S. Fish and Wildl. Serv., Resource Publ. 131, 1978) presented 14 models based on an array of explicit assumptions for the study of survival in avian populations. These methods are replacing the life table methods previously used to estimate survival rates (e.g., Burnham and Anderson, *J. Wildl. Manage.,* **43:** 356–366, 1979). The new methods allow survival or recovery rates, or both, to be constant, time-specific, or time- and age-specific.

In studies to estimate survival rates for birds the data are often from recoveries of birds shot or found dead during the hunting season and reported to the Bird Banding Laboratory by sportsmen, conservation agency employees, or the general public. This note examines the bias in estimating annual survival due to a proportion of the recoveries being incorrectly reported a year late. Specifically, a few recoveries each year of, for example, adult male American Widgeon (*Anas americana*) banded in California are reported as being recovered in year i + 1 when in fact they were actually recovered the previous year i. Delayed reporting might typically be caused by people finding a band in their heavy clothing in the fall of the year and, being embarrassed about their failure to report the band when it was taken, report it a year late not mentioning the actual year of recovery. Heuristically, delayed reporting should bias estimated annual survival rates upwards because it appears from the data that the birds corresponding to the "delayed" recoveries actually lived an additional year.

METHODS

Results here are based on Seber's (*Biometrika,* **57:** 313–318, 1970) model (see Model 1 in Brownie et al., op. cit.) but with allowance for delayed reporting of a proportion q of the recoveries each year.

Let p = the probability that a band is reported in year i given that the bird also was shot in year i

$q = 1 - p$ = the probability that report of the band is delayed one year.

We assume all recoveries are either reported in year i (as all the models of Brownie et al., op. cit., assume) or one year later. That is, we assume people do not wait 2, 3, . . . , ℓ years before reporting a band recovered in year 1. In this study we allow p to have the values 0.95, 0.98, and 0.99 because these seem to represent realistic values (5%, 2%, and 1% rate of delayed reporting). Of course, if $p = 1.0$ no delayed reporting exists.

The magnitude of the bias will be influenced by the true survival rates and possibly, the true recovery rates. Therefore, we computed the the-

TABLE 1.

Symbolic representation of band recovery data assuming (a) no delayed reporting and (b) proportion $(1 - p)$ of the bands are reported to the Bird Banding Laboratory one year late.

(a) No delayed reporting, $p = 1.0$

Year banded	Number banded	Number of recoveries by year				
		1	2	3	• • •	ℓ
1	N_1	R_{11}	R_{12}	R_{13}	• • •	$R_{1\ell}$
2	N_2		R_{22}	R_{23}	• • •	$R_{2\ell}$
3	N_3			R_{33}	• • •	$R_{3\ell}$
•	•				•	•
•	•				•	•
•	•				•	•
k	N_k					$R_{k\ell}$

(b) Delayed reporting of one year, $p < 1.0$ $(q = 1 - p)$

Year banded	Number banded	Number of recoveries by year				
		1	2	3	• • •	ℓ
1	N_1	$R_{11}p$	$R_{12}p + R_{11}q$	$R_{13}p + R_{12}q$	• • •	$R_{1\ell}p + R_{1\ell-1}q$
2	N_2		$R_{22}p$	$R_{23}p + R_{22}q$	• • •	$R_{2\ell}p + R_{2\ell-1}q$
3	N_3			$R_{33}p$	• • •	$R_{3\ell}p + R_{3\ell-1}q$
•	•				•	•
•	•				•	•
•	•				•	•
k	N_k					$R_{k\ell}p + R_{k\ell-1}q$

oretical bias for three values of annual survival rate (S_i = 0.35, 0.60, and 0.85) and four values of recovery rate (0.01, 0.03, 0.06, 0.10). We examined the bias assuming banding was done over a 10-year period. In all, we examined 36 sets of expected recoveries generated from Table 1b: three survival rate values × four recovery rate values × three rates of delayed reporting = 36.

We computed the expected value of the estimator $\hat{S}_i$, $E(\hat{S}_i)$, for each of the 36 "data" sets using the adjusted maximum likelihood estimator for Model 1 (see Brownie et al., op. cit., p. 16). Because the estimator of S_i under Model 1 is unbiased assuming no delayed reporting, we can assess the bias of the estimator due to delayed reporting by generating data under the model structure shown in Table 1b. In addition, we made analyses under Models 0, 2 and 3 and intend to present these results qualitatively (see Brownie et al., op. cit., for details on these models). Two definitions are required for clarity:

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

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

TABLE 2.

Percent relative bias in the estimator of annual survival due to delayed reporting.

	Survival rate		
	35%	60%	85%
	7.31[1]	1.85	0.74
1%	2.91[2]	0.88	0.06
	2.40[3]	0.33	-0.21
	7.17	2.38	0.74
3%	3.06	0.83	0.35
	1.71	0.42	0.09
	6.60	2.30	1.04
6%	2.37	0.85	0.38
	0.94	0.38	0.17
	7.11	2.38	1.07
10%	2.91	0.92	0.41
	1.40	0.95	0.19

[1] $p = 0.95$ (5% delay)
[2] $p = 0.98$ (2% delay)
[3] $p = 0.99$ (1% delay)

RESULTS

We found, as might be expected, that the bias in the estimator of annual survival rate is independent of the number of birds banded. Furthermore, bias is not strongly affected by variation in recovery rates. Therefore, our results are much more general than the specific examples reported.

The percent relative bias (PRB) of the estimated average annual survival rate, $\hat{S}$ for each of the 36 cases is presented in Table 2. The bias is little affected by differing recovery rates. For survival rates of 60 and 85 percent, the PRB is less than 2.5 percent (e.g., if $S = 0.60$, then 2.5 PRB corresponds to $E(\hat{S}) = 0.615$) and is essentially negligible compared to the magnitude of the standard error commonly found in analyzing real data. The PRB was substantial only for survival rates of 35 percent where $p = 0.95$ (hence for low values of S and high values of q) ranging from 6.60 to 7.31 percent. Still, the size of the standard error is generally larger than this in most banding studies.

The PRB varied somewhat for the individual annual survival rates. Typically, the first and last estimates of annual survival were slightly more biased (e.g., years 1 and 9 in this study) than the estimates in the middle years of the study (e.g., years 3–7). This variation was slight and the estimates of PRB shown in Table 2 are indicative of what to expect for PRB on individual years.

The goodness of fit test for Model 1 (or Models 2 or 3) presented by Brownie et al. (op. cit.) will detect delayed reporting if it is substantial or if the sample size is large, or both. Of special interest is the fact that the tests of Model 1 vs. Model 0 (see Brownie et al., op. cit.) are quite sensitive to delayed reporting. This is indeed fortunate. If delayed reporting of recoveries is serious, the tests should indicate that Model 0 is appropriate and this model is less biased with respect to delayed reporting. The PRB for Model 0 ranged from −1.51 to 1.25 percent with most of the 36 cases studied having a slight negative bias. Of course, it is important to recall the fact that Model 1 is little biased by delayed reporting. In addition, we found Models 2 and 3 were also robust to delayed reporting.

A final remark concerns the direction of the bias. Except for Model 0 which is nearly unbiased, the other models have estimators that are slightly positively biased because of delayed reporting. In contrast, Nelson et al. (*J. Field Ornithol.*, **51:** 30–38, 1980) show that these same estimators were slightly negatively biased due to band loss. In nearly all sets of banding data we can expect some band loss and some delayed reporting of recoveries. Although we certainly cannot claim the two biases will cancel each other, it is at least satisfying that they do not magnify the overall bias.

CONCLUSION

The estimators of annual survival under Models 0, 1, 2 and 3 (Brownie et al., op. cit.) are generally robust to delayed reporting of band recoveries. If real data were analyzed under one of these models, the bias due to delayed reporting could probably be expected to be nearly negligible, especially considering the magnitude of the standard error of the estimates of annual or average annual survival. If banded samples are large and the proportion of recoveries reported a year late is large, then the tests should indicate that Model 0 is appropriate. This model is nearly unbiased with respect to problems in delayed reporting of recoveries. Finally, the direction of the bias in annual survival rate estimates is positive for most models due to delayed reporting and negative due to band loss.

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TESTS OF THE ASSUMPTIONS UNDERLYING LIFE TABLE METHODS FOR ESTIMATING PARAMETERS FROM COHORT DATA[1]

David R. Anderson,[2] Alice P. Wywialowski,[3] and
Kenneth P. Burnham[4]

Since the late 1940's, life table methods have been used to estimate annual, age-specific mortality rates from tagged or banded animal populations. Deterministic methods in the form of a dynamic or composite dynamic life table were developed and used by Bellrose and Chase (1950) and Hickey (1952), and discussed by Geis and Tabor (1963). Seber (1971) used the same basic model, formulated it in the proper stochastic framework, and provided closed form estimators of the survival parameters based on approximations to the maximum likelihood (*ML*) estimators. Cormack (1970) found the *ML* estimates from the same stochastic model by numerical methods; however, identifiability was not explicitly addressed. Recently, North and Morgan (1979) proposed an extension of the same model by allowing the age-specific annual mortality rate to be a function of weather (i.e., they recognized time-dependent variation). Seber (1972, 1981) and Eberhardt (1972) provided further information on this basic model and its assumptions. Finally, we note that these same assumptions are often applied to capture-recapture data, which can then be analyzed by exactly these same life table methods applied to the final capture only (see, e.g., Mardekian and McDonald 1981).

Given this long-used model (i.e., the assumptions), there are a wide variety of ways to attempt to estimate its parameters. However, we question the fundamental assumptions that the model rests upon. In the general context here, there are two assumptions of primary concern:

1) Annual survival is assumed to be age specific only, hence independent of year,
2) The reporting rate λ is assumed to be a constant over all ages and years.

These assumptions are very restrictive and have been shown to be false for hunted waterfowl (Burnham and Anderson 1979). Furthermore, it can be argued that a model allowing each age to have a different survival is not parsimonious. Our objective here is to assess the validity of these assumptions for bird species that are not hunted.

Basic Model and Assumptions

The following notation will be required:

k = number of years of banding,
l = number of years during which recoveries are recorded, $l \geq k$,
S_i = $1 - M_i$ = annual survival rate (probability) for birds of age i,
M_i = $1 - S_i$ = annual mortality rate (probability) for birds of age i,
N_i = number of birds banded in year i, $i = 1, 2, \ldots, k$,
R_{ij} = number of banded birds recovered in year j from birds banded in year i, $i = 1, 2, \ldots, k$, $j = i, i + 1, \ldots, l$,
R_i = total recoveries from birds banded in year i, $= \sum_{j=1}^{l} R_{ij}$,
λ = band reporting rate.

The observed band recovery data can be symbolized as follows:

Number banded	Number recovered in year			Total recovered
	1	2	3 . . . k . . . l	
N_1	R_{11}	R_{12}	$R_{13} \ldots R_{1k} \ldots R_{1l}$	$R_{1.}$
N_2		R_{22}	$R_{23} \ldots R_{2k} \ldots R_{2l}$	$R_{2.}$
$\vdots$			$\ddots \quad \vdots \quad \vdots$	$\vdots$
N_k			$R_{kk} \ldots R_{kl}$	$R_{k.}$

Additional information on the theoretical basis for modeling banding data is contained in Brownie et al. (1978).

The model and its assumptions are expressed by the following expectations for the number of recoveries reported 1, 2, . . . , l yr after being banded as young in year i:

$$N_i(1-S_1)\lambda,\ N_iS_1(1-S_2)\lambda,\ N_iS_1S_2(1-S_3)\lambda,\ \ldots,\ N_iS_1S_2\ldots S_{l-1}(1-S_l)\lambda.$$

These expectations are obvious when one considers that for a bird to be recovered the 1st yr, it must die, its body be recovered, and its band be reported in that year. For a bird to be recovered in the 2nd yr after banding it must survive the 1st yr, die during the

2nd yr, and its body be recovered and its band reported, and so on (Cormack 1970:24). It is important to note the assumption that the reporting rate λ is constant for all years regardless of the age of the bird.

If we define $f_i \equiv (1 - S_i)\lambda$ then the expectations can be written more succinctly:

$$N_i f_1,\ N_i S_1 f_2,\ N_i S_1 S_2 f_3, \ldots,\ N_i S_1 S_2 \ldots S_{l-1} f_l.$$

In this form, Anderson and Burnham (1976:54–59) show that $f_i/(1 - S_i)$ must be constant for all ages, i. Tests of these assumptions constitute the subject of the paper.

Methods

We used the general goodness-of-fit test of Burnham and Anderson (1979:359–360), denoted as Test 1 here, to assess the overall assumptions of the method. Often the expectations for $j \gg i$ will be very small. If the expectations are <2, the chi-square approximation is of doubtful validity. Therefore, it becomes necessary to pool expected values within a row, and corresponding data, if $E(R_{ij})$ is <2. This results in a valid test, but loses 1 df for each pooled R_{ij} value (Brownie et al. 1978:20).

For the assumption that the 1st-yr recovery rates are constant, i.e., are age dependent only, hence not varying by year, we used the test of Burnham and Anderson (1979:360), denoted here as Test 2.

Selection of data for testing model assumptions.— We wished to analyze 20–40 data sets from unhunted species in an effort to assess the assumptions of the life table methods. After considerable effort, we could find only 10 data sets for critical evaluation. We searched *Bird-Banding, Bird Study,* and *North American Bird Bander* on the following key words: banding, band recovery, dynamics, life tables, mortality, populations, and survival. We sent letters to ornithologists and avian ecologists, scanned the *Literature Cited* sections of certain papers, and contacted many banders in an attempt to obtain more data sets for study. Table 1 provides detailed information on each data set.

Results

The results of the overall goodness-of-fit test (Test 1) of the 10 data sets to the life table model are presented in Table 1. For seven cases the significance levels range from .0000 to .0004 and provide strong evidence to reject the assumptions of the model except for the three sets of gull data. Significance levels for the three gull data sets ranged from .2546 to .8553, indicating a good fit.

The significance levels resulting from the application of Test 2 (Table 1) indicate a strong rejection of the null hypothesis that the 1st-yr recovery rates are independent of year for Great Blue Herons, Herring Gulls (New Brunswick), Brown Pelicans, White-Crowned Sparrows, and Chimney Swifts (significance levels varied from .0000 to .0007). Results of this test for Black-Crowned Night Herons and Grey Herons are significant at about the .05 level (.0610 and .0531, respectively). Only in Herring Gulls (Massachusetts), Dominican Gulls, and Great Horned Owls do the 1st-yr recovery rates appear to satisfy this assumption of the life table model. Overall, eight of the 10 data sets clearly do not fit the life table model; Herring Gulls (Massachusetts) and Dominican Gulls represent the exceptions.

Valid inferences must generally stem from a model employing valid assumptions, or, at least, the inferences must be robust, in practical terms, when certain underlying assumptions are violated. From the results presented here and those in Burnham and Anderson (1979) there is now conclusive evidence that the assumptions of the life table method are rarely met for bird banding data. Furthermore, the estimators of model parameters are quite sensitive to the failure of model assumptions (i.e., the estimators of survival are not robust to failure of assumptions). Further development and derivation of alternative estimation methods based on this model and its restrictive assumptions seem pointless, primarily because λ appears to be time specific and age specific (for at least the first or second age classes).

Discussion

It is important to note that the tests used to assess the structure and assumptions of the model are not dependent upon how the model parameters might be estimated. In fact, no parameters are estimated in doing the testing. The most severe problem concerns the reporting rate (λ) which is assumed to be a constant regardless of the age of the bird and the year in which it died. From the results of Test 2, λ clearly varies by year in most cases. Furthermore, because the spatial distribution of recoveries differs by age (e.g., young birds tend to be recovered nearer the banding site than adults), it seems likely that λ is also age specific. Finally, young birds are generally recovered earlier in time (in any given year) than adults.

Estimators of annual survival rate are substantially biased if λ is year and age specific. For example, $E(\hat{M}_1) \doteq M_1\ (\lambda^*/\lambda)$, where λ^* and λ are the reporting rates for young and adult birds, respectively. For this reason alone, most mortality rates published in the literature are overestimated. Essentially, the age-specific variation in the reporting rate manifests itself as an overestimate of mortality rate because the assumption that λ is constant over all ages and years is not met.

TABLE 1. Results of tests of goodness of fit to the assumptions of the life table methods for 10 unhunted species of birds banded as young. Test 1 examined the overall assumptions of the method and Test 2 the assumption that 1st-yr recovery rates are dependent on age only and not on year.

Species (reference)	Banding area	Banding years	*k**	Total banded	Total recoveries	Test 1 significance level	Test 2 significance level
Black-Crowned Night Heron (Henny 1972)	North America	1946–1965	20	13471	287	.0000	.0610
Great Blue Heron (Henny 1972)	North America	1946–1965	20	5330	246	.0000	.0072
Grey Heron (Mead et al. 1979)	Great Britain and Ireland	1955–1974	20	4955	757	.0000	.0531
Herring Gull (Kadlec 1975)	Massachusetts	1967–1969	3	23066	499	.8553	.9256
Herring Gull (Paynter 1966)	New Brunswick	1934–1939	6	31694	1095	.2729	.0004
Dominican Gull (Fordham 1970)	New Zealand	1960–1965	6	7051	388	.2456	.6219
Great Horned Owl (Henny 1972)	North America	1951–1965	15	1896	163	.0001	.5920
Brown Pelican (Henny 1972)	North and South Carolina	1959–1965	7	6465	278	.0004	.0001
†White-Crowned Sparrow (L. Mewaldt, *personal communication*)	California	1973–1978	6	1568	648	.0001	.0000
†Chimney Swift (Henny 1972)	Tennessee	1946–1958	13	73047	2997	.0000	.0000

* Number of years of banding.
† Recaptures.

While it is becoming more clear that λ is age and year specific, it seems likely that the annual survival rate is also year specific. Certainly, there is year-specific variation in survival rate among many exploited species. North and Morgan (1979) found that annual survival might be a function of weather and hence, exhibits year-specific variation.

Substantial bias in parameter estimates is probably the most undesirable result of using a model based on invalid assumptions. Another problem with the life table method is that sampling variation is underestimated. This is because additional parameters are needed to account for the real variability in observed data. The life table model has too few parameters and, therefore, the sampling variance of the survival rate is underestimated. This leads to confidence intervals that have less than the nominal coverage and tests of hypotheses that are greater than α-level tests. The combination of substantial bias and underestimates of sampling variance result in a highly precise, incorrect answer.

Testing of assumptions has been largely neglected in the analysis of data from bird banding studies and, in fact, from animal tagging studies in general. If the numbers banded each year are not available, then tests will have almost no power. Even if large numbers are banded, but the recovery rate is very low, the tests will have limited power because so few data are available for evaluation. This may be the reason, in part, for failure to reject the assumptions for some of these data sets with few years of recovery data.

Conclusions

A variety of schemes has been proposed over the past three decades to estimate age-specific survival or mortality rates. A great many of these "life table methods" are based on the same model. This model assumes that annual survival varies only by age of the bird, and not by year. A second assumption is that the reporting rate is constant over all ages and years. These restrictive assumptions are not valid for most bird banding studies. This prevents valid inferences from being made using analysis of the sample data and, therefore, we recommend against the continued use of this approach.

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PROBLEMS IN ESTIMATING AGE-SPECIFIC SURVIVAL RATES FROM RECOVERY DATA OF BIRDS RINGED AS YOUNG

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SUMMARY

(1) The life table model is frequently employed in the analysis of ringed samples of young in bird populations. The basic model is biologically unrealistic and of little use in making inferences concerning age-specific survival probabilities.

(2) This model rests on a number of restrictive assumptions, the failure of which causes serious biases. Several important assumptions are not met with real data and the estimators of age-specific survival are not robust enough to these failures.

(3) Five major problems in the use of the life table method are reviewed. Examples are provided to illustrate several of the problems involved in using this method in making inferences about survival rates and its age-specific nature.

(4) We conclude that this is an invalid procedure and it should not be used. Furthermore, ringing studies involving only young birds are pointless as regards survival estimation because no valid method exists for estimating age-specific or time-specific survival rates from such data.

(5) In our view, inferences about age-specific survival rates are possible only if both young and adult (or young, subadult and adult) age classes are ringed each year for k years ($k \geqslant 2$).

INTRODUCTION

Analysis methods for estimating age-specific survival rates from the ringing of young birds have generally been based on a single underlying model, or special case of this model. Our objective is to review this model that we will call the life table model, its assumptions, approaches to estimation of the model's unknown parameters and problems in making inference concerning age-specific survival rates. Our work was motivated, to some extent, by the recent paper by Lakhani & Newton (1983).

Basic model and notation

The following notation is required:

k = number of years of ringing,
l = numbers of years during which ring recoveries are recorded, $k \leqslant l$,

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Age-specific survival rates

TABLE 1. Ringing and recovery data for young birds ringed over k years and recovered over l years ($l > k$)

Ringing year i	Number ringed N_i	Recoveries (R_{ij}) in year j						
		1	2	3	$\cdots$	k	$\cdots$	l
1	N_1	R_{11}	R_{12}	R_{13}	$\cdots$	R_{1k}	$\cdots$	R_{1l}
2	N_2		R_{22}	R_{23}	$\cdots$	R_{2k}	$\cdots$	R_{2l}
3	N_3			R_{33}	$\cdots$	R_{3k}	$\cdots$	R_{3l}
·	·				·	·		·
·	·				·	·		·
·	·				·	·		·
k	N_k					R_{kk}	$\cdots$	R_{kl}

ϕ_i = annual survival rate (probability) for birds of age i,
$M_i = l - \phi_i$ = annual mortality rate (probability) for birds of age i,
N_i = number of young birds ringed in year i, $i = 1, 2, \ldots, k$
R_{ij} = number of ringed birds recovered in year j from birds ringed as young in year i, $i = 1, 2, \ldots, k, j = i, i + 1, \ldots, l$,
λ = reporting rate (probability); sometimes used as a subscripted variable to indicate age-specific or time-specific parameters.

Ringing recovery data, the vector N_i and the matrix R_{ij}, are shown in Table 1. The expectations, under the life table model, as functions of the unknown parameters of interest, are found in Table 2.

Assumptions

Several assumptions are necessary in making inference from the life table model:

(1) The ringed sample is representative of the population of interest,
(2) There is no loss of rings,
(3) Survival rates are not affected by ringing,
(4) The year of recovery for those ringed birds recovered is correctly tabulated,
(5) The fate of each ringed bird is independent of the fate of other ringed birds,
(6) Annual survival ϕ_i is age-specific only, independent of year,
(7) The reporting rate λ is a constant over all age classes and years, and
(8) Every ringed bird experiences homogeneous rate parameters ϕ_i and λ (i.e., no population subgroups having heterogeneous parameters.

Assumptions 1, 2, 3, 4, 5 and 8 are not testable without additional data other than the N_i and R_{ij}. Statistical tests of assumptions 6 and 7 are possible using only the ringing data. However, if the general goodness-of-fit test shows lack of fit, it may not be clear which particular assumptions are rejected. Although assumptions 2, 6, and 7 are critical ones under this model, they are not especially critical with certain other models for the analysis of ringing data (e.g., Model H_2 in Brownie *et al.* 1978).

Estimation of parameters

Early attempts to derive estimators of the unknown parameters include Lack (1943), Franer (1945), Bellrose & Chase (1950), Hickey (1952), Haldane (1955), and Balham & Miers (1959). Of these, only Haldane explored optimal estimation, using maximum likelihood theory. He studied the special case of the life table model where $\phi_1 = \phi_2 = \ldots =$

TABLE 2. The life table model for the recovery of ringed birds banded as young ($l > k$)

Banded	Expected number of ring returns in year j from ringing in year i*						
	1	2	3	$\cdots$	k	$\cdots$	l
N_1	$N_1(1-\phi_1)\lambda$	$N_1\phi_1(1-\phi_2)\lambda$	$N_1\phi_1\phi_2(1-\phi_3)\lambda$	$\cdots$	$N_1\phi_1\phi_2 \cdots \phi_{k-1}(1-\phi_k)\lambda$	$\cdots$	$N_1\phi_1\phi_2 \cdots \phi_{i-1}(1-\phi_l)\lambda$
N_2		$N_2(1-\phi_1)\lambda$	$N_2\phi_1(1-\phi_2)\lambda$	$\cdots$	$N_2\phi_1\phi_2 \cdots \phi_{k-2}(1-\phi_{k-1})\lambda$	$\cdots$	$N_2\phi_1\phi_2 \cdots \phi_{l-2}(1-\phi_{l-1})\lambda$
N_3			$N_3(1-\phi_1)\lambda$	$\cdots$	$N_3\phi_1\phi_2 \cdots \phi_{k-3}(1-\phi_{k-2})\lambda$	$\cdots$	$N_3\phi_1\phi_2 \cdots \phi_{l-3}(1-\phi_{l-2})\lambda$
.				.	.		.
.				.	.		.
.				.	.		.
N_k					$N_k(1-\phi_1)\lambda$	$\cdots$	$N_k\phi_1\phi_2 \cdots \phi_{l-k}(1-\phi_{l-k+1})\lambda$

* All subscripts relate to the age of the bird; the parameters λ and ϕ_i are assumed to be independent of year.

$\phi_l = \phi$. His estimators allowed the R_{ij} matrix to be truncated; i.e., before some recoveries in later years were reported. Eberhardt (1972), Caughley (1977), and Seber (1972, 1982) provide details of these early methods.

Maximum likelihood methods for the general model (Table 2) were not fully considered until the work of Cormack (1970) and Seber (1971); also see North & Cormack (1981).

State-of-the-science estimation

Computer algorithms developed by Lebreton (1977) and White (1983) represent optimal estimation from this model and are flexible numerical procedures. Both computer programs require at least one constraint to allow identifiability of the unknown parameters (see Anderson & Burnham 1976, Brownie *et al.* 1978; Burnham & Anderson 1979; Seber 1971, 1972, 1982). Lakhani & Newton (1983) show that the imposition of such an identifiability constraint can produce substantial bias even when the true parameters deviate only slightly from the constraint. Both algorithms use maximum likelihood theory for estimation and testing of a sequence of models for arbitrary k and l without bias due to truncation. The sequence is illustrated in Table 3, depending on the constraints.

Log-likelihood ratio tests and goodness-of-fit tests are provided to allow an appropriate model to be used in making inference from a particular data set (Lebreton 1977; White 1983). These methods and their associated computer algorithms should replace all previous estimation methods for the life table model (however, in the unusual case where $l \to \infty$, closed form estimators and tests can be derived—see Botkin & Miller 1974; Seber 1972), but Lakhani & Newton (1983) have demonstrated that the resulting estimates are liable to be untrustworthy.

PROBLEMS

Although the underlying stochastic model is well defined, cf. Seber (1971), and optimal estimation algorithms have been developed (subject to an identifiability constraint), the life table model is a very poor basis for the analysis of ringing data. Support for this appears in the following sections.

Reporting rate not a constant

Estimates of ϕ_i are critically dependent on the assumption that the reporting rate λ is constant over all years and age classes. The reporting rate λ is the product of the probability of finding a ringed dead bird times the probability of reporting it. The latter probability is unlikely to be age- or year-specific. However, the probability of finding a

TABLE 3.

Model	Constraint(s)	Number of parameters
Full (Table 2)	$\phi_{l-1} = \phi_l$	l
Reduced	$\phi_{l-2} = \phi_{l-1} = \phi_l$	$l-1$
Reduced	$\phi_{l-3} = \phi_{l-2} = \phi_{l-1} = \phi_l$	$l-2$
Reduced	$\phi_{l-4} = \ldots = \phi_l$	$l-3$
.	.	.
.	.	.
.	.	.
Null	All $\phi_i = \phi$	2 (i.e., ϕ and λ)

ringed dead bird is likely to be a function of the cause of death, geographic location of the bird, and the time of the year. This can be easily shown by mapping and tabulating the spatial and temporal distribution of recoveries for the two age groups, young and adult (or young, subadult, and adult classes) (see Hopper, Funk & Anderson 1978). Biologically, we might expect λ to vary by age for, at least, young *v.* adults. Young birds often die due to different causes of mortality, at different times of the year, and in different geographical locations than adults. These basic concepts can be formulated as hypotheses and routinely and statistically tested. Typically, the reporting rate of young birds λ_l is higher than adult birds λ.

The approximate expection of the estimators of age-independent survival (where $\phi_i = \phi$ for all ages) when the reporting rate is age-specific for 2 years (λ_1 and λ_2) is

$$E(\hat{\phi}) \doteq 1 - \frac{M\lambda_1}{M\lambda_1 + \phi\lambda_2}$$

(see example 1a in Table 4). If survival is age-specific for three age classes (i.e., young, subadult, and adult, ϕ_1, ϕ_2 and ϕ_3, respectively), and reporting rate also varies for these three ages classes (λ_1, λ_2 and λ_3, respectively), the following approximations are useful:

$$E(\hat{\phi}_1) \doteq 1 - \frac{M_1\lambda_1}{M_1\lambda_1 + \phi_1 M_2\lambda_2 + \phi_1\phi_2\lambda},$$

$$E(\hat{\phi}_2) \doteq 1 - \frac{M_2\lambda_2}{M_2\lambda_2 + \phi_2\lambda}.$$

The expectations indicate a serious problem with the life table method. Implicitly, the model assumes that the same proportion of ringed birds are found and reported, regardless

TABLE 4. Examples illustrating the approximate age-specific bias in life table estimates of survival when reporting rate is also age-specific

Example	Quantity	Reporting rate λ_1	λ_2	λ_3	λ_4	Survival rate ϕ_1	ϕ_2	ϕ_3	ϕ_4	ϕ_5	ϕ_6
1a	Parameter	0·12	0·06	0·06	0·06	0·6	0·6	0·6	0·6	0·6	0·6
	Estimate*	0·086	—	—	—	0·41	0·58	0·58	0·58	0·58	0·58
	PRB†	−28	43			−32	−3	−3	−3	−3	−3
1b	Parameter	0·015	0·008	0·008	0·008	0·6	0·6	0·6	0·6	0·6	0·6
	Estimate	0·013	—	—	—	0·43	0·64	0·53	0·53	0·53	0·53
	PRB	−13	38			−28	+7	−12	−12	−12	−12
2a	Parameter	0·10	0·06	0·05	0·05	0·6	0·7	0·85	0·85	0·85	0·85
	Estimate	0·076	—	—	—	0·44	0·69	0·87	0·87	0·87	0·87
	PRB	−24	27	52		−27	−1	+2	+2	+2	+2
2b	Parameter	0·010	0·006	0·005	0·005	0·6	0·7	0·85	0·85	0·85	0·85
	Estimate	0·008	—	—	—	0·42	0·64	0·83	0·83	0·83	0·83
	PRB	−20	33	60		−30	−9	−2	−2	−2	−2
3	Parameter	0·18	0·19	0·25	0·29	0·53	0·37	0·59	0·61	0·47	0·61
	Estimate	0·17	—	—	—	0·42	0·59	0·61	0·63	0·60	0·61
	PRB	−6	−12	−32	−41	−21	+60	+3	+3	+28	0
4	Parameter	0·28	0·29	0·24	0·24	0·64	0·49	0·79	0·79	0·79	0·79
	Estimate	0·27	—	—	—	0·44	0·56	0·73	0·73	0·73	0·73
	PRB	−4	−7	13		−31	+12	−8	−8	−8	−8

* Approximate expected value of the estimator.

‡ Per cent relative bias, $(E(\phi) - \phi/\phi) \times 100$.

of the number or the proportion that die in a given year. Furthermore, this proportion is the same for all years $j = 1, 2, \ldots, l$. This is a very restrictive assumption if viewed on biological grounds. The estimators are particularly sensitive to large bias if λ varies by age (a violation of assumption 7, an assumption which is biologically unlikely). The expressions above allow the magnitude of the bias in $\hat{\phi}$ to be approximated as functions of age-specific reporting rates.

We developed a statistical test of the null hypothesis that λ was independent of year in Burnham & Anderson (1979). This test is useful for data sets where few recoveries are available. The test-statistic is distributed as chi square with $k - 1$ degrees of freedom under the null hypothesis that $\phi_1\lambda$ is constant,

$$N^2 \sum_{i=1}^{k} \frac{[R_{ii} - N_i(\frac{R}{N})]^2}{N_i R(N-R)} = \chi^2_{k-1}$$

where N is the total number banded ($N = N_1 + \ldots + N_k$) and R is the total number of first-year recoveries ($R = R_{11} + R_{22} + \ldots + R_{kk}$). For better data sets, additional tests are useful. An extensive analysis of forty-five sets of data on ringed waterfowl rejected this hypothesis in all but six cases ($P < 0{\cdot}05$). In a similar analysis of ten unhunted species we found rejection of the hypothesis in five cases (Anderson, Wywialowski & Burnham 1981).

In general, it seems that the reporting rate is usually age- and time-specific. This is a violation of the assumptions of the life table model and the estimates are quite sensitive to the failure of this assumption (also see Brownie *et al.* 1978).

Constraints

It was not until Seber (1971) that it was realized that the parameters in the life table model could not be uniquely estimated without at least one constraint on the parameters. The full model has $l + 1$ parameters, but only l unique data cells; thus, a fundamental problem is lack of identifiability. This problem is alleviated only if $l \gg k$ or if $(l - k) >$ potential longevity, which is unusual. In examining the older literature, we find the constraint $\phi_l \equiv 0$ was used often implicitly (Burnham & Anderson 1979). This constraint caused a significant age-specific bias in the estimators of survival.

Seber (1971) suggested the constraint $\phi_{l-1} \equiv \phi_l$. This is a minimum to gain identifiability of the unknown parameters. However, Lakhani & Newton (1983) found that such constraints, while seemingly biologically reasonable, could have a marked effect on the estimates of ϕ_i even if λ is constant. They conclude, for this reason alone, "... all hitherto published estimates of age-specific survival are liable to be untrustworthy, if they are based solely on recoveries of dead birds." Additional contraints to reduce the number of parameters, such as $\phi_{l-2} = \phi_{l-1} = \phi_l$, affected the estimates of the remaining parameters.

The necessity of a constraint has not always been recognized. Recently, Piper (1978) derived an estimation scheme for ϕ_i ($i =$ age) and λ_j ($j =$ year). The $\hat{\phi}_i$ are ML estimates found iteratively (under the assumption that λ is a constant over all years and ages) and the λ_j are found analytically (see Piper, Mundy & Ledger 1981). The ϕ_i and λ_j are impossible to estimate uniquely and we warn against the use of Piper's (1978) method.

Fit of model to data

A general goodness-of-fit test was derived by Burnham & Anderson (1979) and allows an assessment of the model using the data. The test can be computed without any constraints on the parameters and without even the need to estimate the parameters. It is a test of model fit, irrespective of the parameter estimation method. Burnham & Anderson (1979) found this model was rejected in forty-three out of forty-five sets of waterfowl data. In fact, the two data sets not rejected had the fewest and fourth fewest recoveries; therefore, probably indicating a lack of power in the test due to small sample size. A similar lack of fit was found in non-hunted bird species by Anderson, Wywialowski & Burnham (1981) where seven out of ten data sets were rejected. It is interesting to note that the remaining three were represented by ringing in only 3–6 years, hence the tests may have low power.

We tested the recovery data from Cape Vultures (*Gyps coprotheres*) ringed as nestlings (see Piper, Mundy & Ledger 1981) to determine if the first-year recovery rate (R_{ii}/N_i) of young birds was constant over all years. This hypothesis was rejected ($\chi^2 \sim 71$, d.f. $= 23$, $P \sim 0.0$). In fact, one can see from the basic data that the first-year recovery rate tends to increase during the years of study. This is a serious violation of the assumptions of the life table model. Piper's (1978) method is incorrect in that the year-specific reporting rates are not uniquely identifiable (see Seber 1971; Anderson & Burnham 1976; Burnham & Anderson 1979). We must conclude that real ringing data rarely fit the life table model.

Sampling correlations

Regardless of the specific constraint used to allow identifiability or reduce the number of parameters to estimate, the parameter estimators can be very highly correlated. For example, the case given by Lakhani & Newton (1983) has sampling correlation coefficients between the estimators of parameters of 0·97 or more. When there are such very high sampling correlations between all the estimated parameters under a given constraint, a small change in the constraint will result in a direct change in all estimated parameters. Thus, different constraints can be expected to have a marked effect on the estimates from a given data set. In fact, we believe that the presence of such very high sampling correlations is indicative that the parameter estimates will be very sensitive to the imposed constraint.

It is very difficult to make inference about age-specific survival processes when the estimators are almost perfectly correlated. Lakhani & Newton (1983) also note problems with the estimated standard errors of the estimates in that they give a "... totally false sense of accuracy and reliability ...." The danger here is that one tends to get highly precise estimates that are very biased; i.e., a precise wrong answer.

Ring loss

The effect of ring loss on estimates of survival is serious for the life table model because it allows survival only to be age-specific. ϕ_i and ring loss rates are seriously confounded and produce a strong age-specific negative bias in estimates of survival (see Ludwig 1967; Botkin & Miller 1974 for reviews). Nelson, Anderson & Burnham (1980) provide an example of this problem whereby an artificial population was analysed with each $\phi_i \equiv 0{\cdot}6$. Using the composite dynamic estimation method for the life table model (Hickey 1952) they computed estimates of survival as 0·56, 0·54, 0·52, 0·48, 0·42, 0·36, 0·25, 0, and 0 for ϕ_1, ϕ_2, ... ϕ_9, respectively. This example was similar to the data on *Larus delawarensis* given by Ludwig (1967) in his study of ring loss. Ring loss cannot be detected by goodness-of-fit tests because ring loss and mortality of ringed birds are confounded. Because of the importance of ring loss and the negative bias in estimates of survival with the life table model, we suspect much of the published literature presents untrustworthy estimates of survival of bird populations. In addition, populations inferred to have age-specific survival beyond about 3 or 4 years may be only losing their rings in later years.

Ring loss is a practical problem that causes large bias in estimators of survival in some models (such as the life table model) while causing negligible bias in other models (e.g., Models 1, 0, H_1 and H_2 of Brownie *et al.* 1978).

EXAMPLES

Six examples (Table 4) illustrate the approximate bias in estimating ϕ_i using the life table model when the reporting rate is age-specific. Expected values were calculated for each example, rounded to the nearest integer, treated as data, and then analysed using program SURVIV (White 1983). The first four examples use $N_i = 3000$, $k = 6$, and $l = 15$. Examples 1a and 1b allow all $\phi_i = \phi$ and let the reporting rate be age-specific for young (λ_1) and adults ($\lambda_2 = \lambda_3 = \lambda_4 = \lambda$). Examples 2a and 2b allow age-specific survival for young ϕ_1, subadults ϕ_2 and adults $\phi_3 = \phi_4 = \phi_5 = \phi_6 = \phi$ while allowing similar age-specificity in the reporting rate λ_1, λ_2, and λ_3. Examples 1a *v.* 1b and 2a *v.* 2b differ only in the magnitude of the reporting rates (see Table 4). Data for Example 3 and the final example were taken from Brownie *et al.* (1978).

Examples 3 and 4 allow the parameters to vary for two and three age classes, respectively. Both allow year-specific variation (another realism not allowed under the life table model). We used reasonable parameter values for many bird populations to illustrate the severe, age-specific bias in estimates from the life table model. The best model in the sequence was selected using the likelihood ratio tests provided by program SURVIV.

The information in Table 4 shows that if the reporting rate varies by age, a substantial negative bias is introduced in $\hat{\phi}_1$. Other estimators of survival are less effected, but frequently reflect negative bias. The mean life span (MLS) is estimated from the estimated survival estimates. The MLS for Experiment 1 is 1·96 years, however, the estimate, computed from the life table estimates of age-specific survival, is only 1·41 years. If ringing of young took place in a remote location where rings were not found or reported, we might expect $\lambda_1 < \lambda_2$ and then a significant positive bias would be expected in $\hat{\phi}_1$.

In is interesting to note that if the reporting rate is age-specific, a violation of the life table model, estimates of λ may be only moderately biased, but will result in much larger biases in $\hat{\phi}_1$. This shows that the estimates of ϕ_1 are very sensitive to age-specific reporting rates.

DISCUSSION

The critical underlying assumptions of the life table model are invalid and the estimators of model parameters are sensitive to these assumption failures, thus rigorous inference about the survival rates of ringed bird populations or their age-specific dynamics, is impossible. The foremost problem arises from the fact that λ varies substantially by age (e.g., young *v.* adults) as this leads to large bias in the estimator for ϕ_1. Even if the key assumptions are met for a particular data set, additional difficulties arise with even optimal estimation methods (e.g., sensitivity of the survival estimates to arbitrary constraints and possibly high sampling correlations among the estimators of ϕ_i and λ). Finally, ring loss is confounded with mortality giving increasing age-specific bias in the survival estimators. This is critical, especially for long-lived species.

Lakhani & Newton (1983) detail some of the major problems with the life table model. They were concerned mainly with the possible effects of constraints, if other model assumptions could be presumed reasonable. The model is even more biologically unreasonable and statistically inept than Lakhani & Newton (1983) document and we believe it is not possible to draw valid inferences from it. We feel it is very unlikely than an accurate and precise estimate of λ (or rather λ_i) or ϕ_1 could be obtained via independent information. For example, $\hat{\phi}_1$ using Cormack's (1964) method, as they mention, is likely to be fairly imprecise. The likely usefulness of $\hat{\lambda}_i$ or $\hat{\phi}_1$ from independent sources diminishes further in examples, such as Lakhani & Newton (1983) give, where the elements in the sampling correlation matrix all exceed 0·97. This is because with such high sampling correlations, the remaining parameters are strongly influenced by the externally estimated parameter any bias or imprecision of that estimate carries over to the other parameter estimates. Use of the life table model is likely only to introduce greater confusion, rather than gaining understanding of population dynamics. The biological and statistical problems of estimation and inference with the life table model may have led to the conclusions forwarded by Botkin & Miller (1974).

The life table method is unacceptable for the analysis of ringing studies of young birds. It is misleading, untrustworthy and gives a false sense of precision (Lakhani & Newton 1983). We cannot recommend its use. We agree with Brownie *et al.* (1978) that, "... based on our current knowledge, there is no valid way to estimate age-specific survival rates from only the banding of young."

The probable solution to problems of estimation and testing is to ring both young and adult (or young, subadult, and adult) age classes each year for $k \geqslant 2$ years. This allows a host of models to be considered that are superior to the life table (see Brownie *et al.* 1978 for twelve models allowing year-specific, age-specific, or year and age-specific survival and reporting parameters).

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THE COMPOSITE DYNAMIC METHOD AS EVIDENCE FOR AGE-SPECIFIC WATERFOWL MORTALITY

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Abstract: For the past 25 years estimation of mortality rates for waterfowl has been based almost entirely on the composite dynamic life table. We examined the specific assumptions for this method and derived a valid goodness of fit test. We performed this test on 45 data sets representing a cross section of banded samples for various waterfowl species, geographic areas, banding periods, and age/sex classes. We found that: (1) the composite dynamic method was rejected ($P < 0.001$) in 37 of the 45 data sets (in fact, 29 were rejected at $P < 0.00001$) and (2) recovery and harvest rates are year-specific (a critical violation of the necessary assumptions). We conclude that the restrictive assumptions required for the composite dynamic method to produce valid estimates of mortality rates are not met in waterfowl data. Also we demonstrate that even when the required assumptions are met, the method produces very biased estimates of age-specific mortality rates. We believe the composite dynamic method should not be used in the analysis of waterfowl banding data. Furthermore, the composite dynamic method does not provide valid evidence for age-specific mortality rates in waterfowl.

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The composite dynamic (CD) life table has been the primary method used to estimate annual mortality rates of waterfowl populations for the past 25 years. Early descriptions and use of the method are found in Bellrose and Chase (1950) and Hickey (1952). The model underlying this estimation method, the properties of the method, and explicit computing formulas are usually not specified clearly (see Geis and Tabor 1963; Geis 1972*a,b*). Nevertheless, use of the method has been widespread (e.g., Moisan et al. 1967; Geis et al. 1971) and not at all restricted to waterfowl. Anderson and Burnham (1976), Eberhardt (1972), and Seber (1972, 1973) present recent material on the validity and usefulness of the method.

Three crucial assumptions are necessary for the composite dynamic method to be valid: (1) annual mortality rate (M_i) varies only by the age (i) of the bird, no time-specific variation of the M_i is allowed; (2) annual recovery rate is a constant fraction of annual mortality rate; and (3) virtually none of the banded birds remains alive when the data are analyzed (Geis 1972*a*:16).

A variety of implications follow from these assumptions, perhaps the most important one is that no year to year (time-specific) variation in either harvest rates, or band reporting rates is allowed. These 2 implicit assumptions are generally recognized as untrue (e.g., Anderson 1975; Henny and Burnham 1976). Assumption (3) means the recovery data from a banding study cannot be validly analyzed with the CD method for many years after banding has stopped. We believe that few biologists recognize the assumptions implicit in the method nor the degree to which the estimators of M_i may be sensitive to departures from these important assumptions.

In addition to these specific assumptions needed for the CD method, a number of general assumptions are necessary for meaningful analysis of banding data under any model (Brownie et al. 1978:6–7). In particular there must be no band loss. Band loss is indistinguishable from age-specific mortality, and is especially serious under the CD method of analysis.

A large scientific literature on various species of birds contains the results from a CD analysis of band recovery data. It has focused on 3 main areas: (1) the estimation of 1st-year mortality rate (M_1) from birds banded as young and estimation of average annual mortality rate from birds banded as adults (i.e., for adults, M_1 is interpreted as an average); (2) studying age-specificity of the mortality process; i.e., estimating $M_1, M_2, M_3, \ldots$; and (3) studying the effect of hunting on total annual mortality rates. We wish to address the 1st and 2nd of these as the 3rd has already been discussed by Anderson and Burnham (1976).

It is surprising that no one has reported results of any statistical tests of the assumptions required for the CD method to perform validly. Recently, Hickey (1972:264) believed, "... it seems particularly necessary that the basic assumptions underlying these calculations be subjected to an adequate review." That is our purpose here. The 4 objectives of this paper are: (1) to present the specific assumptions and model necessary for the CD method to be valid; (2) to present 2 statistical tests of these assumptions: (a) a goodness of fit test of the CD model to data, and (b) a test that recovery rates are year-independent; (3) to judge the validity of the CD model by analyzing a cross section of waterfowl data; and (4) to reflect on the CD method as evidence for age-specific mortality in waterfowl.

STATISTICAL CONSIDERATIONS

Assumptions and Model

To specify clearly the assumptions and the model underlying the CD method, and the method itself, we must present some mathematical background. First, we introduce our basic notation; for a more detailed discussion of some of these terms and basic background on analysis of recovery data see Anderson (1975), Anderson and Burnham (1976), and Brownie et al. (1978):

k = Number of years of banding,

l = Number of years during which recoveries are recorded, $l \geq k$,

$S_i = 1 - M_i$ = Annual survival rate (probability) for birds of age i,

$M_i = 1 - S_i$ = Annual mortality rate (probability) for birds of age i,

f_i = Annual band recovery rate (probability) for birds of age i,

N_i = Number of birds banded in year i, $i = 1, \ldots, k$,

R_{ij} = Number of birds recovered in year j from birds banded in year i, $i = 1, \ldots, k$, $j = 1, \ldots, l$,

$R_{i\cdot}$ = Total number of band recoveries from the ith banded cohort (i.e., birds banded in year i) $= \sum_{j=1}^{l} R_{ij}$,

D'_i = All recoveries of bands exactly i years after banding (corresponds to i years of age for birds banded as young) $i = 1, \ldots, l$, and

TN_i = Total number of banded birds that could have contributed to the recoveries D'_i exactly i years after banding (often called "banded birds available" in year i), $i = 1, \ldots, l$.

The above 2 quantities are computed from the R_{ij} and N_i, respectively. In the case of $k = l$ they are (for $i = 1, \ldots, k$)

$$D'_i = \sum_{j=1}^{k-i+1} R_{j,j+i-1},$$

$$TN_i = \sum_{j=1}^{k-i+1} N_j.$$

For example, for $i = 1$, $TN_1 = N_1 + N_2 + \cdots + N_k$ and $D'_1 = R_{11} + R_{22} + \cdots + R_{kk}$, while for $i = k$, $TN_k = N_1$ and $D'_k = R_{1k}$. The mathematical definitions of D'_i and TN_i for $l > k$ are complex and will not be given here. For the general computing formulas of D'_i and TN_i see Anderson and Burnham (1976:55).

Finally we define

$D_i = D_i'/TN_i$ = the proportion of recoveries of all birds aged i, $i = 1, \ldots, l$.

In the wildlife literature, the CD method is often presented only as a sequence of calculations based on the tabulated banding and recovery data. The formula representing these computations for estimating the mortality rate of birds in their ith year of life is:

$$\hat{M}_i = D_i/(D_i + D_{i+1} + \cdots + D_l) \qquad i = 1, \ldots, l-1. \quad (1)$$

Seber (1972) has given a formalization of this method and some of its properties (also see Seber 1971). Our use of the notation D'_i and D_i is the reverse of Seber's use of this same notation.

Given the estimator of formula (1), we specify the exact model necessary for this to produce valid estimates of age-specific mortality rates. It is beyond the scope of this paper to present all the needed background material on modeling band recovery data (see Brownie et al. 1978). Only key results will be given.

The CD procedure is meant to apply only in cases of age-specific survival and recovery rates. Therefore the general model structure in terms of expected band recoveries is

$$E(R_{ij}) = \begin{cases} N_i f_1 & i = 1 \\ N_i S_1 S_2 \ldots S_{j-i} f_{j-i+1} & i > 1. \end{cases} \quad (2)$$

To complete the statistical model for the recoveries R_{ij}, we note that the recoveries from each banded cohort are multinomial random variables. Thus given N_i birds banded in year i, we have R_{ii}, $R_{i,i+1}$, $\ldots$, R_{il}, $N_i - R_{i\cdot}$ are multinomial random variables with expectations given by (2). Note that:

$$E(R_{i\cdot}) = E(R_{ii}) + E(R_{i,i+1}) + \cdots + E(R_{i,l}).$$

Recognition of this multinomial model as the correct sampling model for the data allows rigorous consideration of estimation of parameters and tests of the assumptions (see Brownie et al. 1978).

We mention that a special case of the CD model is that of assuming constant recovery and survival rates; that is $f_i \equiv f$ and $S_i \equiv S$ for all i.

From formula (2) we derive:

$$E(D_i) = \begin{cases} f_1 & i = 1 \\ S_1 S_2 \ldots S_{i-1} f_i & i > 1. \end{cases} \quad (3)$$

A fundamental property of estimators is that they should be consistent; that is for large samples their expected value converges to the true parameter value (this is related to unbiasedness). Based on formulas (1) and (3) and the requirement of consistency, Anderson and Burnham (1976:54–55) showed that the CD method is valid only if the ratio f_i/M_i is constant for all i. Thus we must assume that:

$$\frac{f_i}{M_i} \equiv a \qquad i = 1, \ldots, l \qquad (4)$$

for some constant a. This is a very restrictive assumption, and unless it is tested there is no reason to believe it is true for waterfowl (Anderson and Burnham 1976:55–56). Finally, the CD estimator of the parameter a is

$$\hat{a} = D_1 + D_2 + \cdots + D_l.$$

Estimation

The CD estimation method was developed long before the complete statistical model given above was formalized. The question of optimal inference under the CD assumptions has never been considered in the literature, nor have sampling variances been developed for $\hat{M}_i$ of formula (1). In fact the estimator of (1) can be improved upon in several ways; e.g., standard maximum likelihood theory.

Identifiability of parameters is an important subject, albeit a quite technical one (cf. Brownie et al. 1978:112). A key result in this regard is Seber's (1971) proof that the parameters $M_1, M_2, \ldots, M_l$ and a of the CD model are not even uniquely identifiable. The basic problem is that given any set of banding data or expected recoveries, numerous different sets of parameters under the CD model could generate exactly these same data. For example, let $k = l = 3$; the following parameters will produce exactly the same expected values, $E(R_{ij})$, for any numbers banded N_i:

$$a = 0.1, \qquad S_1 = 0.6, \qquad S_2 = 0.5, \qquad S_3 = 0.4$$

and

$$a = 0.2, \qquad S_1 = 0.8, \qquad S_2 = 0.8125, \qquad S_3 = \frac{11.2}{13} = 0.86154.$$

In order to estimate the parameters of the CD model at least 1 constraint must be imposed. The types of constraint allowable are to either (1) arbitarily specify 1 (or more) mortality rate(s), or (2) set 2 or more mortality rates equal. Seber (1971) assumed $M_{l-1} = M_l$ and derived estimators which differ from those of the CD method. A thorough statistical treatment of this model will require sequential testing for differences in age-specific mortality rates. Thus one would adopt constraints such as $M_j = M_{j+1} = \cdots = M_l$ and test the adequacy of the model for increasing values of j.

The CD method employs the first approach; arbitrarily specifying that $M_l = 1$. This implicit constraint is unrealistic. It also implies that all products such as $S_iS_{i+1} \ldots S_l$ are are zero, and this implies the usually stated condition required for validity of the CD estimators.

Using formula (3) we can show the estimator $\hat{M}_i$ is consistent for the parameter

$$M_i^* = \frac{M_i}{1 - S_iS_{i+1} \ldots S_l} \qquad i = 1, \ldots, l-1.$$

This means that the expected value of $\hat{M}_i$ is approximately M_i^*, with the approximation getting better for large samples of banded birds. Another way to say this is that $\hat{M}_i$ is a biased estimator (it overestimates M_i) unless the product $S_iS_{i+1} \ldots S_l$ is zero. This will be true only if l is much larger than i, i.e., one does not analyze the data until several years after the last cohort is banded (cf. Seber 1972). Two facts are apparent: (1) the bias in $\hat{M}_i$ is due to the implicit constraint $M_l = 1$, and (2) if a realistic constraint such as $M_{l-1} = M_l$ were used, the statistical bias would vanish as sample size increases.

Goodness of Fit Test

Let $\hat{E}(R_{ij})$ be an (asymptotically efficient) estimator of the expected value of the random variable R_{ij} under the assumptions of the CD method. Then the general goodness of fit test for this model is simply the classical chi-square test based on (observed − expected)²/expected. Symbolically the test statistic is:

$$\chi^2 = \left\{ \sum_{i=1}^{k} \sum_{j=1}^{l} \frac{[R_{ij} - \hat{E}(R_{ij})]^2}{\hat{E}(R_{ij})} \right\} + \left\{ \sum_{i=1}^{k} \frac{[R_{i\cdot} - \hat{E}(R_{i\cdot})]^2}{[N_i - \hat{E}(R_{i\cdot})]} \right\}. \qquad (5)$$

The 1st term is based on the recoveries, while the 2nd term accounts for those bands that were never recovered. The quantity $\hat{E}(R_{i\cdot})$ is computed as

$$\hat{E}(R_{i\cdot}) = \sum_{j=i}^{l} \hat{E}(R_{ij}).$$

Under the null hypothesis that the CD model fits the data this test statistic has a chi-square distribution with

$$\frac{k(k+1)}{2} + k(l - k + 1) - l$$

degrees of freedom. Often the expectations for j much greater than i will be very small. If they are less than 2, the chi-square approximation is of doubtful validity. Therefore, it becomes necessary to pool expected values within a row, and corresponding data, if $\hat{E}(R_{ij})$ is less than 2. This results in a valid test, but loses 1 degree of freedom for each pooled R_{ij} value.

Usually the values of $\hat{E}(R_{ij})$ are found by substituting estimated parameter values in the formula for $E(R_{ij})$ (formula 2); in so doing we use $\hat{f}_i = \hat{a}\hat{M}_i$. Using the CD estimators of these parameters (and the constraint $\hat{M}_l \equiv 1$) leads to the simple formulas:

$$\hat{E}(R_{ij}) = N_i D_{j-i+1} \qquad i = 1, \ldots, k \quad j = i, \ldots, l.$$

For example,

$$\hat{E}(R_{ii}) = N_i \hat{f}_1 = N_i \hat{a} \hat{M}_i = N_i D_1.$$

We note that $E(R_{ij})$ is estimable without constraints needed to allow identifiability of the parameters. Therefore, the goodness of fit test (5) is not dependent upon how the parameters are estimated. In fact, this test can be computed without estimating any parameters by computing the conditional expectation of R_{ij} given the statistics $D_1, \ldots, D_l$ (many of the goodness of fit tests in Brownie et al. (1978) were constructed following this procedure). It can be shown that:

$$E(R_{ij} | D_1, \ldots, D_l) = N_i D_{j-i+1},$$

and mathematically a valid goodness of fit test results from using $\hat{E}(R_{ij}) = E(R_{ij} | D_1, \ldots, D_l)$. The validity of this test is unaffected by truncation; i.e., it is valid for all values of k and l.

This goodness of fit test provides a valid test of the 2 assumptions critical to the CD model (the M_i are age-specific only, and $f_i = aM_i$). If the test indicates that the model does not fit we are saying 1 or both of these assumptions is false. Therefore, the method cannot be used in the analysis of data and the estimates of parameters are not useful.

A more specific test can be used to assess the assumption that 1st-year recovery rates are constant, i.e., are age-dependent only, hence not varying with time. Under the assumptions of the CD method we must have $E(R_{ii}) = N_i f_1$ or the ratios R_{ii}/N_i have a constant expectation, independent of the year (i) of banding. A simple k by 2 chi-square contingency table test of this assumption can be written as:

$$\chi^2 = (N.) \sum_{i=1}^{k} \frac{\left[R_{ii} - N_i\left(\frac{R..}{N.}\right)\right]^2}{(R..)(N_i - R..)}, \quad (6)$$

where $R..$ = total 1st-year recoveries and $N.$ = total number banded $\equiv TN_1$. This test has $k - 1$ degrees of freedom. If this test rejects the null hypothesis of constant first-year recovery rate then the CD model is invalid. This is because of time variation in the 1st-year recovery rates as would result if harvest rates vary over time.

SELECTION OF WATERFOWL DATA

An objective of this paper is to assess the validity of the CD model for waterfowl banding data in general (excepting geese and swans). Thus we want to test the null hypothesis that the CD model generally fits waterfowl data, versus it does not generally fit such data. This is not the same as testing whether the model fits a given set of data. To meet this more general objective a proper scientific approach is to select a representative sample of all banded waterfowl populations and conduct the tests of assumptions on these data sets. The inference is then not just that the model does or does not fit these given data sets but that it does or does not fit waterfowl banding data in general.

To meet this objective we started with a large tabulation of most of the duck banding data in Canada and the United States from 1955 to 1972. Then we established criteria for selecting data sets. The 2 primary criteria were that the data sets selected be representative of (banded) waterfowl populations and that the banded samples be large enough to yield a reliable test of the assumptions.

To be representative of waterfowl banding we sought to cover a variety of geographic areas, ages, sexes, species, and banding periods (i.e., preseason vs. winter). Before selecting these data sets we established some criterion for a "good" data set; by "good" we mean sufficient numbers of birds banded and of recoveries to yield a meaningful test of the CD method assumptions. Our target goals for each data set were to have at least 5 years of banding ($k \geq 5$), an average number banded per year of at least 300, and an average 1st-year recovery rate of at least 3%. In general we met these criteria, however, occasionally we used $k = 4$ and for some data sets average recovery rate was lower than 3% (but in these cases annual numbers banded were in the thousands).

Using these guidelines we selected 45 data sets relating to 9 species from the large tabulation. We emphasize that the tabulation showed only raw data and had never been analyzed by us. Thus we made our selection of data sets before ever knowing the outcome of the tests of assumptions. Once these 45 data sets were selected, we used all of them; there was no subsequent deletion or addition of data sets after the analyses. Thirty-four data sets were from preseason banding (8 adult and 26 young data sets) and 11 sets were from winter banding (all adults). Table 1 provides detailed information on each data set.

RESULTS

Year-specific Recovery Rates

The CD model allows recovery rates to be age-specific only, and these rates must be directly proportional to the age-specific mortality rates. However, waterfowl hunting regulations in North America have fluctuated greatly over the past 25 years (Martin and Carney 1977). It seems logical that recovery rates do vary by year—a violation of a necessary condition of the CD method (Anderson and Burnham 1976:13).

We tested the null hypothesis that 1st-year recovery rates are constant across years using (6); the results appear in Table 1. The test results indicate a sound rejection of the null hypothesis. We conclude that recovery rates in ducks vary significantly by years, a major violation of the CD model assumptions. The idea that year-specific variation is "averaged out" by combining data over a number of years in a "composite" is not correct. For example, this procedure produces severe overestimates of age-specific mortality rates and severe underestimates of their sampling variances. In other words, a highly precise, incorrect estimate is produced.

Goodness of Fit Test of the CD Method

Valid inferences must stem from a model employing valid assumptions. We tested the assumptions necessary for the CD method to be valid using the simple goodness of fit test (formula 5; Table 2). Information in Table 2 provides conclusive evidence that the assumptions of the

Table 1. Results of the test that 1st-year recovery rates are constant across years for 45 sets of waterfowl banding data in North America.

Banding period	Species	State or province	Age and sex	Banding years	k^a	Total banded	Total recoveries	Significance level
Preseason	Mallard	Montana	Adult ♂	1959–69	11	12,105	1,512	0.00189
		Saskatchewan	Adult ♂	1961–72	12	21,015	2,236	0.00000
		Minnesota	Adult ♀	1959–72	14	10,949	1,077	0.00000
		Wisconsin	Adult ♀	1961–72	12	16,803	1,682	0.00000
		Minnesota	Young ♂	1961–72	12	19,645	3,014	0.00000
		New York	Young ♂	1960–72	13	13,466	2,150	0.00000
		Ontario	Young ♂	1965–72	8	19,792	2,790	0.00140
		Saskatchewan	Young ♂	1955–72	18	30,627	4,263	0.00000
		Minnesota	Young ♀	1961–72	12	16,731	1,993	0.00000
		New York	Young ♀	1960–72	13	13,221	1,837	0.00000
		Ontario	Young ♀	1965–72	8	16,417	2,002	0.00019
		Saskatchewan	Young ♀	1955–72	18	28,198	2,770	0.00000
Preseason	Blue-winged teal	Iowa	Young ♂	1963–72	10	15,510	910	0.00000
		Manitoba	Young ♂	1962–72	11	17,115	691	0.00032
		Minnesota	Young ♂	1963–71	9	10,458	468	0.09759
		Ontario	Young ♂	1963–72	10	11,765	523	0.00108
		Iowa	Young ♀	1963–72	10	13,928	947	0.00000
		Manitoba	Young ♀	1962–72	11	15,723	686	0.00270
		Minnesota	Young ♀	1963–71	9	9,683	520	0.00063
		Ontario	Young ♀	1963–72	10	10,977	583	0.00295
Preseason	Pintail	California	Adult ♂	1955–72	18	34,788	3,356	0.00000
		Saskatchewan	Adult ♂	1955–58	4	22,279	1,403	0.00000
		California	Young ♂	1955–58	4	15,405	1,940	0.07258
		Alberta	Young ♀	1965–71	7	6,386	415	0.41488
		California	Young ♀	1955–58	4	10,216	1,015	0.50003
		Saskatchewan	Young ♀	1964–71	8	9,245	464	0.02668
Preseason	Wood duck	Wisconsin	Adult ♂	1962–72	11	8,126	818	0.00041
		Illinois	Young ♂	1962–72	11	11,690	1,081	0.00375
		Iowa	Young ♂	1962–72	11	9,342	1,026	0.00000
		Wisconsin	Young ♂	1960–70	11	9,197	1,067	0.00000
		Illinois	Young ♀	1962–72	11	10,335	716	0.00410
		Iowa	Young ♀	1962–72	11	8,661	855	0.00000
		Wisconsin	Young ♀	1960–70	11	7,894	816	0.00000
Preseason	Lesser scaup	Alaska	Adult ♂	1960–66	7	26,135	1,012	0.00002
Winter	Mallard	Illinois	Adult ♂	1963–72	10	27,691	2,905	0.00000
		Nebraska	Adult ♂	1965–72	8	15,272	1,562	0.00002
		Illinois	Adult ♀	1963–72	10	12,911	787	0.00723
		Nebraska	Adult ♀	1965–72	8	7,880	322	0.53884
Winter	Green-winged teal	California	Adult ♂	1955–70	16	13,731	919	0.00006
Winter	Pintail	California	Adult ♂	1955–72	18	27,727	2,263	0.00001
		California	Adult ♀	1957–72	16	17,747	764	0.01416
Winter	Redhead	New York	Adult ♂	1955–72	13	20,549	1,776	0.00000
		New York	Adult ♀	1963–72	10	4,629	371	0.00146
Winter	Canvasback	New York	Adult ♂	1955–59	5	6,123	808	0.00000
Winter	Wigeon	California	Adult ♂	1955–68	14	16,992	1,754	0.30970
				TOTALS:		685,079	62,869	

[a] Number of years of banding.

Table 2. Results of goodness of fit test for the composite dynamic model and modern methods applied to 45 sets of waterfowl-banding data in North America.

					Composite dynamic model	Modern methods[a]	
Banding period	Species	State or province	Age and sex	Banding years	Significance level	Significance level	Model
Preseason	Mallard	Montana	Adult ♂	1959–69	0.00006	0.59843	1
		Saskatchewan	Adult ♂	1961–72	0.00000	0.18843	1
		Minnesota	Adult ♀	1959–72	0.00000	0.00425	1
		Wisconsin	Adult ♀	1961–72	0.00000	0.00834	1
		Minnesota	Young ♂	1961–72	0.00000	0.17011	0[b]
		New York	Young ♂	1960–72	0.00000	0.00836	0
		Ontario	Young ♂	1965–72	0.00027	0.07432	0
		Saskatchewan	Young ♂	1955–72	0.00000	0.00631	0
		Minnesota	Young ♀	1961–72	0.00000	0.13044	0
		New York	Young ♀	1960–72	0.00000	0.28056	0
		Ontario	Young ♀	1965–72	0.00270	0.58030	0
		Sakatchewan	Young ♀	1955–72	0.00000	0.85574	0
Preseason	Blue-winged teal	Iowa	Young ♂	1963–72	0.00000	0.40978	0
		Manitoba	Young ♂	1962–72	0.00015	0.94543	0
		Minnesota	Young ♂	1963–71	0.05430	0.54376	0
		Ontario	Young ♂	1963–71	0.00042	0.01402	0
		Iowa	Young ♀	1963–72	0.00000	0.23395	0
		Manitoba	Young ♀	1962–72	0.00000	0.63155	0
		Minnesota	Young ♀	1963–71	0.00050	0.06369	0
		Ontario	Young ♀	1963–72	0.01422	0.27058	0
Preseason	Pintail	California	Adult ♂	1955–72	0.00000	0.00003	0
		Saskatchewan	Adult ♂	1955–58	0.00000	0.72319	1
		California	Young ♂	1955–58	0.00000	0.00590	0
		Alberta	Young ♀	1965–71	0.00889	0.01171	0
		California	Young ♀	1955–58	0.01128	0.00677	0
		Saskatchewan	Young ♀	1964–71	0.03752	0.30592	0
Preseason	Wood duck	Wisconsin	Adult ♂	1962–72	0.00000	0.96056	0
		Illinois	Young ♂	1962–72	0.00000	0.06970	0
		Iowa	Young ♂	1962–72	0.00001	0.94273	0
		Wisconsin	Young ♂	1960–70	0.00000	0.42157	0
		Illinois	Young ♀	1962–72	0.00014	0.22382	0
		Iowa	Young ♀	1962–72	0.00000	0.35093	0
		Wisconsin	Young ♀	1960–70	0.00000	0.02904	0
Preseason	Lesser scaup	Alaska	Adult ♂	1960–66	0.00000	0.00064	1
Winter	Mallard	Illinois	Adult ♂	1963–72	0.00000	0.42132	1
		Nebraska	Adult ♂	1965–72	0.00001	0.28064	1
		Illinois	Adult ♀	1963–72	0.00023	0.28552	1
		Nebraska	Adult ♀	1965–72	0.68993	0.61217	1
Winter	Green-winged teal	California	Adult ♂	1955–70	0.00000	0.33859	1
Winter	Pintail	California	Adult ♂	1955–72	0.00000	0.04601	1
		California	Adult ♀	1957–72	0.00000	0.02080	1
Winter	Redhead	New York	Adult ♂	1955–72	0.00000	0.01708	1
		New York	Adult ♀	1963–72	0.00489	0.64865	1
Winter	Canvasback	New York	Adult ♂	1955–59	0.00000	0.52254	1
Winter	Wigeon	California	Adult ♂	1955–68	0.00051	0.11472	0

[a] See Brownie et al. (1978).

[b] Tests of assumptions can be made for bandings of only young birds via Model 0; however, estimation is not possible unless a matching sample of adults is also available for analysis (Brownie et al. 1978:33–34).

CD method are not met (e.g., an adequate fit is rejected for 37 of the 45 data sets [82%] at the 0.001 level). This is an overall test of the assumptions necessary for the CD model. Moreover, the test results are not dependent on the particular estimation method used (the same conclusions would be reached if the constraint $M_{l-1} = M_l$ were used, rather than $M_l \equiv 1$). We conclude that the CD method is not appropriate for the analysis of waterfowl-banding data.

Goodness of Fit Tests of Modern Methods

Brownie et al. (1978) present a series of recently developed (i.e., "modern") estimation models and testing procedures to allow selection of the "best" model for a specific data set. It seems appropriate to assess the assumptions made by these modern methods. Relevant information is presented in Table 2 to allow comparisons. Only 8 data sets (18%) are rejected at the 0.01 level and only 2 data sets (4%) are rejected at the 0.001 level. Additional information of this type is given for mallards by Anderson (1975). These results generally indicate that modern methods are adequte for the analysis of waterfowl data—at the very least, they are a considerable improvement over the older methods. In addition, these modern procedures provide statistical tests (i.e., goodness of fit tests, likelihood ratio tests, and contingency-type tests) to assess the assumptions being made for a particular model. If these tests indicate that the assumptions are not met for a particular data set, the model should not be used for the analysis of that data set. Finally, none of the modern methods is affected by truncation of the recovery data and most are not affected by changes or trends in annual band reporting rates.

Bias in Age-specific Mortality Rate Estimates

We pointed out that bias will occur in the mortality rates estimates $\hat{M}_i$ unless $S_i S_{i+1} \ldots S_l$ is essentially zero. This product has not been zero in the vast majority of analyses of banding data. Truncation has occurred almost without exception (e.g., Moisan et al. 1967; Geis et al. 1971). To illustrate the effect of truncation, consider a case where mortality rate for all ages is 0.4 (i.e., $S_i \equiv S$ for all ages). Expected values of the estimator of mortality rate under the CD method can be computed using

$$E(\hat{M}_i) \doteq \frac{M}{1 - S^{k-i+1}} .$$

Although the true $M_i \equiv 0.4$, the CD method would produce the following average estimates for $i = 1, \ldots, 7$: 0.412, 0.420, 0.434, 0.460, 0.510, 0.625, and 1.000. This bias in the CD estimation procedure has frequently been incorrectly interpreted as evidence for age-specific mortality in waterfowl.

We stress that these biases occur even when the assumptions required by the CD model are true; they are an inherent property of the estimation method (primarily because of the implicit constraint $M_l = 1$). One might conclude that mortality rates increase with age when, in fact, only bias increases with age when the CD method is used.

DISCUSSION AND RECOMMENDATIONS

We contend that valid estimates and sound inference must come from a proper model and estimation procedure based on reasonable assumptions. We have found the CD model to be inappropriate as a basis for analysis of waterfowl banding data because: (1) the assumption that recovery rates do not vary by time is unrealistic; there is substantial direct information that hunting regulations influence harvest and harvest rate, and that recovery rate is closely correlated with harvest rate (Henny and Burnham 1976); (2) goodness of fit tests soundly reject the restrictive assumptions required; and (3) logical inconsistencies occur, as for example in applying the method to adults which are a mix of unknown ages when banded (cf. Anderson and Burnham 1976:55–56). Thus, our main point is that the necessary assumptions behind the CD method are logically and demonstratively invalid. Therefore, the CD method should not be used.

A 2nd point, of lesser significance, is that the estimation method itself is poor even if the necessary assumptions are true. It must be recognized that the $l + 1$ parameters $M_1, \ldots, M_l$ and a are not separately estimable unless the mortality rates are subjected to at least 1 appropriate constraint (cf. Seber 1971). The CD method is implicitly based on the constraint $M_l \equiv 1$, which is simply not justified. If there are situations where the CD assumptions are tenable (e.g., recovery data from a few species of nongame birds) improved estimators should be developed for the analyses. We note, however, that the goodness of fit test (5) is valid and independent of the specific estimation method used and is not affected by truncation of the data.

It seems important to recognize that 2 results commonly found in the literature are now suspect. First, the estimates of 1st-year mortality rates of birds banded as young are severely overestimated (e.g., Jessen 1970) because the necessary condition $a = f_i/M_i$ is violated. Second, the notion that mortality increases with age is not validly supported. This notion is an artifact of the CD method due to truncation of data and the implied constraint $M_l = 1$. The concept that mortality in waterfowl is age-specific is not validly supported by analyses using the CD method.

We recommend against the use of the CD method in the analysis of waterfowl banding data. We suggest caution in interpreting published results based on CD method concerning estimate of age-specific mortality rates; differences between mortality rates by sex and geographic areas; and the effect of hunting on total annual mortality rates. We recommend use of the more modern methods. Their advantages are discussed by Anderson and Burnham (1976:18).

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A General Methodology for Maximum Likelihood Inference from Band-Recovery Data

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SUMMARY

A numerical procedure is described for obtaining maximum likelihood estimates and associated maximum likelihood inference from band-recovery data. The procedure allows the specification of a very general form for band-recovery models, by means of which constraints on model parameters can be easily imposed by simple transformations. The method is illustrated for previously developed one-age-class band-recovery models, and is extended to new models, including the analysis with a covariate for survival rates and variable-time-period recovery models. Extensions to *R*-age-class band-recovery, mark–recapture models, and twice-yearly marking are discussed. A FORTRAN program, available from the authors, provides computations for the models described, and can be adapted for additional user-defined models.

1. Introduction

In band-recovery problems, birds are marked in each of several periods (for example, July–September in a series of years) and the sample consists of recoveries of bands during periods following banding. The probability that a bird banded in Year *i* is recovered in a subsequent Year *j* can be modelled as a function of time- and age-specific survival and recovery rates.

Seber (1970) and, in an unpublished report, D. S. Robson and W. D. Youngs (Cornell University Biometrics Unit Paper No. BU-360, 1971) have modelled recoveries with multinomial distributions and have developed maximum likelihood estimates (MLEs) for time-specific survival and recovery probabilities when all animals are marked as adults. Johnson (1974) and Brownie and Robson (1976) extended this methodology to allow age-specific survival and recovery probabilities for birds marked as adults and as young, and Brownie *et al.* (1978) summarized previous models, developed reduced-parameter models, and presented algorithms for estimation and hypothesis testing among a hierarchy of models.

In modelling band-recovery data, we believe that it is desirable to start with a model structure that allows specification of the sources of variability likely to occur in nature. For North American game birds these include, at a minimum, allowance for time-specificity in both survival and recovery probabilities, and where two age classes are considered, for age-specificity as well. All of these features have been incorporated into the models described by Brownie *et al.* (1978). For many well-structured data sets, and for relatively straightforward hypotheses regarding survival and recovery rates, these models have been quite adequate. However, we have encountered many examples of bird-banding experiments in which either variations in the design (for example, banding years were missing) or biological questions addressed (for example, tests of functional relationships between survival rates and exogenous variables) have suggested parameterizations which did not fit into the framework specified by Brownie *et al.* (1978).

Key words: Band recoveries; Hypothesis testing; Maximum likelihood; Multinomial models; Numerical estimation; Ring recoveries.

In the past, unique biological questions or data sets have required special developments for each case. We present a methodology which enables an investigator to specify a hypothesized relationship, H_0, among the parameters in terms of constraints on a very general band-recovery model, H_A. We also show how to obtain MLEs and associated test statistics under H_A and H_0, and we use the procedure to analyze several new models, illustrating each with a data example.

2. Estimation and Hypothesis Testing

2.1 *Definitions*

Initially we restrict our development to the one-age-class band-recovery problem, although R-age-class problems are a straightforward extension. Our notation follows Brownie *et al.* (1978):

N_i, the number of animals marked and released in Year i, $i = 1, \ldots, k$;
R_{ij}, the number of animals that were marked in Year i and recovered in Year j, $j = i, \ldots, l$;
$R_{i,l+1}$ $\equiv N_i - \sum_{j=i}^{l} R_{ij}$, the number of animals marked in Year i and not recovered;
π_{ij}, the probability that an animal marked in Year i is recovered in Year j;
S_i, the probability that an animal which is alive at the midpoint of the marking period of Year i survives to the midpoint of the marking period of Year $i + 1$;
f_i, the probability that a marked animal which is alive at the midpoint of the marking period in Year i is recovered in the subsequent recovery period (for example, hunting season following banding).

We note that for North American game birds, f_i has a straightforward interpretation when the recovery period is a hunting season immediately following the banding period (i.e. 'preseason' banding). In cases in which there is a significant lag between banding and recovery, f_i implicitly incorporates a mortality component.

2.2 *Fully-Parameterized Models, H_A*

The statistical treatment of the band-recovery problem by Seber (1970, 1971) and Brownie *et al.* (1978) was based on the product of independent multinomials

$$\mathrm{pr}(\{R_{ij}\}) = \binom{N_i}{\{R_{ij}\}} \prod_{j=i}^{l+1} \pi_{ij}^{R_{ij}}$$

for i banding periods, $i = 1, \ldots, k$, and j recovery periods, $j = i, \ldots, l$, so the overall likelihood function is

$$L(\{\pi_{ij}\}) = \prod_{i=1}^{k} \mathrm{pr}(\{R_{ij}\})$$

with π_{ij} being a function of $\{f_j, S_i, \; j = 1, \ldots, l, \; i = 1, \ldots, l - 1\}$.

Initially we will consider H_A to be equivalent to Model $M1$ (Brownie *et al.*, 1978, p. 15) in which f_j and S_i are time-specific. For Model $M1$ (H_A)

$$\pi_{ij} \equiv \begin{cases} f_j, & j = i, \\ \prod_{m=i}^{j-1} S_m f_j, & i < j < l + 1, \\ 1 - \sum_{m=i}^{l} \pi_{im}, & j = l + 1. \end{cases} \tag{1}$$

Since H_A is a fully-parameterized member of the exponential family, it can be shown (Brownie *et al.*, 1978) that for the parameter vector

$$\boldsymbol{\theta}_A \equiv (f_1, \ldots, f_k, S_1, \ldots, S_{k-1}, \alpha_1, \ldots, \alpha_{l-k})$$

with

$$\alpha_j \equiv f_{k+j} \prod_{m=k}^{k+j-1} S_m, \quad j = 1, \ldots, l-k,$$

moment-type estimators and MLEs are identical (Davidson and Solomon, 1974). This gives rise to a simple method of producing closed-form estimators of survival and recovery rates. Model H_A is of particular importance because most other one-age-class models of interest are obtained by constraining the parameters of H_A and will be reduced-parameter models, i.e. the number of parameters estimated is less than the number of elements of the minimal sufficient statistic.

2.3 *Reduced-Parameter Models, H_0*

Brownie *et al.* (1978) described two reduced-parameter models for one-age-class recovery problems. In one of the models, survival rates are constrained to be constant, whereas in the other, both survival and recovery rates are constrained thus. Moment-type estimators cannot be obtained, and closed-form solutions of the likelihood equations do not exist for either model. Since the likelihood must be redefined each time $\boldsymbol{\theta}_A$ is constrained under a particular H_0, it is understandable that only a few reduced-parameter models have been developed. We will show how this procedure can be considerably simplified by exploiting the simple multiplicative structure of the cell probabilities π_{ij}.

A commonly used procedure for obtaining MLEs when explicit solutions to the likelihood equations do not exist is the method of scoring (Kale, 1962; Rao, 1965, pp. 302–309):

$$\hat{\boldsymbol{\theta}}_{i+1} = \hat{\boldsymbol{\theta}}_i + I^{-1}(\hat{\boldsymbol{\theta}}_i) g(\hat{\boldsymbol{\theta}}_i), \tag{2}$$

where $\hat{\boldsymbol{\theta}}_i$ are the estimates of $\boldsymbol{\theta}$ at the ith iteration. The method requires a starting value $\boldsymbol{\theta}^*$, which in practice can be obtained by guesswork or by estimation from a fully-parameterized model. Also required are expressions for $g(\boldsymbol{\theta})$ and $I(\boldsymbol{\theta})$, where

$$g(\boldsymbol{\theta}) = \sum_{i=1}^{k} \sum_{j=i}^{l+1} \left(\frac{R_{ij}}{\pi_{ij}}\right)\left(\frac{\partial \pi_{ij}}{\partial \boldsymbol{\theta}}\right) \tag{3}$$

and

$$I(\boldsymbol{\theta}) = \sum_{i=1}^{k} N_i \sum_{j=i}^{l+1} \frac{1}{\pi_{ij}} \left(\frac{\partial \pi_{ij}}{\partial \boldsymbol{\theta}}\right)\left(\frac{\partial \pi_{ij}}{\partial \boldsymbol{\theta}'}\right). \tag{4}$$

Both functions can thus be obtained simply from first partial derivatives of the cell probabilities. Since the approach taken here involves constraining the parameter space of the general model H_A, we express partial derivatives $\partial \pi_{ij}/\partial \boldsymbol{\theta}_0$ by means of the chain rule

$$\frac{\partial \pi_{ij}}{\partial \boldsymbol{\theta}_0} = \left(\frac{\partial \boldsymbol{\theta}_A}{\partial \boldsymbol{\theta}_0}\right)\left(\frac{\partial \pi_{ij}}{\partial \boldsymbol{\theta}_A}\right). \tag{5}$$

The partial derivatives $\partial \pi_{ij}/\partial \boldsymbol{\theta}_A$ are, of course, constant for any Model H_0 obtained by constraining H_A, so the scoring procedure for Model H_0 is determined by a functional relationship of the form $\boldsymbol{\theta}_A = f(\boldsymbol{\theta}_0)$, with the assumption that the derivatives $\partial \boldsymbol{\theta}_A/\partial \boldsymbol{\theta}_0$ exist.

For example, if H_0 is defined by constant survivorship $S_i = S$, $i = 1, \ldots, k-1$, then

$$\frac{\partial \boldsymbol{\theta}_A}{\partial \boldsymbol{\theta}_0} = \begin{array}{c|cccc|cccc|} & S_1 & S_2 & \cdots & S_{k-1} & f_1 & f_2 & \cdots & f_k \\ \hline S & 1 & 1 & \cdots & 1 & 0 & 0 & \cdots & 0 \\ \hline f_1 & & & & & 1 & & 0 & \\ f_2 & & & 0 & & & \ddots & & \\ \vdots & & & & & & & \ddots & \\ f_k & & & & & 0 & & & 1 \end{array}$$

After the parameters of a model have been fitted as described, the Pearson goodness-of-fit statistic (cf. Brownie *et al.*, 1978, pp. 19–20; North and Morgan, 1979) can be used to test for model adequacy. It is usually necessary to pool cells because expected counts are small, and alternatives for the classical test have been suggested (cf. North and Morgan, 1979). Models under null hypotheses (H_0) can be compared to that under an alternative (H_A) by likelihood ratio test statistics (Kendall and Stuart, 1961, Ch. 24).

2.4 *Computing Algorithm*

The expressions in §§2.2 and 2.3 have been coded in FORTRAN for an HP-3000 computer. A main program reads the data and initial values for $\boldsymbol{\theta}$, and calls subroutines to compute the statistics needed for the scoring procedure. General forms for the cell probabilities, π_{ij}, and their derivatives for the model structures described in §3 are coded in subroutines. Models under specific null hypotheses are then obtained by $\partial\boldsymbol{\theta}_A/\partial\boldsymbol{\theta}_0$, coded as additional subroutines. Coding is provided for all of the hypotheses described in §3, and for several additional models. Additional hypotheses may be constructed by the addition of brief coding for $\partial\boldsymbol{\theta}_A/\partial\boldsymbol{\theta}_0$. No further modification of the program is required provided H_0 fits into one of the previously coded general forms. Convergence ($\| \hat{\boldsymbol{\theta}}_{i+1} - \hat{\boldsymbol{\theta}}_i \| < \varepsilon$) is rapid (usually <10 iterations) for most models and data sets. Our FORTRAN coding of these algorithms is quite general and should be compatible, with minor modifications, with most FORTRAN compilers. A documented listing and detailed instructions are available upon request from the authors.

3. Specific Models

3.1 *Unequal Time Intervals Between Sampling Periods*

Background and development. Brownie *et al.* (1978, p. 179) briefly considered the case in which intervals between marking periods are of variable length. This situation often occurs with species for which marking efforts have been sporadic, resulting in gaps of missing years in the records. Survival rates, S_i, may still be estimated, but S_i is now defined as the probability of survival over an interval $[t_i, t_{i+1}]$ of length d_i, where d_i may vary with i. A parameter of interest is the single-interval survival rate, ϕ_i, where S_i and ϕ_i are related by

$$S_i = \phi_i^{d_i}. \tag{6}$$

It is assumed here that the survival rate S_i is simply a product of the survival rates ϕ_{ij} over each of the d_i intervals in $[t_i, t_{i+1}]$:

$$S_i = \prod_{j=1}^{d_i} \phi_{ij}.$$

Setting $\phi_{ij} = \phi_i$ yields (6). Estimates of ϕ_i, $i = 1, \ldots, k-1$, may be obtained from $\boldsymbol{\theta}_A$ by the relationship $\phi_i = (S_i)^{1/d_i}$. Similarly, $\text{var}(\hat{\phi}_i)$ may be obtained by application of the delta

Table 1

Band recoveries from male ring-necked ducks banded in Maryland, Virginia and North Carolina, December–February 1953–1964

Banding year	Interval (years)	Number banded	Recovery year 1953	1955	1956	1958	1960	1961	1963	1964
1953	2	220	9	8	1	0	0	0	0	0
1955	1	386		36	16	4	1	0	1	0
1956	2	223			16	2	1	0	1	1
1958	2	102				6	1	0	2	0
1960	1	212					11	2	3	2
1961	2	433						16	7	7
1963	1	140							4	1
1964	1	313								12

method (Seber, 1973, p. 7). However, tests of H_0: $S_i = S$ make little biological sense, because S_i depends on d_i as well as on ϕ_i, and H_0 will usually be rejected unless $d_i = d$. A more useful test is that of H_0: $\phi_i = \phi$. Reparameterization of H_A by (6) yields

$$\boldsymbol{\theta}_A = (f_1, f_2, \ldots, f_k, \ \phi_1, \phi_2, \ldots, \phi_{k-1}), \tag{7}$$

and under H_0: $\phi_i = \phi$ we have

$$\boldsymbol{\theta}_0 = (f_1^*, f_2^*, \ldots, f_k^*, \phi),$$

where

$$f_i^* = f_i, \quad S_i = \phi^{d_i}, \quad i = 1, \ldots, k.$$

The likelihood function and its derivatives follow from application of the methods in §2.3, and the relationship between $\boldsymbol{\theta}_A$ and $\boldsymbol{\theta}_0$.

Example. Ring-necked ducks (*Aythya collaris*) were trapped and banded in December–February in Maryland, Virginia and North Carolina. After 1964, several contiguous years of adequate bandings enabled estimation of annual survival rates (Conroy and Eberhardt, 1983). There were several years between 1953 and 1964 in which few if any ringnecks were banded in these areas, resulting in gaps in the data (Table 1). We used the model defined in this section to estimate f_i and ϕ_i for these data (Table 2) and to test the null hypothesis that annual survival rates, ϕ_i, were temporally constant (Table 3). The models under both hypotheses fit the data ($P > .10$), and the hypothesis of constant ϕ was not rejected

Table 2

Maximum likelihood estimates of survival rates, ϕ_i, and band-recovery rates, f_i, for ring-necked-duck data in Table 1

Banding year	H_A: ϕ_i unconstrained $\hat{f}_i$	$\widehat{\text{SE}}$	$\hat{\phi}_i$	$\widehat{\text{SE}}$	H_0: $\phi_i = \phi$ $\hat{f}_i$	$\widehat{\text{SE}}$	$\hat{\phi}_i$	$\widehat{\text{SE}}$
1953	0.0409	0.0134	0.5218	0.0918	0.0403	0.0132	0.6120	0.0346
1955	0.0987	0.0148	0.5477	0.1609	0.0937	0.0137	0.6120	0.0346
1956	0.0706	0.0159	0.5165	0.1191	0.0648	0.0114	0.6120	0.0346
1958	0.0529	0.0194	0.6447	0.1536	0.0413	0.0125	0.6120	0.0346
1960	0.0457	0.0132	0.5656	0.2014	0.0439	0.0119	0.6120	0.0346
1961	0.0297	0.0074	1.0530	0.2588	0.0289	0.0068	0.6120	0.0346
1963	0.0222	0.0103	0.3533	0.2028	0.0476	0.0119	0.6120	0.0346
1964	0.0383	0.0109			0.0422	0.0091	0.6120	0.0346
Average estimate:	0.0499	0.0048	0.6004	0.0400	0.0503	0.0042	0.6120	0.0346

Table 3
Likelihood ratio test of hypothesis that survival rates are constant for ring-necked-duck data in Table 1

Model	df	χ^2	P
H_A	4	6.655	.155
H_0	12	12.496	.407
H_0 vs H_A	6	8.543	.201

($P > .10$), suggesting a temporally constant annual survival rate of .61 with an estimated asymptotic standard error of .03.

3.2 *Survival Rate as a Function of a Covariate*

Background and development. In this model, annual survival rates, S_i, are hypothesized to be a function of an independent variable, X_i. Examples of X_i could include weather conditions, availability of habitats or food, and densities of conspecifics, competitors or predators. Previous investigations of the effects of environmental variables on S_i have generally involved estimation of S_i followed by regression of $\hat{S}_i$ on X_i. This approach makes less effective use of the data, and requires two separate analyses. Furthermore, because of autocorrelation among the $\hat{S}_i$, the usual assumptions for regression are not met. North and Morgan (1979) modelled annual survival rates of herons as a logistic function of winter temperature, but required assumptions about recovery probabilities which are unlikely to be appropriate for North American birds that are hunted. Our approach is to reparameterize H_A under the hypothesis

$$H_0\colon S_i = g(X_i), \quad i = 1, \ldots, k. \tag{8}$$

In particular, it may be reasonable to hypothesize a linear relation between S_i and X_i,

$$H_0\colon S_i = a + bX_i,$$

or between S_i' and X_i,

$$H_0\colon S_i' = a + bX_i,$$

where

$$S_i' = \ln\{S_i/(1 - S_i)\}.$$

This approach requires estimation of two parameters, a and b, in addition to f_i, as opposed to the estimation of S_i followed by the appropriate linear regression or linear logistic regression. The parameters under H_0 are

$$\boldsymbol{\theta}_0 = (f_1, f_2, \ldots, f_k, a, b),$$

and specification of the mathematical relationship between S_i and X_i in terms of a and b enables derivation of the likelihood and the maximum likelihood inference.

Example. Adult female mallards (*Anas platyrhynchos*) were banded in Manitoba, Saskatchewan and eastern Alberta in August–September 1966–1977. It was believed that annual survival rates over the interval August i–August $i + 1$ were negatively influenced by high densities of mallards per pond in May of Year $i + 1$ (Nichols, Pospahala and Hines, 1982). A plot of $\hat{S}_i$ (under the fully-parameterized model) suggested a linear relation

$$H_0\colon S_i = a + bX_i,$$

where S_i is the annual survival rate of adult females (August i–August $i + 1$), X_i is the number of mallards per pond in May $i + 1$, and a and b are parameters to be estimated.

Table 4

Band recoveries from adult female mallards banded in prairie Canada, July–September 1966–1979, and densities of ducks per pond for May of following years

Banding year	Number banded	Recovery year 1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	Ducks/Pond
1966	926	39	20	6	3	7	2	2	1	0	0	0	0	0	0	0.9787
1967	1413		53	18	17	9	8	5	4	0	0	1	0	0	0	2.2445
1968	1147			34	27	23	11	5	3	0	2	1	0	0	0	1.2638
1969	1233				57	33	21	14	5	2	1	2	0	1	0	1.0898
1970	1674					82	35	22	8	2	4	3	1	1	0	1.3363
1971	1727						71	30	13	1	8	6	2	0	2	1.3067
1972	1864							67	32	12	12	4	4	3	0	2.2601
1973	1438								46	23	21	13	5	4	7	0.6647
1974	1235									43	27	15	10	7	4	0.8903
1975	2351										67	56	26	13	10	1.3183
1976	5215											180	91	56	33	2.1163
1977	5256												167	89	61	0.8707
1978	3615													114	66	

Table 5

Maximum likelihood estimates of survival rates, S_i, and band-recovery rates, f_i, for mallard data in Table 4

Banding year	H_A: S_i unconstrained				H_{01}: $S_i = a + bX_i$		H_{02}: $S_i = S$	
	$\hat{f}_i$	$\widehat{\text{SE}}$	$\hat{S}_i$	$\widehat{\text{SE}}$	$\hat{f}_i$	$\widehat{\text{SE}}$	$\hat{f}_i$	$\widehat{\text{SE}}$
1966	0.0421	0.0066	0.5440	0.0962	0.0418	0.0066	0.4184	0.0066
1967	0.0381	0.0047	0.4686	0.0698	0.0364	0.0042	0.0371	0.0043
1968	0.0283	0.0041	0.5890	0.0767	0.0273	0.0036	0.0253	0.0033
1969	0.0430	0.0048	0.7130	0.0864	0.0415	0.0041	0.0405	0.0040
1970	0.0452	0.0043	0.6376	0.0795	0.0475	0.0038	0.0483	0.0039
1971	0.0380	0.0039	0.5428	0.0710	0.0403	0.0033	0.0409	0.0034
1972	0.0364	0.0037	0.4283	0.0578	0.0357	0.0030	0.0362	0.0030
1973	0.0348	0.0040	0.5488	0.0761	0.0328	0.0033	0.0297	0.0028
1974	0.0280	0.0036	0.7898	0.0997	0.0236	0.0026	0.0242	0.0027
1975	0.0303	0.0030	0.6211	0.0622	0.0307	0.0027	0.0325	0.0028
1976	0.0346	0.0023	0.5712	0.0489	0.0352	0.0021	0.0360	0.0022
1977	0.0309	0.0021	0.5904	0.0591	0.0329	0.0020	0.0311	0.0018
1978	0.0304	0.0025			0.0298	0.0018	0.0306	0.0019
Average estimate:	0.0355	0.0011	0.5864	0.0118	0.0351	0.0010	0.0349	0.0010
					$\hat{a}$:	0.7514		
					$\widehat{\text{SE}}$:	0.0554	$\hat{S}$:	0.5879
							$\widehat{\text{SE}}$:	0.0099
					$\hat{b}$:	−0.1170		
					$\widehat{\text{SE}}$:	0.0380		

Three models were analyzed: H_A, the fully-parameterized model with S_i and f_i varying with time; H_{01}, a reduced-parameter model with $S_i = a + bX_i$; and H_{02}, a reduced-parameter model with $S_i = S$, this model being equivalent to H_0: $b = 0$ in the linear parameterization. The relevant banding, recovery and covariate data are given in Table 4. Parameter estimates and associated standard errors for the models are shown in Table 5.

Test results indicate that all three models provide an adequate fit ($P > .50$) to the data (Table 6). The test of H_{01} versus H_A was not rejected ($P > .10$), which suggests that modelling survival rates by year-specific values, S_i, provides no more information than does the covariate model. The tests of H_{02} versus H_A and H_{01} were both rejected ($P < .01$), which suggests that survival rates are not temporally constant and that a significant linear relationship exists between S_i and X_i. A similar inference may be obtained by regression of the $\hat{S}_i$ under H_A against X_i, but this requires two analyses and the estimation of 12 additional parameters.

Table 6

Likelihood ratio tests of hypotheses that survival rates are constant, and that survival rates are a linear function of ducks/pond for the mallard data in Table 4

Model	df	χ^2	P
H_A	51	38.009	.916
H_{01}	62	52.849	.619
H_{02}	62	55.553	.517
Comparison			
H_{01} vs H_A	10	14.020	.172
H_{02} vs H_A	11	22.360	.022
H_{02} vs H_{01}	1	8.340	.004

4. Extensions

In addition to the models described in §3, we have extended this methodology to several other types of model. For example, if birds are marked twice a year, it is possible to estimate survival rates over portions of the year. In hunted species, particular interest may focus on the proportion of mortality, $1 - S_i$, that occurs during the hunting season (usually September–February) and during the remainder of the year (cf. Brownie *et al.*, 1978, p. 159).

If age classes can be identified at the time of banding, then the data and corresponding parameters can be stratified accordingly. Estimation of parameters and tests of hypotheses (for example, constant but age-specific survival rates) are a straightforward extension of the methods described in §2, and several two-age-class models have been programmed in our algorithms. Furthermore, although we assumed in §2 that the banded samples, N_i, were known and we conditioned the observations on them, our methodology could be extended to cases in which N_i are not known and the likelihood is conditioned on the total number of recoveries (Lebreton, 1977; North and Morgan, 1979).

We have also successfully employed a two-stage iterative procedure for obtaining solutions to fully-parameterized and reduced-parameter Jolly–Seber mark–recapture problems (Jolly, 1965, 1982; Seber, 1965). However, this procedure can be very sensitive to starting values and may not prove as useful for these problems as for band-recovery problems.

5. Discussion

Modelling band-recovery data in a biologically realistic manner often requires a large number of parameters. One application of our methodology is to reduce the number of parameters needed to model a population. It is important, however, that a reduction in parameters be pursued in a framework that allows objective comparison of biological hypotheses. The strength of our approach lies in the simplicity with which models under various null hypotheses can be obtained and compared by maximum likelihood methods. Once a sufficiently general model, H_A, has been specified, estimation and testing for biological hypotheses, H_0, are based on the mathematical relationship between H_A and H_0. This simple relationship avoids the necessity of developing new likelihood equations each time a new H_0 is specified. Because reduced-parameter models require numerical solutions, a procedure for testing alternative models, which requires minimum coding, has obvious advantages. In our algorithm we provide the coding for a very general model structure and for several models under specific hypotheses. Additional models, not described above, can be obtained with a minimal amount of extra coding. Users of this procedure are welcome to expand this methodology to other hypotheses, and we will provide assistance as requested.

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RÉSUMÉ

On décrit une procédure numérique permettant d'obtenir les estimations du maximum de vraisemblance et les statistiques associées adaptées à des données de reprises d'individus bagués. La procédure permet de travailler sur des modèles très généraux; des contraintes sur les paramètres du modèle peuvent être facilement imposées par des transformations simples. La méthode est illustrée sur des modèles à une classe d'âge déjà développés; elle est étendue à de nouveaux modèles incluant l'analyse avec une covariable pour des modèles de taux de survie et de reprise variable avec le temps. On discute d'extensions à la reprise d'individus bagués appartenant à R classes d'âge, de modèles de marquage-recapture et de marquage deux fois par an. Un programme FORTRAN, disponible auprès des auteurs permet de traiter les modèles décrits; il permet de traiter d'autres modèles définis par l'utilisateur.

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SIMULTANEOUS ANALYSIS OF BAND-RECOVERY AND LIVE-RECAPTURE DATA

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Brownie et al. (U.S. Fish and Wildl. Serv., Resour. Publ. 131, 1978) presented 14 interrelated models for the analysis of band-recovery data. In addition, they discussed computer programs ESTIMATE (for animals banded as adults) and BROWNIE (for simultaneous banding of 2 or 3 age-groups) that fit the data to the various models and computed estimates of survival and recovery rates. The banding studies on which such models can be used involve capturing, banding, and releasing a sample of animals at the same location at regular intervals (usually 1 year). For k such banding occasions, let $N_1, N_2, \ldots, N_k$ be the numbers of adults banded and released. Further, let R_{ij} be the number of band recoveries in period j from adult animals banded on the ith occasion. In general, there are ℓ periods of recover, $\ell \geqslant k$. Brownie et al. (1978) expressed this recovery information conveniently in matrix form. When possible, the notation used by Brownie et al. (1978) will be followed in this paper, and it is assumed that the reader is familiar with their work.

The fate of a banded animal will be 1 of 3 mutually exclusive events. Each animal will (1) be killed or found dead and the band reported, (2) return to the banding site and be recaptured alive in a subsequent year, or (3) not be seen again and the band not reported. An animal could be recaptured alive on any number of occasions, and its ultimate fate be case 1 above. Because the models used to analyze band-recovery data are based on the multinomial distribution, we will be able to use only the *last* time an animal (band) is seen (reported); i.e., each animal is recorded only once in the summary—either as a live recapture on the occasion of its last recapture or as a band recovery, but not both.

Analysis of recovery data alone is well developed, and the same is true for recapture data. It is only the joint analysis of recovery and recapture data from a single banding program that is not well developed in the literature. Brownie et al. (1978, Section 8.2) dealt with this problem, but suggested including the intermediate recaptures and applying a recovery model (for bands from dead animals) to these recapture data. That approach keeps all the recapture data, and uses a model that is an approximation. To get an exact model in which the variance formulae for estimated survival rates are valid, this paper discards the intermediate recapture data. The proposed technique cannot be optimal because the intermediate recaptures are ignored. However, it is a simple and relatively efficient method of combining recoveries and recaptures and the existing computer programs ESTIMATE and BROWNIE. These programs can be used to examine the data.

MODELS AND ANALYSIS

To examine the method as applied to the models for animals banded as adults,

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Table 1. Expected numbers of band recoveries under Model 1, with $k = 3$ and $\ell = 4$.

Banding occasion	Number banded	Period of recovery (between banding occasions)			
		1	2	3	4
1	N_1	N_1f_1	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2S_3f_4$
2	N_2		N_2f_2	$N_2S_2f_3$	$N_2S_2S_3f_4$
3	N_3			N_3f_3	$N_3S_3f_4$

we will use Model 1 (Brownie et al. 1978) as the primary example. The assumptions of Model 1 are (1) age-independent survival and recovery rates and (2) time-specific survival and reporting rates independent of the date of banding. Parameters f (recovery rate) and S (survival rate) are subscripted to indicate dependence on a specific time period. For illustration, the general form of Model 1 in terms of 3 years of banding and 4 years of recovery is given (Table 1).

The corresponding expected numbers of terminal live recaptures of the banded animals is defined to be Model 1′ (Table 2). The parameter S again is subscripted to indicate dependence on a specific time period. It is assumed that all multiple recaptures have been eliminated, so the new parameter, p_i, is the probability of an animal returning to the banding site, being recaptured on the ith banding occasion, and neither the animal nor its band being reported again. In this model there are no live recaptures during the 1st period after banding, because recaptures will occur only when the banding operation is carried out again. Note that on the 3rd banding occasion the parameters S_2p_3 occur together, on the 4th occasion S_3p_4, and in general on the jth occasion ($j \geq 2$) $S_{j-1}p_j$ occur together. These parameters are estimable as a product, but not separately.

Comparing Model 1′ with Model 1, it can be seen that they are of the same form for estimation of survival rates S_1, S_2, . . . , S_{k-1} if we ignore the blanks on the diagonal and shift the columns of Model 1′ one place to the left. The term $q_{i+1} = S_ip_{i+1}$ in Model 1′ corresponds to the recovery rate, f_i, in Model 1. In general, existing computer programs for analysis of band recoveries can be used to analyze these recapture data. However, consider the addition of corresponding elements of the data matrices; that is, add the number of band recoveries in the jth period, R_{ij}, to the number of terminal live recaptures on the (j + 1)th banding occasion, R'_{ij}. Factoring out the common terms, define Model 1* (Table 3) for the expected value of $R_{ij} + R'_{ij}$, the "total" recoveries in the jth recovery period (i.e., period j, or on the [j + 1]th banding occasion) from the ith banding occasion. The survival rates, S_1, S_2, . . . , S_{k-1}, are separately estimable and can be directly

Table 2. Expected numbers of terminal live recaptures under Model 1′, with $k = 3$ and $\ell = 4$.

Banding occasion	Number banded	Banding occasion			
		1	2	3	4
1	N_1		$N_1S_1p_2$	$N_1S_1S_2p_3$	$N_1S_1S_2S_3p_4$
2	N_2			$N_2S_2p_3$	$N_2S_2S_3p_4$
3	N_3				$N_3S_3p_4$

Table 3. Model 1* for expected numbers of terminal live recaptures and band recoveries, with $k = 3$ and $\ell = 3$.

Banding occasion	Number banded	Recovery period 1	 2	 3
1	N_1	$N_1(f_1 + q_2)$	$N_1S_1(f_2 + q_3)$	$N_1S_1S_2(f_3 + q_4)$
2	N_2		$N_2(f_2 + q_3)$	$N_2S_2(f_3 + q_4)$
3	N_3			$N_3(f_3 + q_4)$

obtained from the computer program ESTIMATE. The 2nd set of parameters, $f_i + q_{i+1}$, is estimable; however, there is no clear, useful interpretation.

The other models (i.e., 0, 2, and 3) reported by Brownie et al. (1978) can be similarly transformed to, say, models 0*, 2*, and 3* for combined recoveries and recaptures. Model 2* assumes constant survival rate period to period, and thus is the same as Model 1*, except that there are no subscripts on S. Model 3* is too restrictive to be applicable in many natural cases, because it assumes that not only survival rates, but also recovery rates and probabilities of returning and being recaptured, remain constant from period to period. Model 0*, which allows newly banded animals to have different recovery rates than those previously banded, is the same as Model 1*, with the quantity $f_i' + q_{i+1}'$ replacing $f_i + q_{i+1}$ on the diagonal elements of the combined recovery and recapture matrix.

Several of the authors' colleagues and 1 of the referees have suggested that with recapture data taken during banding operations at the same (small) site, if an animal does not return exactly to that site in subsequent years, it is no longer in the sampled population, as some emigration is possible. If E represents the probability of emigration, the suggestion is that you might not estimate survival rate S, but rather $S \cdot (1 - E)$, assuming the events are independent. The models herein propose to solve this problem by embedding the term $(1 - E)$ in p. That is, consider the 3 events: (A) an animal returns to the banding site; (B) an animal is recaptured, given (A); and (C) neither the animal nor its band is reported again, given (A) and (B). If $(1 - E)$, B', and C' represent the probabilities of the 3 events, A, B and C, respectively, then $p = (1 - E) \cdot B' \cdot C'$. Under the assumption that the parameter p has the same properties as the recovery rate, f (e.g., in models 1, 1', and 1* they are to be independent of the date of banding), then the survival rates are estimable by the maximum likelihood method developed by Brownie et al. (1978). This argument is based totally on deductive logic. It would also be advisable to conduct a statistical test of the equality of survival rates in the 2 data sets before combining them. Unfortunately such a test is not available, and development of one is beyond the scope of this note. We hope that interest in this aspect of the analysis is stimulated.

Each banded animal should be recorded only once in the combined recovery and recapture matrix for the multinomial likelihood functions to be applicable. The usual implicit assumption is made that the recovery of bands from, and live recaptures of, banded birds yield a representative sample from the overall banded population. Also, one assumes the banded population is representative of the whole population.

Analysis of the combined recoveries and recaptures under models 0*, 1*, 2*, and 3* (and choice among the models)

Table 4. Expected numbers of recoveries and terminal recaptures under H_1^*, with $k = 3$ and $\ell = 3$.

Banding occasion	Number banded	Recovery period 1	Recovery period 2	Recovery period 3
Birds banded and released as adults				
1	N_1	$N_1(f_1 + q_2)$	$N_1S_1(f_2 + q_3)$	$N_1S_1S_2(f_3 + q_4)$
2	N_2		$N_2(f_2 + q_3)$	$N_2S_2(f_3 + q_4)$
3	N_3			$N_3(f_3 + q_4)$
Birds banded and released as young				
1	M_1	$M_1(f_1' + q_2')$	$M_1S_1'(f_2 + q_3)$	$M_1S_1'S_2(f_3 + q_4)$
2	M_2		$M_2(f_2' + q_3')$	$M_2S_2'(f_3 + q_4)$
3	M_3			$M_3(f_3' + q_4')$

would be difficult were it not that program ESTIMATE exists for analysis of band recoveries under models 0, 1, 2, and 3, and is directly applicable. All tests of fit and comparisons of models are valid, as are the point and interval estimates of survival rates.

Brownie et al. (1978) also considered the case when there are 2 or 3 age-classes of banded animals (e.g., young, subadults, and/or adults). A similar method of combining band recoveries with live recaptures can be used in these cases. We will consider 2 age-classes and the model under H_1. Under H_1, annual survival and recovery rates (S and f) are time-specific, and young and adults have different survival and recovery rates. For the young, the symbols S' and f' are used. It is assumed that after the 1st period of life, a young animal becomes an adult.

For the expected number of terminal live recaptures, we define the model H_1'. Parameters are defined as in H_1, with 2 new parameters, p_i and p_i', representing the probability of returning to the banding site, being recaptured, and the band not being reported again, for adult and young birds, respectively. Letting $S_{i-1}p_i = q_i$ and $S_{i-1}'p_i' = q_i'$, the recoveries and recaptures can be added together as before, yielding Model H_1^* for combined recoveries and recaptures in a given period (Table 4).

Survival rates are separately estimable,

Table 5. Recovery matrices for band recoveries and terminal live recaptures of Canada geese banded at Turbid Lake, Yellowstone National Park, Wyoming, 1967–71.

Banding occasion	Number banded	Year recovered 1967	1968	1969	1970	1971	1972
Band recoveries from birds shot or found dead							
1967	198	30	14	7	8	5	
1968	157		24	11	10	8	
1969	119			10	6	9	
1970	275				34	13	
1971	249					26	
Terminal live recaptures							
1967	198		1	29	14	4	8
1968	157			17	9	7	4
1969	119				19	12	4
1970	275					42	16
1971	249						43

Table 6. Total recoveries and terminal recaptures of Canada geese banded at Turbid Lake, Yellowstone National Park, Wyoming, 1967–71.

Banding occasion	Number banded	Recovery period				
		1	2	3	4	5
1967	198	31	43	21	12	13
1968	157		41	20	17	12
1969	119			29	18	13
1970	275				76	29
1971	249					69

whereas parameters $f_i + q_{i+1}$ and $f_i' + q_{i+1}'$ are estimable as sums. In a similar manner, the other models considered by Brownie et al. (1978) can be defined for combined recoveries and recaptures. The computer program BROWNIE can be used to fit the new models.

APPLICATION

Band-recovery and live-recapture data are available for normal wild Canada geese (*Branta canadensis*) banded at Turbid Lake in Yellowstone National Park, Wyoming, from 1967 to 1971. Recovery matrices are given for band recoveries and live recaptures (Table 5) and for the combined data (Table 6) (Mardekian, M.S. Thesis, Univ. Wyoming, Laramie, 1979). All intermediate recaptures have been eliminated.

Each of the 3 recovery matrices was analyzed with program ESTIMATE. Model 2 best described the band-recovery data, giving an estimate of the constant survival rate (estimate ± SE) of 69.41 ± 3.53%. On the live-recapture data, Model 1 fit best; the estimated mean survival rate ($\bar{x}$ ± SE) is 65.14 ± 5.35%. On the combined data set, ESTIMATE fit Model 2 (Model 2* in the new notation), with an estimate of constant survival rate of 66.45 ± 2.93%. As expected, this estimate is between the other 2, but has a smaller standard error.

SUMMARY

Models are developed for the analysis of combined band-recovery and live-recapture data. They are similar in structure to the band-recovery models reported in Brownie et al. (1978), and provide an improvement in the estimation of survival rates under the assumption that the recovery of bands from, and live recaptures of, banded birds yields a representative sample from the population. An example is given of the application of these models, using existing computer programs for the analysis.

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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 i	Number banded N_i	Year of recovery			
		1	2	3	4
1	N_1	$N_1\theta_0f_1$	$N_1\theta_1S_1f_2$	$N_1\theta_2S_1S_2f_3$	$N_1\theta_3S_1S_2S_3f_4$
2	N_2		$N_2\theta_0f_2$	$N_2\theta_1S_2f_3$	$N_2\theta_2S_2S_3f_4$
3	N_3			$N_3\theta_0f_3$	$N_3\theta_1S_3f_4$
4	N_4				$N_4\theta_0f_4$

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.

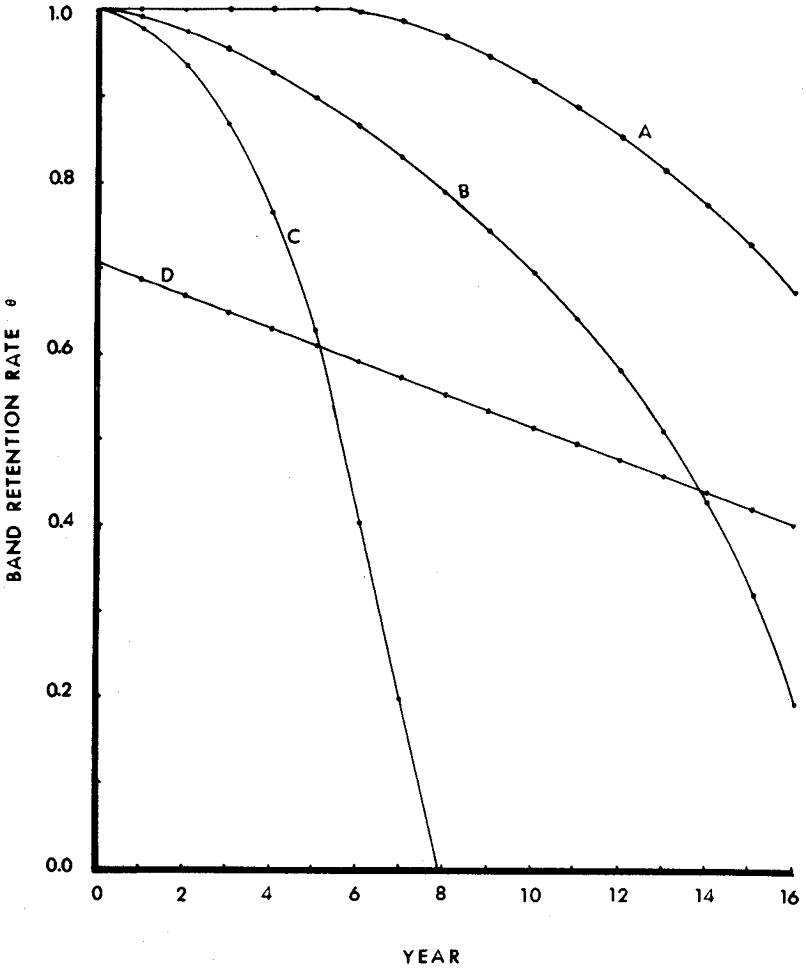

FIGURE 1. Band retention rate as a function of the number of years after banding.

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., $i = 1, 2, \ldots, 16$). 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 $\hat{S}_i \pm 1.96$ 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, $\hat{S}_i \pm 1.96$ se($\hat{S}_i$), by calculating the bias relative to the standard error. Therefore, let

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

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., $\hat{S}_i \times 100$).

Year (i)	Band retention function A Annual survival rate ($\hat{S}_i$)		Band retention function B Annual survival rate ($\hat{S}_i$)		Band retention function C Annual survival rate ($\hat{S}_i$)		Band retention function D Annual survival rate ($\hat{S}_i$)	
		Percent relative bias (PRB)		Percent relative bias (PRB)		Percent relative bias (PRB)		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 ($\delta = \text{bias}/\text{se}(\hat{S}_i)$) 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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ADDITIONAL COMMENTS ON THE ASSUMPTION OF HOMOGENEOUS SURVIVAL RATES IN MODERN BIRD BANDING ESTIMATION MODELS

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Abstract: We examined the problem of heterogeneous survival and recovery rates in bird banding estimation models. We suggest that positively correlated subgroup survival and recovery probabilities may result from winter banding operations and that this situation will produce positively biased survival rate estimates. The magnitude of the survival estimate bias depends on the proportion of the population in each subgroup. Power of the suggested goodness-of-fit test to reject the inappropriate model for heterogeneous data sets was low for all situations examined and was poorest for positively related subgroup survival and recovery rates. Despite the magnitude of some of the biases reported and the relative inability to detect heterogeneity, we suggest that levels of heterogeneity normally encountered in real data sets will produce relatively small biases of average survival rates.

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Pollock and Raveling (1982) recently emphasized the importance of considering the assumptions underlying modern bird banding estimation models (e.g., Seber 1970, Robson and Youngs 1971, Brownie and Robson 1976, Brownie et al. 1978), and devoted special attention to the assumption that all banded individuals of an identifiable demographic group (e.g., an age-sex class) have identical survival and recovery probabilities for any given year. They pointed out that in a large number of instances this assumption is biologically unrealistic, and they approximated the bias of recovery and survival rate estimators that could be expected to result from heterogeneous survival and recovery rates. Here, we present additional results that are relevant to the problem of heterogeneous survival and recovery rates.

Pollock and Raveling (1982) presented results on bias for cases in which (1) there is a negative relationship between survival and recovery probabilities of an individual and (2) individual survival probabilities differ but recovery probabilities are similar. They did not consider the situation in which survival and recovery probabilities are positively correlated. We expect this situation to occur frequently when the banding and recovery periods are separated by time spans that are not negligible with respect to mortality.

Let p_i be the conditional probability that a bird is recovered in the hunting season of year i given that it is alive at the beginning of season i. Let $S_{bh,i}$ be the probability that a bird alive at the midpoint of the banding period in year i survives until the beginning of the hunting season in year i. Let $S_{hb,i}$ be the analogous probability of surviving the interval between the beginning of the hunting season of year i and the banding period of year $i + 1$. The annual survival probability between banding periods, S_i, is then given by the product, $S_{bh,i}S_{hb,i}$. If the banding period immediately precedes the hunting season (i.e., preseason banding), then $S_{bh,i} \simeq 1.0$. If the banding period is not preseason, then $S_{bh,i} < 1.0$, with smaller $S_{bh,i}$ corresponding to longer intervals (and hence more mortality) between the banding period and the hunting season. The recovery probability of the Brownie et al. (1978) models can be defined as $f_i = S_{bh,i}p_i$.

In the case of preseason banding ($S_{bh,i} \simeq 1.0$), it seems reasonable to expect either no relationship or a negative relationship between subgroup S_i and f_i, depending on whether or not there is a negative relationship between hunting mortality (which should be reflected in p_i) and $S_{hb,i}$ and on whether or not this relationship is the basis for subgroup differences. When banding and recovery periods are separated by time spans that are not negligible with respect to mortality (i.e., when $S_{bh,i} < 1.0$), then positive, negative, or no relationship between subgroup S_i and f_i is possible. If the main difference between subgroups involves hunting mortality and $S_{hb,i}$, then a negative relationship between f_i and S_i could easily result. If the subgroups differed primarily in $S_{hb,i}$, but if this difference was not associated with differences in hunting mortality (or p_i), then no relationship would be expected between subgroup S_i and f_i. However, if the principal difference between subgroups occurs in the $S_{bh,i}$, then we would expect a positive relationship between S_i and f_i. In postseason or winter banding operations, we suspect (see Discussion) that subgroup differences in $S_{bh,i}$ will be common, and sufficiently important to produce such positive relationships between S_i and f_i.

Our objectives are to: (1) consider the magnitude and direction of bias resulting from positively correlated subgroup survival and recovery rates; (2) consider the importance of subgroup proportions in the population to the magnitude of bias, and (3) consider the power of standard goodness-of-fit tests to detect heterogeneity in survival and recovery probabilities.

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METHODS

Like Pollock and Raveling (1982) we considered Model 1 of Brownie et al. (1978:15–20; see also Seber 1970, and Robson and Youngs 1971). This model was developed for adult birds and is parameterized with year-specific survival and recovery rates. The model assumes that all banded birds alive in year *i* have identical survival and recovery probabilities, S_i and f_i, respectively. We used 2 methods of approximating the bias resulting from violation of this assumption. The 1st method involved the use of Taylor series approximations and is apparently identical to that used by Pollock and Raveling (1982).

The 2nd method of approximating bias involved the use of computer simulation. For a fixed total banded sample size, we first used pseudorandom numbers to generate binomial variates corresponding to the number of birds banded in each demographic subgroup. Then, for each subgroup, we used pseudorandom numbers to generate the multinomial random vectors comprising its recovery matrix. The specific methods used to generate these matrices are similar to those described in Anderson and Burnham (1976: 66). The recovery matrix for the entire heterogeneous population is obtained by summing the subgroup matrices, and the estimators, $\hat{f}_i$ and $\tilde{S}_i$ (where $\tilde{S}_i$ is the bias-adjusted survival probability estimator), are then computed from the population matrix using the equations of Brownie et al. (1978:16). This process was repeated *n* times for each experimental situation considered, and bias was estimated as the difference between the mean of the *n* estimates and the true parameter value.

Following Pollock and Raveling (1982), we report the percent relative bias defined, for example with survival rate, as:

$$100[E(\tilde{S}_i) - S_i]/S_i$$

where $E(\tilde{S}_i)$ denotes the expected value of $\tilde{S}_i$, and S_i denotes the true survival probability. We define average percent relative bias as the arithmetic mean percent relative bias for all years of the experiment for which estimates are obtained.

We were also interested in the power of the Pearson chi-square goodness-of-fit test for Model 1 (Brownie et al. 1978: 19–20) with respect to violation of the homogeneity assumption. This was examined via computer simulation using the same basic program used to compute the bias expression. For each of n heterogeneous-model data sets, we computed the chi-square goodness-of-fit test statistic (we used the same cell pooling algorithm as in program ESTIMATE) and its associated probability level. We obtained the total number of data sets resulting in model rejection, m, and estimated power as $(m/n)_\alpha$, where power is defined as the probability of rejecting the null hypothesis when α is used as the rejection level for the chi-square test.

RESULTS

Using the Taylor series approximations, analytical expressions for the large sample bias of $\tilde{S}_i$ and $\hat{f}_i$ can be derived for any given relationship between S and f. In general, the expressions are quite complex and of little practical interest. However, in certain situations, the sign and a general feel for the magnitude of the bias can be gained by examining the expressions. For example, consider the banding experiment consisting of k banding and recovery years where there are assumed to be 2 heterogeneous subgroups within the population having proportions r and $1 - r$. These subgroups may differ in survival and/or recovery probabilities. We make the simplifying assumption that the survival and recovery rates remain constant throughout the experiment within each subgroup and we denote the parameters within each subgroup by f, S and f', S'. (The numerical results of Pollock and Raveling [1982, Table 4] are a special case of this situation.) By examining the expressions for asymptotic bias in survival and recovery rates (Appendix), we see that:

1. The bias in $\hat{f}$, although small, is always negative.
2. The bias in $\tilde{S}$ is positive if
   $$S > S' \text{ and } f > f'$$
   $$\text{or } S < S' \text{ and } f < f'.$$
3. The bias in $\tilde{S}$ may be either positive or negative when the relationship between S and f is negative. However, for the usual magnitudes of S and f, the bias will be negative, since for a positive bias to result, ΔS (defined as $|S - S'|$) would have to be quite large relative to Δf (defined as $|f - f'|$).
4. The bias in $\tilde{S}$ is not greatly affected by the annual banded sample size, N_i.

These results are illustrated via numerical examples (Figs. 1, 2). Figure 1 contains 3 curves representing Taylor series approximations of average percent relative bias plotted as a function of the difference between subgroup survival probabilities (ΔS). The 6 plotted points corresponding to each line represent the bias as estimated from Monte Carlo simulations (each point obtained from 1,000 iterations). The simulated bias estimates correspond closely to the Taylor series approximations and indicate that the approximations are quite reasonable. We assumed 2 subgroups with survival probabilities of $S = 0.5 - \Delta S/2$, $S' = 0.5 + \Delta S/2$.

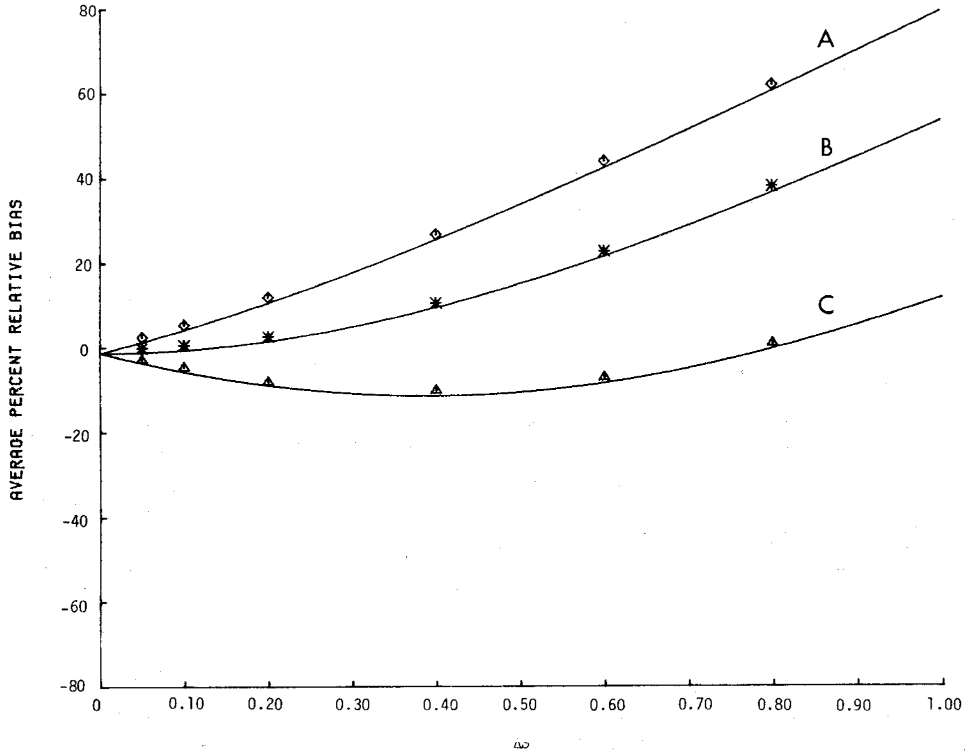

Fig. 1. Average percent relative bias of $\hat{S}_i$ plotted as a function of the difference between true subgroup survival probabilities, ΔS. In all plots, $S = 0.50 - \Delta S/2$, $S' = 0.50 + \Delta S/2$. Subgroup recovery probabilities are: plot A, $f = 0.025$, $f' = 0.075$; plot B, $f = f' = 0.05$; plot C, $f = 0.075$, $f' = 0.025$. All plots assume equal proportions (0.50) of the population and banded sample in each subgroup, and 2,000 birds banded annually for 5 years. The curves represent Taylor series approximations while the plotted points represent Monte Carlo simulation results (1,000 iterations each).

The 3 curves correspond to the following 3 sets of subgroup recovery probabilities: plot A, $f = 0.025$, $f' = 0.075$; plot B, $f = f' = 0.05$; plot C, $f = 0.075$, $f' = 0.025$. We assumed 0.50 of the population and banded sample in each subgroup. Finally, we assumed a 5-year banding program with 2,000 birds banded annually. Figure 2 assumes the same experimental situation as Fig. 1 but includes bias plotted as a function of the difference between subgroup recovery probabilities (Δf). The 3 curves in Fig. 2 correspond to the following sets of survival probabilities: plot A, $S = 0.40$, $S' = 0.60$; plot B, $S = S' = 0.50$; plot C, $S = 0.60$, $S' = 0.40$. Both Figs. 1 and 2 demonstrate the importance of the relationship between survival and recovery probabilities to the magnitude and direction of bias. Although a negative relationship does generally result in negative bias, as reported by Pollock and Raveling (1982), a positive relationship between the probabilities can result in large positive bias (Figs. 1, 2).

Most of the numerical examples of Pollock and Raveling (1982) assume equal sizes for all subgroups. However, the bias resulting from survival rate heterogeneity is a function of the proportions in each subgroup (see bias expression in Appen-

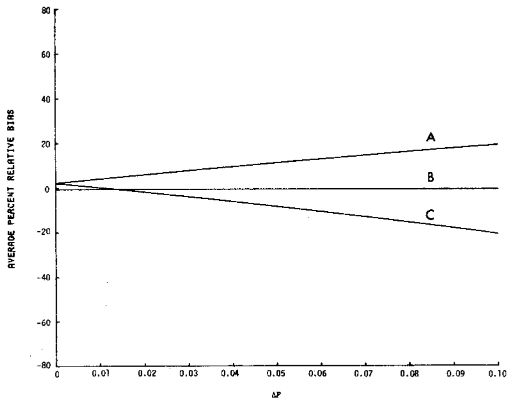

Fig. 2. Average percent relative bias of $\tilde{S}_i$ plotted as a function of the difference between subgroup recovery probabilities (Δf). In all plots, $f = 0.05 - \Delta f/2$, $f' = 0.05 + \Delta f/2$. Subgroup survival probabilities are: plot A, $S = 0.40$, $S' = 0.60$; plot B, $S = S' = 0.50$; plot C, $S = 0.60$, $S' = 0.40$. All plots assume equal proportions (0.50) of the population and banded sample in each subgroup, and 2,000 birds banded annually for 5 years. The curves represent Taylor series approximations.

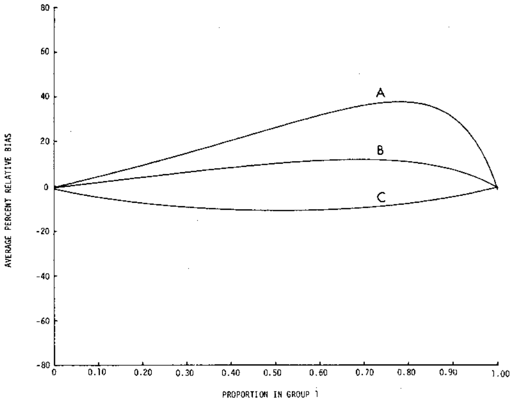

Fig. 3. Average percent relative bias of $\tilde{S}_i$ plotted as a function of the proportion of the population and banded sample in subgroup 1 (the subgroup characterized by S and f). Subgroup survival and recovery probabilities are: plot A, $S = 0.30$, $f = 0.025$, $S' = 0.70$, $f' = 0.075$; plot B, $S = 0.30$, $f = f' = 0.05$, $S' = 0.70$; plot C, $S = 0.30$, $f = 0.075$, $S' = 0.70$, $f' = 0.025$. All plots assume 2,000 birds banded annually for 5 years. The curves represent Taylor series approximations.

dix). We plotted Taylor series approximations of average percent relative bias as a function of the proportion of the population in subgroup 1 (characterized by S and f), for the following parameter values: plot A, $S = 0.30$, $S' = 0.70$, $f = 0.025$, $f' = 0.075$; plot B, $S = 0.30$, $S' = 0.70$, $f = f' = 0.05$; plot C, $S = 0.30$, $S' = 0.70$, $f = 0.075$, $f' = 0.025$ (Fig. 3). We assumed a 5-year banding program with 2,000 total birds banded annually. Monte Carlo simulations with extreme subgroup proportions (e.g., 0.05, 0.95) again indicated that the Taylor series approximations were quite reasonable. Plot C (negative relationship between f and S) is fairly symmetrical with the greatest bias occurring around equal subgroup proportions of 0.5. However, in plots A and B (positive relationship between S and f, and no relationship), bias is greater when a larger proportion of individuals is in the low survival probability subgroup (and, in the case of plot A, the low recovery probability subgroup). This skewness with positive relationship and no relationship between S and f is even more pronounced with greater differences in subgroup survival probabilities (greater ΔS).

Brownie et al. (1978) provided goodness-of-fit tests to determine whether or not a given model seems to fit a particular band recovery data set. If these tests are likely to detect violations of the homogeneous survival and recovery probability assumption, then biased estimators will not present as big a problem as when the violations are not detectable. We plotted empirical power estimates ($\alpha = 0.05$) for the Model 1 goodness-of-fit test (Brownie et al. 1978:19–20) (Fig. 4). Plots A, B, and C represent the same sets of subgroup recovery probabilities as in Fig. 1. We again assumed 5 years of banding, equal proportions in each subgroup, and 2,000 total birds banded annually. The estimated power of the goodness-of-fit test to reject the inappropriate Model 1 was low for lower values of ΔS in all plots

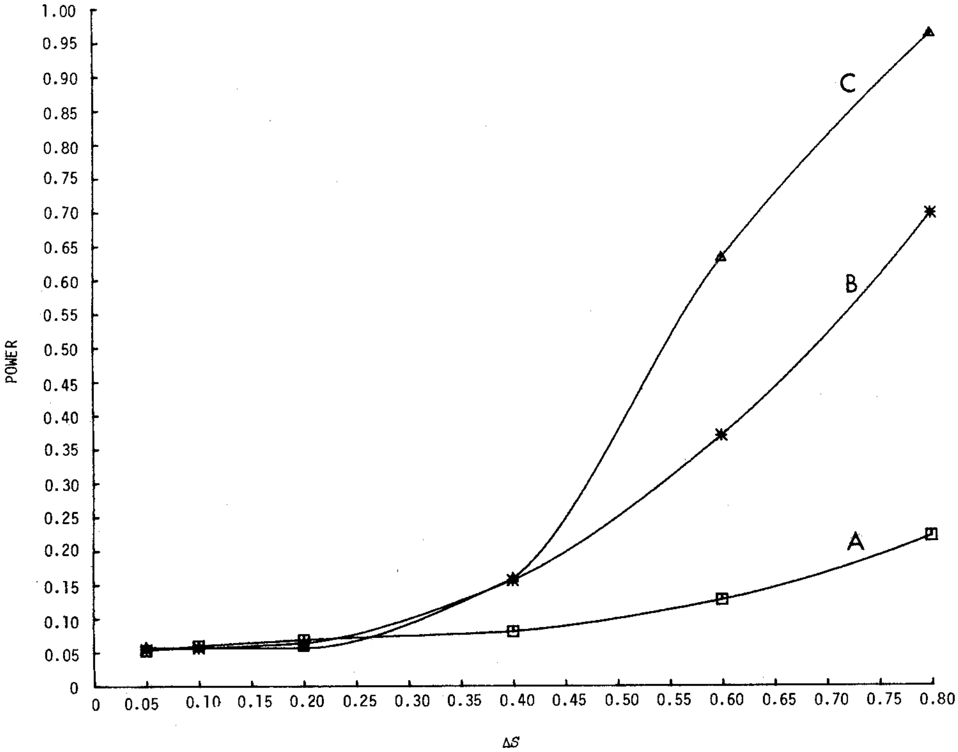

Fig. 4. Estimated power ($\alpha = 0.05$) of the goodness-of-fit test to reject Model 1, plotted as a function of the difference between subgroup survival probabilities (ΔS). In all plots $S = 0.50 - \Delta S/2$, $S' = 0.50 + \Delta S/2$. Subgroup recovery probabilities are: plot A, $f = 0.025$, $f' = 0.075$; plot B, $f = f' = 0.05$; plot C, $f = 0.075$, $f' = 0.025$. All plotted points assume equal proportions (0.50) of the population and banded sample in each subgroup, and 2,000 birds banded annually for 5 years. The plotted points represent Monte Carlo simulation results (1,000 iterations each).

(Fig. 4). These lower ΔS values also correspond to the smaller biases of survival rate estimates (Fig. 1). At larger values of ΔS (e.g., $\Delta S > 0.40$), estimated power differed substantially for the 3 kinds of subgroups considered. The test was most powerful in the case of a negative relationship between subgroup survival and recovery probabilities and least powerful when a positive relationship existed.

We also plotted estimated power of the goodness-of-fit test as a function of banded sample size (Fig. 5). Plots A, B, and C correspond to the same sets of subgroup survival and recovery probabilities as in Fig. 3. We again assumed 5 years of banding. In all 3 plots, the estimated power of the test increased with banded sample size. The 3 plots differed substantially, with the greatest power corresponding to the subgroup with negatively related S and f.

DISCUSSION

When considering the implications of our results for actual banding studies it is important to keep in mind the kinds of heterogeneity that might exist in migratory bird populations. Pollock and Raveling (1982) provided an example of Canada geese (*Branta canadensis maxima*) banded at Marshy Point on Lake Mani-

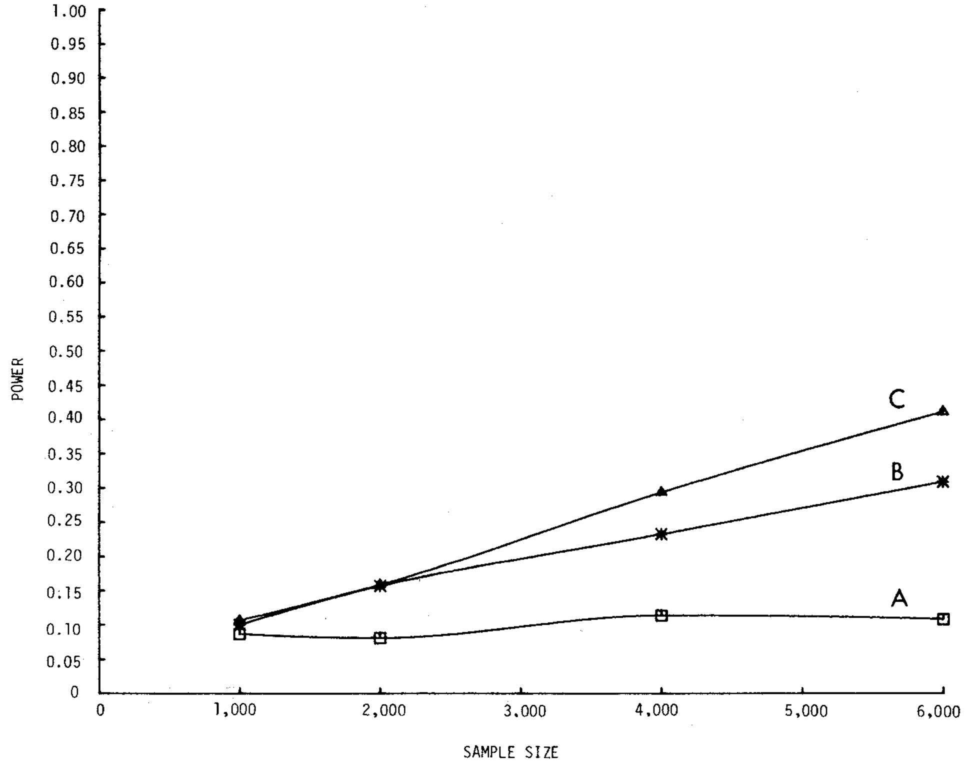

Fig. 5. Estimated power ($\alpha = 0.05$) of the goodness-of-fit test to reject Model 1, plotted as a function of total annual banded sample size. Subgroup survival and recovery probabilities are: plot A, $S = 0.30$, $f = 0.025$, $S' = 0.70$, $f' = 0.075$; plot B, $S = 0.30$, $f = f' = 0.05$, $S' = 0.70$; plot C, $S = 0.30$, $f = 0.075$, $S' = 0.70$, $f' = 0.025$. All plotted points assume equal proportions (0.50) of the population and banded sample in each subgroup, and a 5-year banding experiment. The plotted points represent Monte Carlo simulation results (1,000 iterations each).

toba, Canada, which represented 2 population segments that wintered in different areas. In most duck species, it is not unusual to find birds banded in specific breeding areas and recovered in a variety of different wintering areas. Similarly, birds from a particular winter-banded sample are often recovered in different breeding and staging areas in the fall. In banding analyses it is common to combine different banding stations within a relatively large geographic area into banding reference areas. While such areas are usually defined based on similarity of recovery distribution of birds banded at the included stations, it is certainly possible that the use of reference areas might result in the combination of population segments that differ to some degree in migration pathways. In any case, differences in migration pathways, breeding grounds and wintering grounds are expected to result in differences in environmental conditions and hunting pressure, and thus in possible differences in survival and recovery probabilities.

If reproduction increases mortality risks of birds (Johnson and Sargeant 1977, Bailey 1981) then breeding and nonbreeding segments of a population would be expected to exhibit different survival probabilities. Age may represent another source of heterogeneity in survival and recovery probabilities. Winter-banded birds of many species are not separated by age-classes when banded. Although survival and recovery rates of first year vs. older winter-banded mallards (*Anas platyrhynchos*) from Colorado were similar (Hopper et al. 1978), it is certainly possible that this is not true of all other waterfowl species (e.g., diving ducks seem to exhibit greater age-specific dimorphism in winter). Preseason-banded birds are generally assigned to either of 2 age-classes (adult or young), but test results of Anderson (1975:18–19) suggest that in some areas subadult mallards may exhibit different survival and recovery probabilities than either adults or young.

In many of the previous examples of sources of heterogeneity, it is probably most useful to think of a population or banded sample as consisting of discrete population segments. However, when some sources of heterogeneity are considered it may be more useful to think of survival rates as differing from individual to individual and following some probability distribution (see model M_h of Otis et al. 1978). For example, phenotypic variation in the ability to withstand periods of severe winter stress and even variation in tendency to follow different migration pathways might be assumed to vary from individual to individual in a population, resulting in a specific survival and recovery probability being associated with each individual. Pollock and Raveling (1982) modeled this situation by allowing individual survival rates to follow a series of beta distributions, but their conclusions about estimator bias were qualitatively similar to those they obtained with the discrete population segment model. Because of the qualitatively similar results of the 2 approaches and because of our interest in sources of heterogeneity that are likely to result in population segments, we only considered this approach in the present work.

Our results have emphasized the importance of the relationship between individual survival and recovery probabilities to the bias resulting from such heterogeneity. In general, presence of a negative relationship between S and f tends to result in negatively biased survival estimates. Uncorrelated and positively correlated S and f tend to produce positively biased survival estimates, often of greater magnitude. We expect winter banding operations (or any banding operation separated from the recovery period by a substantial amount of time) to often result in positively related S and f, while preseason-banded birds may exhibit either no relationship or a negative relationship between S and f. This observation may explain the tendency in some species (mallards, J. Nichols, unpubl. data; black ducks, *Anas rubripes*, W. Blandin, unpubl. data) for survival estimates of winter-banded birds to be somewhat higher than those of preseason-banded birds. The proportion of individuals in each population subgroup also influences the magnitude of the resulting bias of survival rate estimates. In the cases we examined (which included a number of situations in addition to those presented in Fig. 3), negatively related S and f tended to exhibit the greatest biases when subgroup proportions were similar (~0.50). However, with uncorrelated and positively correlated S and f, the largest biases occurred when a larger proportion of the population was in the subgroup with the lower S.

Our empirical power estimates of the Brownie et al. (1978) goodness-of-fit test were low for small to moderate differences between subgroup survival probabilities (ΔS), but biases were also relatively small for such differences. In the case of positively correlated S and f, the power of the test was low for all ΔS examined. Therefore, among the situations we examined, the power of the goodness-of-fit test was lowest for the situation (positively related S and f) producing the largest relative bias. Power of the test increased with increasing banded sample sizes, as expected.

Our suspicion that winter banding programs of heterogeneous populations tend to produce a positive correlation between subgroup survival and recovery probabilities leads us to suggest that preseason banding programs should offer somewhat more protection from survival estimate bias resulting from heterogeneity. The absolute value of relative bias of the $\hat{S}_i$ resulting from negatively correlated and uncorrelated S and f (as expected from preseason programs) is smaller than for the situation of a positive correlation. In addition, the goodness-of-fit test was more powerful in the situations expected to accompany preseason banding, although even then this test is not expected to be of much use in detecting heterogeneity at expected levels with normal sample sizes. Finally, we emphasize that portions of our figures represent situations that are unrealistic. For example, we allowed the difference between subgroup survival probabilities (ΔS) to range between 0.0 and 1.0 in Figs. 1 and 4. When considering the possible biological sources of heterogeneity that we have discussed, it seems that most situations would probably involve $\Delta S \leq 0.20$, with $\Delta S \leq 0.10$ being most common. For ΔS in this range, relative biases of the $\hat{S}_i$ are small, especially when considered in relation to their standard errors (estimated standard errors of the annual survival estimates generally would be expected to range from approximately 0.05 to 0.10 for the situations considered in Figs. 1–4, and would be larger with smaller banded sample sizes). Larger ΔS may exist in some instances (Pollock and Raveling 1982), but we suspect they will represent rare situations.

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APPENDIX

An analytical expression for the large sample bias of $\hat{f}_i$ and $\tilde{S}_i$ is given for the situation described in the text. We assume that

1. There are 2 heterogeneous subgroups within the population which differ in recovery and/or survival rate. Let r and $1 - r$ denote the proportions of the population in subgroups 1 and 2, respectively.
2. There are k banding and recovery seasons within the banding experiments.
3. The recovery and survival rates are constant within each subgroup over the course of the experiment.

We define $\bar{f} = rf + (1 - r)f'$ and $\bar{S} = rS + (1 - r)S'$ to be the "average" recovery and survival rates in the population. Let

$$\delta_i = ff'r(1 - r) \sum_{j=1}^{k-i} (S^j - S'^j),$$

$$\gamma_i = \sum_{j=1}^{i-1} N_j(S^{i-j} - S'^{i-j}),$$

and $$\beta_i = r(1 - r)(S - S') \sum_{j=1}^{k-i} \cdot (S^{j-1}f - S'^{j-1}f').$$

Then for large samples we have

$$E(\hat{f}_i) \approx \bar{f} - \delta_i\gamma_i/E(T_i),$$

and $$E(\tilde{S}_i) \approx \bar{S} + [\delta_i\gamma_i/E(T_i) + \beta_i]/\rho_{i+1},$$

where $$\rho_i = \sum_{j=0}^{k-i} [rS^jf + (1 - r)S'^jf']$$

is the probability of ever recovering a bird banded in year i, and T_i is the ith block total of the recovery matrix (see Brownie et al. 1978:13).

Then $$\text{Bias}\ (\hat{f}_i) = -\delta_i\gamma_i/E(T_i) < 0,$$

and $$\text{Bias}\ (\tilde{S}_i) = [\delta_i\gamma_i/E(T_i) + \beta_i]/\rho_{i+1} > 0$$

if $S > S'$ and $f \geq f'$

or $S < S'$ and $f \leq f'$.

ASSUMPTIONS OF MODERN BAND-RECOVERY MODELS, WITH EMPHASIS ON HETEROGENEOUS SURVIVAL RATES

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Abstract: The assumptions inherent in modern band-recovery models are reviewed with particular attention to homogeneity of survival and band-recovery rates for all individuals in the population. If this assumption fails, the following implications emerge: (1) the models only enable estimation of average annual survival and band-recovery rates; (2) estimators of these averages probably give underestimates; (3) the degree of underestimation in practical studies is difficult to assess, but may sometimes be important for survival estimates; (4) if sampling is nonrandom and heterogeneity of survival and recovery rates is present in the population, then any estimates could be misleading; and (5) if survival rates are homogeneous but recovery rates are heterogeneous (due perhaps to geographical variation in hunting pressure and reporting rates), then there is no bias in survival estimates. An example where data from neck-collared birds showed heterogeneity in segments of a Canada goose (*Branta canadensis*) population is discussed. We believe that the practical limitations of bird-banding studies deserve careful review by population biologists and managers.

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Band-recovery data have long been used to estimate mortality rates in exploited migratory bird populations. However, it is only in recent years that methods of analysis of banding data have been rigorously considered. By making certain assumptions, Seber (1970, 1971, 1972, 1973) formulated a rigorous statistical model that gave rise to explicit maximum-likelihood estimators of survival- and recovery-rate parameters. Extensions allowing for age dependence of survival and recovery rates were made by Johnson (1974), Brownie and Robson (1976), and Brownie et al. (1978), who, in a comprehensive monograph, detailed a variety of age-dependent models.

Development of modern methods clearly identified the weaknesses of some of the older procedures such as the composite dynamic life table. Burnham and Anderson (1979) analyzed 45 substantial data sets from migratory waterfowl band recoveries and demonstrated that the composite dynamic life table should no longer be used, as only 2 data sets (4%) fit the model at $\alpha = 0.05$.

Burnham and Anderson (1979) also found that modern methods are not necessarily always adequate for analyzing banding data, as 14 of 45 data sets (30%) did not fit. In this paper we further examine the assumptions of the modern methods.

An important assumption of all recovery models is that all banded individuals of an identifiable class (e.g., by species, age, sex) in the sample have the same annual survival and recovery rates (Brownie et al. 1978:6). We consider what happens when this assumption fails, and the importance of random sampling in conjunction with homogeneity of survival and recovery rates.

First, we consider a specific model (Model 1: Adults Only Banded) when the homogeneity assumption holds. We shall refer to this as the Homogeneous Population Model. This will be followed by the same model when the homogeneity assumption fails, the Heterogeneous Population Model. We discuss a popula-

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tion of Canada geese for which segments with heterogeneous survival and recovery rates are known to exist from the use of individually identifiable neck-collared birds (Raveling 1978). Finally, we provide a general discussion of all the assumptions underlying modern band-recovery models, with an emphasis on the practical implications of assumption failure.

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Table 1. The algebraic representation of band recoveries with k banding and recovery years.

			Recoveries by hunting season					
Year banded	Number banded		1	2	3	...	k	Row totals
1	N_1		R_{11}	R_{12}	R_{13}	...	R_{1k}	R_1
2	N_2	T_1[a]		R_{22}	R_{23}	...	R_{2k}	R_2
3	N_3		T_2		R_{33}	...	R_{3k}	R_3
⋮	⋮			T_3		⋮	⋮	⋮
k	N_k						R_{kk}	R_k
Column totals			C_1	C_2	C_3	...	C_k	

[a] T_i is a rectangular block of data with $T_1 = R_1$, $T_i = R_i + T_{i-1} - C_{i-1}$ for $i = 2, \ldots, k$, where R_i is the ith-row total and C_i is the ith-column total for $i = 1, \ldots, k$.

HOMOGENEOUS POPULATION MODEL

Here we consider the situation where all birds are banded as adults and all birds have the same survival and recovery rates in a particular year (Model 1 of Brownie et al. 1978:15). For simplicity, we will also assume the number of years of recoveries is the same as the number of years of banding.

The data matrix for observed recoveries is given in Table 1. Under this model, each row of recoveries follows a multinomial distribution, and the expected recoveries take the form given in Table 2.

The maximum-likelihood estimators of the survival- and recovery-rate parameters are given by the following equations:

$$\hat{S}_i = \left(\frac{R_i}{N_i} - \hat{f}_i\right) \Big/ \left(\frac{R_{i+1}}{N_{i+1}}\right) \tag{1}$$

$$\hat{f}_i = \frac{R_i C_i}{N_i T_i}. \tag{2}$$

If we assume the model is correct, then Eq. (2) gives unbiased estimators of the recovery rates. The survival-rate estimators (Eq. [1]) are biased, but the bias is small for banding studies of reasonable size. The maximum-likelihood estimator adjusted for bias is

$$\hat{S}_i = \left(\frac{R_i}{N_i} - \hat{f}_i\right) \Big/ \left(\frac{R_{i+1} + 1}{N_{i+1} + 1}\right). \tag{3}$$

HETEROGENEOUS POPULATION MODEL

This is the same model, except now each bird has its own specific survival and recovery probability for a given year. Also, all survival and recovery rates for the birds banded are a random sample from a multivariate probability distribution. Under this model, it is easy to show (Seber 1973:316) that each row of recoveries is still multinomially distributed as before, but now the expected numbers of band recoveries differ (Table 3).

All expectations $E(\cdot)$ are with respect to the appropriate multivariate probability distribution. Suppose, for example, we consider $E(S_1 S_2 f_3)$, then

$$E(S_1 S_2 f_3) = \int_0^1 \int_0^1 \int_0^1 S_1 S_2 f_3 f(S_1, S_2, f_3)\, dS_1\, dS_2\, df_3$$

with $f(S_1, S_2, f_3)$ the joint distribution of S_1, S_2, and f_3 for the whole population of animals. Put in simple terms, $E(S_1 S_2 f_3)$

Table 2. The expected number of band recoveries under the Homogeneous Population Model.

Year banded	Number banded	Recoveries by hunting season				
		1	2	3	...	k
1	N_1	N_1f_1[a]	$N_1S_1f_2$	$N_1S_1S_2f_3$[b]	...	$N_1S_1 \ldots S_{k-1}f_k$
2	N_2		N_2f_2	$N_2S_2f_3$	...	$N_2S_2 \ldots S_{k-1}f_k$
3	N_3			N_3f_3	...	$N_3S_3 \ldots S_{k-1}f_k$
⋮	⋮				⋮	⋮
k	N_k					N_kf_k

[a] f_i is the recovery rate for year i, i.e., the probability of a bird being killed, retrieved by hunter, and its band reported for $i = 1, \ldots, k$.

[b] S_i is the survival rate from year i to year $i + 1$, for $i = 1, \ldots, k - 1$.

is the average value of the product $S_1S_2f_3$ over the whole population. If results like

$$E(S_1S_2f_3) = E(S_1)E(S_2)E(f_3) \qquad (4)$$

were true for all the products, then Table 3 would have the same form as Table 2, with average values replacing the 1 constant value for all animals. In this instance, the estimators (Eqs. [1] and [2]) would have the same properties as before, except they would be estimating average survival and recovery rates. Actually, the result is only true if animals' survival rates and band-recovery rates are completely independent of each other. This is extremely unlikely in practice. It is likely that survival rates from year to year for the same animal will have a strong positive relationship. Also, the relationship between survival and recovery rates is likely to be negative, because recovery typically occurs for those animals killed by hunters.

Using Taylor Series approximations (Seber 1973:7), approximate expectations can be derived for the estimators $\tilde{S}_i$ and $\hat{f}_i$ in Eqs. (3) and (2). We find

$$E(\tilde{S}_i) \simeq \left[E\left(\frac{R_i}{N_i}\right) - E(\hat{f}_i)\right] \Big/ E\left(\frac{R_{i+1} + 1}{N_{i+1} + 1}\right)$$

and

$$E(\hat{f}_i) \simeq E\left(\frac{R_i}{N_i}\right)\frac{E(C_i)}{E(T_i)}, \qquad (5)$$

which can be expressed in terms of the expected values (Table 3).

$$E(\tilde{S}_i) \simeq \frac{\begin{gathered} E(f_i) - E(\hat{f}_i) + E(S_if_{i+1}) \\ + E(S_iS_{i+1}f_{i+2}) + \ldots \\ + E(S_i \ldots S_{k-1}f_k) \end{gathered}}{\begin{gathered} E(f_{i+1}) + E(S_{i+1}f_{i+2}) + \ldots \\ + E(S_{i+1} \ldots S_{k-1}f_k) \end{gathered}}. \qquad (6)$$

The expected value of $\tilde{S}_i$ given in Eq. (6) is a very good approximation because of the independence of numerator and denominator in the estimator (Eq. [3]).

To find the $E(\hat{f}_i)$ in Eq. (5), it is only necessary to give expressions for $E(R_i/N_i)$, $E(C_i)$, and $E(T_i)$, which are summations of the appropriate cells (Table 3). Bias expressions are then calculated as follows:

$$B(\tilde{S}_i) = E(\tilde{S}_i) - E(S_i) \qquad (7)$$

$$B(\hat{f}_i) = E(\hat{f}_i) - E(f_i). \qquad (8)$$

The percent relative bias is determined by dividing the bias by the true value of the parameter and expressing as a percentage.

NUMERICAL ANALYSIS OF BIAS

The dynamics of exploited populations are poorly understood. Although it is likely (from density-dependent factors influencing survival) that hunting mortality is partially compensated for by a decrease in natural mortality (Anderson and

Table 3. The expected number of band recoveries under the Heterogeneous Population Model.

Year banded	Number banded	Recoveries by hunting season				
		1	2	3	…	k
1	N_1	$N_1E(f_1)$[a]	$N_1E(S_1f_2)$	$N_1E(S_1S_2f_3)$	…	$N_1E(S_1 \ldots S_{k-1}f_k)$
2	N_2		$N_2E(f_2)$	$N_2E(S_2f_3)$	…	$N_2E(S_2 \ldots S_{k-1}f_k)$
3	N_3			$N_3E(f_3)$	…	$N_3E(S_3 \ldots S_{k-1}f_k)$
⋮	⋮				⋮	⋮
k	N_k					$N_kE(f_k)$

[a] $E(\cdot)$ are expectations.

Burnham 1976, 1978), the exact relationship is unknown. This uncertainty makes analysis of the bias due to the existence of heterogeneity of individuals with respect to survival and recovery extremely difficult.

First, let us consider the situation of 2 or 3 population segments of equal size with a wide range of heterogeneous survival rates such that the average annual survival rate of the whole population is held constant at either 0.3 or 0.6. For each case, we consider a wide range of heterogeneous recovery rates with a constant average of 0.05. The averages of the percent relative bias values for the yearly survival-rate estimators over a 3- or 5-year banding study are presented in Tables 4 and 5. These results show that for a given amount of heterogeneity in the survival rates, the bias moves from positive to negative as the recovery rates of the segments become more different. The values for 2 population segments (Table 4) are more extreme than those for 3 population segments (Table 5).

Now we consider the more realistic situation of a heterogeneous population where individual survival rates follow a series of beta distributions (Johnson and Kotz 1970), with the average annual survival rate held constant at 0.33, 0.5, or 0.67. For each case, we consider 2 very different relationships for the recovery rates. First, we assume that the individual's recovery rate is independent of its survival rate and that the average annual recovery rate over the population is 0.05. Second, we assume that the individual's recovery rate is a constant proportion of its mortality rate (1 minus the survival rate), so $f = a(1 - s)$, and that the average

Table 4. Average percent relative bias of survival-rate estimators for a heterogeneous population with 2 population segments for 3 and 5 years of banding data.

	Expected survival rates					
	$E(S) = 0.3$			$E(S) = 0.6$		
	Survival rates of segments			Survival rates of segments		
	0.35, 0.25	0.4, 0.2	0.45, 0.15	0.7, 0.5	0.8, 0.4	0.9, 0.3
I[a]	+ 0.5 (+ 1.3)[b]	+ 2.3 (+ 5.0)	+ 5.0 (+10.9)	+ 0.8 (+ 2.3)	+ 3.3 (+ 8.7)	+ 7.5 (+18.5)
II	− 3.7 (− 2.9)	− 6.2 (− 3.5)	− 7.5 (− 1.5)	− 3.3 (− 2.0)	− 5.1 (+ 0.5)	− 5.0 (+ 7.2)
III	− 8.0 (− 7.3)	−14.8 (−12.6)	−20.8 (−15.6)	− 7.7 (− 6.5)	−13.9 (− 8.8)	−18.5 (− 6.8)
IV	−12.3 (−11.8)	−23.8 (−22.6)	−35.0 (−31.5)	−12.1 (−11.3)	−23.3 (−19.9)	−33.4 (−24.7)
V	−16.7 (−16.7)	−33.3 (−33.3)	−50.0 (−50.0)	−16.7 (−16.7)	−33.3 (−33.3)	−50.0 (−50.0)

[a] The recovery rates of the 2 population segments are I: 0.05, 0.05; II: 0.0375, 0.0625; III: 0.025, 0.075; IV: 0.0125, 0.0875; and V: 0, 0.1. In all cases $E(f) = 0.05$.

[b] Figures in parentheses are 5-year values.

Table 5. Average percent relative bias of survival-rate estimators for a heterogeneous population with 3 population segments for 3 and 5 years of banding data.

	Expected survival rates					
	$E(S) = 0.3$			$E(S) = 0.6$		
	Survival rates of segments			Survival rates of segments		
	0.35–0.25[a]	0.4–0.2	0.45–0.15	0.7–0.5	0.8–0.4	0.9–0.3
I[b]	+ 0.4 (+ 0.8)[c]	+ 1.5 (+ 3.3)	+ 3.4 (+ 7.4)	+ 0.6 (+ 1.5)	+ 2.2 (+ 5.9)	+ 5.0 (+12.8)
II	− 2.4 (− 2.0)	− 4.1 (− 2.3)	− 5.0 (− 1.0)	− 2.2 (− 1.3)	− 3.3 (+ 0.4)	− 3.3 (+ 4.8)
III	− 5.2 (− 4.8)	− 9.8 (− 8.2)	−13.7 (−10.1)	− 5.1 (− 4.2)	− 9.1 (− 5.7)	−12.1 (− 4.4)
IV	− 8.1 (− 7.8)	−15.7 (−14.5)	−22.7 (−19.9)	− 8.0 (− 7.3)	−15.1 (−12.4)	−21.4 (−15.2)
V	−11.0 (−10.8)	−21.7 (−21.1)	−32.1 (−30.7)	−10.9 (−10.6)	−21.4 (−20.0)	−31.3 (−28.2)

[a] There are 3 population segments with survival rates of 0.35, 0.3 and 0.25. In all cases the middle survival rate is the same as $E(S)$.

[b] The recovery rates of the 3 population segments are I: 0.05, 0.05, 0.05; II: 0.0375, 0.05, 0.0625; III: 0.025, 0.05, 0.075; IV: 0.0125, 0.05, 0.0875; and V: 0, 0.05, 0.1.

[c] Figures in parentheses are 5-year values.

annual recovery rate over the population is 0.05. The average percent relative bias of survival-rate estimators over a 3- or 5-year study varies (Table 6). These results show that the bias in the survival-rate estimators is very dependent on which relationship between recovery rate (f) and survival rate (s) is considered. If the recovery rate is independent of the survival rate, then there is a positive bias that is most severe in longer studies and when the average annual survivial rate is low. If the relationship is $f = a(1 - s)$, then there is a negative bias that is most severe in shorter studies and when the average annual survival rate is high.

DISCUSSION

It is difficult to make strong quantitative statements about the nature of the bias of survival- and recovery-rate estimators in banding studies. First, the exact nature of the relationship between survival and recovery rates is unknown. Second, few data are available documenting the nature of heterogeneity for

Table 6. Average percent relative bias of survival-rate estimators for a heterogeneous population where individual survival rates follow a beta distribution for 3 and 5 years of banding data.

$E(S) = 0.33$				
Parameter values	$\alpha = 1, \beta = 2$	$\alpha = 3, \beta = 6$	$\alpha = 6, \beta = 12$	$\alpha = 25, \beta = 50$
SE of beta distributions	0.236	0.149	0.108	0.053
f independent of s	+10.8 (+26.0)[a]	+4.4 (+10.2)	+2.3 (+5.3)	+0.6 (+1.3)
$f = 0.075(1 - s)$	−17.0 (− 6.2)	−6.1 (− 1.1)	−3.1 (−0.3)	−0.7 (0)
$E(S) = 0.5$				
Parameter values	$\alpha = 1, \beta = 1$	$\alpha = 5, \beta = 5$	$\alpha = 10, \beta = 10$	$\alpha = 40, \beta = 40$
SE of beta distributions	0.290	0.151	0.109	0.056
f independent of s	+ 9.1 (+21.7)	+2.5 (+6.3)	+1.3 (+3.3)	+0.3 (+0.9)
$f = 0.1(1 - s)$	−26.1 (−16.0)	−6.7 (−3.2)	−3.5 (−1.5)	−0.9 (−0.4)
$E(S) = 0.67$				
Parameter values	$\alpha = 2, \beta = 1$	$\alpha = 6, \beta = 3$	$\alpha = 12, \beta = 6$	$\alpha = 50, \beta = 25$
SE of beta distributions	0.236	0.149	0.108	0.053
f independent of s	+ 4.0 (+ 9.7)	+1.6 (+4.2)	+0.8 (+2.3)	+0.2 (+0.6)
$f = 0.15(1 - s)$	−20.9 (−14.9)	−8.3 (−5.7)	−4.4 (−2.8)	−1.1 (−0.7)

[a] Figures in parentheses are 5-year values.

most species. However, that recoveries frequently occur in widely different geographic areas from banded samples of migratory waterfowl demonstrates that different paths (population segments) exist (Bellrose 1976). In fact, brood mates raised on the same pond may undertake drastically different migrations (Martinson and Hawkins 1968). Therefore, individuals within banded samples are exposed to different environmental conditions including hunting pressure and cooperation in reporting bands (Henny and Burnham 1976). Thus, it is possible to provide some useful new qualitative statements about the nature of possible bias of survival- and recovery-rate estimators when heterogeneity is present in the population. Readers should also keep in mind that bias is of relatively more practical importance in precise studies where the standard errors are small.

Recovery Estimators.—(1) If population segments have the same survival rates but different recovery rates, then there is no bias in the estimator of the average recovery rate. (2) If population segments have heterogeneous survival and recovery rates, then the recovery-rate estimators at the beginning and end of a study always have no bias and those in the middle have a negative bias. The bias is more severe for species where the average survival is high and for studies of longer duration. The degree of bias is much less than for the survival-rate estimators and can probably be ignored for most practical purposes.

Survival Estimators.—(1) If population segments have the same survival rates but different recovery rates, then there is no bias in the survival estimators. This could occur if there were reporting rate changes in different geographical areas (Henny and Burnham 1976). (2) If survival probabilities are heterogeneous over the population, there is likely to be a strong positive relationship between the survival probabilities of an individual from year to year. There is also likely to be a negative relationship between survival and recovery probabilities for an individual. In this situation, survival-rate estimators will generally have a negative bias. The negative bias will be more severe for species where the average survival rate is high and for studies that are of short duration. The seriousness of this negative bias to a banding study will depend on the species under study and will be hard to evaluate in general. (3) It is theoretically possible for the survival-rate estimators to have a positive bias. This could occur if there were segments with markedly different survival rates but similar recovery rates. This implies that the difference in survival of the segments would have to be mostly due to differences in natural mortality. This could occur if drastically different environmental conditions were encountered by the segments (e.g., disease level, food supply, weather). All of these factors can vary on a local or regional scale.

A CANADA GOOSE POPULATION

There has been little documentation of the existence of populations of migratory birds with heterogeneous survival and recovery rates. A major reason is that most studies on the dynamics of migratory bird populations are based on data from band recoveries from dead birds. These data are not suited to a thorough examination of the nature of possible heterogeneity.

The analysis of the geographic distribution of band recoveries does indicate the segments of a population of banded individuals may take different migratory routes. A good example comes from the

Table 7. Characteristics of the Marshy Point adult Canada goose population viewed as 2 distinct segments.

Characteristic	Segment		Average annual population values
	Rochester	Remainder	
Proportion of population	0.75[a]	0.25[a]	
Survival rate	0.83[b]	0.51[b]	0.75[c]
Hunting mortality rate	0.11[d]	0.30[d]	
Recovery rate	0.03[e]	0.08[e]	0.04[e]

[a] From Raveling (1978).

[b] Weighted averages from Raveling (1978)—uses Kirwin, Kansas, data as representative of the remainder. These estimates of survival are based on those birds alive and that returned to Marshy Point. They have approximate standard errors of 0.02 and 0.07, respectively.

[c] This is a weighted average of segment values. The average survival rate is given by $[(3 \times 0.83) + (1 \times 0.51)]/4 = 0.75$.

[d] From Raveling (1978). The Rochester rate is for Manitoba plus Minnesota. The remainder rate was the data from Manitoba plus Kansas plus other Central Flyway states.

[e] These values are obtained by assuming 0.85 of the birds are retrieved and 0.3 are reported (Raveling 1978). For example, the recovery rate for the Rochester segment is: $0.11 \times 0.85 \times 0.3 = 0.03$.

study of Anderson and Sterling (1974) on pintail (*Anas acuta*) drakes banded in Saskatchewan: "Banded pintail drakes were taken by hunters in Canada, all four Flyways in the United States, in Mexico and in Russia, with a single report from Cuba." We believe that it is likely that the pintails undertaking such different migrations had different survival and recovery rates because of different hunting pressures and environmental conditions. Six of the 8 pintail data sets analyzed by Burnham and Anderson (1979) did not fit modern methods of analysis, however, we emphasize that other explanations are possible.

An alternative type of data, not without its own problems, is repeated observations of individually identifiable birds on both the breeding and wintering grounds. This approach was taken by Raveling (1978), who described a population of giant Canada geese (*B. c. maxima*) neck-collared at Marshy Point Goose Sanctuary on the southeastern shore of Lake Manitoba, Canada, during the summers of 1968–70.

From 1968 to 1976, the marked geese were observed on breeding and staging areas at Marshy Point and on wintering grounds at Rochester, Minnesota; Kirwin, Kansas; and Swan Lake, Missouri. Raveling (1978) concluded that this population of geese consisted of segments with differing hunting mortalities and overall survival rates. About 75% of the birds migrated to Rochester, Minnesota, and were subjected to an annual hunting mortality rate of about 19% and total annual mortality of 25%. The remainder of the birds wintered in several areas, with most (15% of the total population) going to Kirwin, Kansas. They had an annual hunting mortality of about 48% and a total annual mortality of 58% (including mortality on breeding grounds in Manitoba). It should be emphasized that these estimates are subject to sampling error and perhaps some bias due to collar loss.

To obtain an approximation of the degree of bias in a traditional banding study on this population, let us assume we have a population of *adult* birds divided into 2 segments (Table 7). These characteristics describe the population based on direct observation of 90% of the marked individuals (Raveling 1978). However, this is admittedly still a simplification of the real population. Based on 3 years of data, the expected value of the survival estimator from Eq. (6) is approximately 0.69, as compared with the average population value of 0.75. This gives a relative bias of about −8%. Over a longer study the bias would be less.

More important to the biologist than any negative bias of the average survival estimate is that a traditional banding study would have revealed almost nothing about the characteristics of the segments. The segment not going to Rochester (25%) was being subjected to a high mortality rate clearly beyond the reproductive potential of geese. Such differential mortality rates for segments could cause rapid distributional changes and have important implications for management (Raveling 1978).

A REVIEW OF THE ASSUMPTIONS OF MODERN BANDING MODELS

Considering the attention given in the literature to the assumptions of capture-recapture sampling (Cormack 1968, Seber 1973), band-recovery models should be subjected to the same scrutiny. Here we consider all of the assumptions of Brownie et al. (1978:6), with an emphasis on the practical implications of assumption failure.

The Sample is Representative of the Target Population

This assumption is important, particularly if heterogeneity of survival and band-recovery rates occurs. Let us take an extreme example for illustration, where we have a population composed 90% of birds with an annual survival rate of 0.8, and 10% of birds with an annual survival rate of 0.4. The average survival rate for the population is 0.76, but suppose nonrandom sampling makes our population appear equally divided into 2 segments. The apparent average survival rate is 0.6, and in a 5-year banding study there would also be a negative bias on survival estimators. The expected value of the survival estimators would be approximately 0.55 if we assume recovery rates of 0.025 and 0.075 for the 2 segments (Eq. [6]).

The following are some possible causes of nonrepresentative samples. (1) Segments may use different parts of a staging or winter area due to behavioral characteristics of the species. This has been demonstrated in the stratification of Canada goose population segments at a migration stopover and winter location (Raveling 1979). If this heterogeneous spatial distribution on a small scale is ignored and only easily accessible areas are sampled rather than using a random sample, large biases could result. (2) Banding at different times on a staging area could be of segments with different timing of migration or different wintering grounds and, hence, possible different survival rates. Canada geese banded at the same trap sites in July, August, and September had different migration patterns, and thus different proportions of segments were sampled in the different time periods (Raveling 1978). Dispersal away from natal sites and concentration at staging areas before autumn migration are common features of many duck populations (Bellrose 1976). It is likely that trapping efforts capture varying components of dispersing birds, which represent different characteristics in terms of their molt and behavior patterns that could be reflected in different migration patterns and vulnerability to hunting. (3) Banding is likely to be nonrandom with respect to age- and sex classes in a population (Raveling 1966). This could be important if age and sex categories cannot be accurately established in the field. It is common during winter banding of several duck species to consider all birds adults, because the molt of juveniles has progressed to make them nearly indistinguishable from adults when plumage criteria are used to separate age-classes. It is well known that different age and sex categories may have different survival rates.

Age and Sex of Individuals are Correctly Determined

This is related to (3) above, and will clearly depend on the species being studied. If the assumption is false, one will, in effect, have segments of different age and sex categories, which is likely to cause heterogeneity of survival and recovery rates.

There is No Band Loss

This is rarely completely true, but it is likely that for recent studies the loss rate is low. Nelson et al. (1980) examined this assumption and found that there is a negative bias on survival estimators that is worse for species with high survival rates. They concluded that, unless band loss was high, this bias would be of little significance. However, it does occur on occasion, especially for sea birds and raptors. Ludwig (1967) documented severe band loss in a study on ring-billed gulls (*Larus delawarensis*) in the Great Lakes.

Survival Rates are Not Influenced by Banding

This assumption is important because if there was substantial mortality due to banding, the survival estimators would not apply to the nonbanded birds. Direct damage will depend on the species and the method of capture, and should usually be detectable by experienced biologists. Detection may not always be easy, however. For example, Lensink (1964:12) concluded that serious injuries to ducklings caught by dogs were frequently undetected, as band-recovery rates from those birds were much lower than from birds caught in traps. Indirect damage by dispersing family groups and other social relationships is more subtle, but may be more common than assumed.

The Year (Hunting Season) of Band Recoveries is Correctly Tabulated

Errors here are probably rather infrequent and should not cause major difficulties in most practical applications of the models (Anderson and Burnham 1980). However, errors do occur and usually involve a hunter reporting a band taken in a later season than when it actually was taken. Raveling (unpubl. data) has 9 records of instances in which a band was sent in with the wrong season identified (of 327 recoveries, or a minimum of 2.8% error). Reasons for this occurring include fears by hunters of government apprehension when sending a band in after a hunting season had closed; sending in bands as taken in a year when a hunter's interest was stimulated by friends or game department officials, but after the banded bird(s) had been obtained; fear of reporting bands of birds killed outside the legal hunting season; and hunters reporting band numbers from birds previously taken by friends or acquaintances as being taken by themselves in the current year. To the extent that such instances occur, they operate to produce a positive bias on survival estimators.

The Fate of Each Banded Individual is Independent of the Fate of Other Banded Individuals

This assumption is probably violated in many practical applications of bird-banding models. Birds are not independent entities in terms of survival or other characteristics (Sulzbach and Cooke 1978). This will not bias any estimators, but will mean that true sampling variances are larger than those given by the statistical models. Thus, any calculated confidence intervals will be narrower than they should be.

A simple example for illustration is to consider a population composed of independent pairs of birds that behave as though they are a single individual. A sample of N individuals from this population is effectively only one-half of N and, hence, any sampling variances will be much larger than those for the models that assume the sample is N independent individuals. The actual situation in real populations is much more complex, with many partially dependent members, but the effective sample size will still be less than the actual sample size. This would impact the confidence intervals of analyses of survival for geese and swans because of their strong pair and family associations.

The Fate of a Given Banded Animal is a Multinomial Random Variable

This is not really an assumption. It follows from the assumption of independence.

All Banded Individuals of an Identifiable Class Have the Same Annual Survival Rates and Recovery Rates

The effects of failure of this assumption have been discussed in detail elsewhere in this paper. We feel it is likely that populations with heterogeneous survival and band-recovery rates exist in practice because: (1) Migration is often on more than 1 flyway, and even on a single flyway there is often a series of wintering points. (2) Hunting pressure varies drastically from state to state and even in different regions of the same state, especially because of the existence of refuges. (3) Habitat on the breeding and wintering grounds is variable.

CONCLUSIONS

We feel that wildlife scientists involved with banding studies should give careful consideration to the model assumptions we have discussed. We believe that particular attention should be given to whether the sampling is random and to whether heterogeneity of survival and band-recovery rates is pronounced. The question of the effect of the banding process itself either directly or indirectly on survival is also important.

If population segments exist and are of interest in their own right, other forms of data such as repeated observations of color-marked, live birds on the breeding and wintering grounds should be considered if possible. Clearly, alternative methods of data collection will not be without their own difficulties.

LITERATURE CITED

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NUMERICAL ESTIMATION OF SURVIVAL RATES FROM BAND-RECOVERY AND BIOTELEMETRY DATA

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Abstract: The estimation of survival rates from tagging or banding data has been well developed by Brownie et al. (1978). However, problems occur when sparse data sets result in undefined estimates, when survival estimates exceed unity, when a hypothesis about the data cannot be tested by any of the available models, and when constraints on model estimators are desired. This paper presents a general analysis method whereby the models of Brownie et al. (1978) and many other methods described in the literature are merely special cases. Models are specified algebraically as cell probabilities consisting of functions of the survival rates and other parameters to be estimated. These algebraic expressions and the observed cell values are input to the computer program SURVIV to provide maximum-likelihood estimates of the unknown parameters and perform hypothesis tests on the data. The generality of the model specification also allows estimation of survival rates from biotelemetry data.

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Estimates of the critical parameters of a wildlife population are required for its sound management. Estimates of recruitment and survival are needed to harvest a population in an optimal fashion. In this paper, numerical methods of maximum-likelihood estimation of survival rates from biotelemetry and banding data are described and a general computer code to perform the estimation is presented.

Maximum-likelihood (ML) estimation is a rigorous statistical method of obtaining estimators for unknown parameters. ML estimators fall into 2 classes: (1) closed form and (2) iterative or numerical. In either case, a likelihood function $L(\theta|X)$ involving the parameters of interest (the vector θ) is formed, given the data (X). In the context here, θ usually represents survival and recovery rates. In all cases, the ML estimators can be found as the solutions of

$$\frac{\partial \ln L(\theta|X)}{\partial \theta_i} = 0.$$

That is, the partial derivative of the natural logarithm of the likelihood function with respect to the ith parameter is set equal to zero and solved for θ_i. From calculus, this procedure is known to find the maximum of the log-likelihood function (hence the name "maximum likelihood"). If θ is a vector of 9 parameters, then there are 9 equations to be solved (usually nonlinear simultaneous equations). Often, these equations can be solved algebraically, such as the ML estimators presented by Seber (1970).

More frequently, it is impossible, or at least difficult, to solve these equations algebraically. In this case, ML estimators of each parameter θ_i can be found by iteratively (using numerical techniques) maximizing the likelihood function $L(\theta|X)$. Systems that can be solved algebraically can also be solved numerically, but not vice versa.

Numerous authors (cf. Robson 1963; Murton 1966; Cormack 1970; Seber 1970, 1971, 1972; Johnson 1974; Youngs and Robson 1975; Brownie et al. 1978; North and Cormack 1981) have developed estimators of survival rates from band- or tag-recovery data, making a wide variety of specific assumptions. In each of the references cited, maximum-likelihood methods were used to derive the estimators and their sampling variances and covariances.

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Jolly (1965:228–230) demonstrated how to build a general model (likelihood function) for capture–recapture sampling for open populations. He then derived estimators for only a few special cases of this model due to the difficulties of algebraically solving the likelihood equations. Numerical solution of complex likelihood equations such as those presented by Jolly (1965) provides a means of obtaining estimates for any particular model, including the most general model, from a complex likelihood function. The biologist or biometrician is no longer constrained by the algebraic complexity of solving the likelihood equations from using a model that provides a realistic representation of the biological situation.

Brownie et al. (1978:9–12) demonstrated how a conceptual model of band-recovery data is used to construct a likelihood function and derive ML estimators. All of the references cited use the technique they describe. The computer program presented here also uses the same technique to perform ML estimation of survival and recovery parameters. Any of the models mentioned in the references cited can be handled by the program, because they are merely special cases of the more general theory. The results of Brownie et al. (1978) are the most recent and comprehensive; thus, comparisons with their work will be made through the remainder of the paper.

Band- or tag-recovery models are more general than needed for biotelemetry data in that the fate of radio-marked animals is usually known, but legbanded birds are often not recovered. Whereas the recovery rate (*f*) of bands must be estimated, the recovery rate of radios is usually known exactly (i.e., $f = 1$). Maximum-likelihood estimation is also useful to obtain estimates of survival rates from biotelemetry data.

Herein are described procedures and a computer program that treat survival-estimation methods as specific cases of a more general model. Methods of estimating parameters and testing general hypotheses about the model parameters are presented. The trade-offs between numerical vs. analytical maximum-likelihood estimation of survival rates are discussed and the necessity of an easy-to-use program illustrated. A Monte Carlo simulation of the effects of bounding parameters on their bias is presented and an example of survival-rate estimation for an elk (*Cervus elaphus nelsoni*) biotelemetry study is provided to illustrate the practical application of the approach described in this paper.

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PARAMETER ESTIMATION BY NUMERICAL METHODS

The general model for estimating survival rates from biotelemetry data is structured identically to that of Brownie et al. (1978:9–12), consisting of a set of multinomial distributions tied together by common parameters to describe the expected cell probabilities, with the numbers of animals banded or tagged treated as fixed observable numbers. The model is best illustrated by considering a simple example. Assume that 40 and 50 animals are radiocollared in years 1 and 2, respectively. The fate of these 90 radio collars is known (Table 1), based on a 3-year battery life. Thus, the "disappearance" of the animal after 3 years is attributed to bat-

Table 1. Simulated and expected recovery history of 90 radio collars placed on elk in years 1 and 2. The true survival rates for years 1–4 were 0.6, 0.7, 0.5, and 0.6, respectively.

Year collared	Number collared	Year collars returned 1	2	3	4	Battery failure
			Simulated Recoveries			
1	40	12	8	13		7
2	50		13	17	7	13
			Expected Recoveries			
1	N_1	$N_1(1 - S_1)$	$N_1S_1(1 - S_2)$	$N_1S_1S_2(1 - S_3)$		$N_1S_1S_2S_3$
2	N_2		$N_2(1 - S_2)$	$N_2S_2(1 - S_3)$	$N_2S_2S_3(1 - S_4)$	$N_2S_2S_3S_4$

tery failure. This simple example assumes no animals are lost due to radio failure or emigration from the study area.

Brownie et al. (1978:9–12) used the cell probabilities of models such as that in Table 1 (Boyd 1956, Seber 1970) to construct a likelihood function and derive ML estimators of the unknown parameters (in the example S_1, S_2, S_3, and S_4). The computer programs they described are the current "state-of-the-art" for estimating survival rates from band-recovery data. Several limitations occur with their approach. First, the parameter estimates are not constrained in a bounded region; thus, estimates of survival rates greater than unity occasionally occur, particularly if samples are small. Second, if a sparse data matrix happens to occur (i.e., certain critical cells have zeros), some estimators are undefined, even though the estimated survival for that cell could be unity (cf. North and Cormack 1981).

The restrictions of the programs provided by Brownie et al. (1978) can be alleviated by optimizing the likelihood function numerically, with the parameter space restricted to the range of admissible parameter values. Several other advantages are incurred by using numerical procedures. Sets of parameters can be constrained to a common value. Thus, in the simple example, S_1 and S_2 can be constrained to a common value, and likewise S_3 and S_4. Thus, the parameter space can be reduced from 4 to 2 and, if this model is still appropriate for the data, more precise estimates of the parameters are achieved.

An additional extension of the models presented in Brownie et al. (1978) is that models can be developed that allow the same survival parameters for 2 sexes at 1 age-class, but different survival rates at a later age-class. Consider as an example the estimation of survival of a cervid species. The survival of male and female young may be identical to develop a parsimonious model. However, when the age-class is reached where sex differences become obvious (such as antlers), the survival rates could differ. Thus, models to estimate the survival rates of cervid species should allow common survival rates for the young animals of both sexes, but different survival rates for the sexes at later age-classes. Tests of the hypothesis of identical survival of the young should be made before this hypothesis is supported, however.

The drawback to the numerical optimization approach is formulating the algebraic expression of the likelihood function. A computer program described in a later section is available to construct the likelihood function from the algebraic expressions for the expected cell probabilities, perform optimization (with constraints), and construct likelihood-ratio tests between models. However, the user must thoroughly understand the formulation of the expected cell probabilities to use this program.

A 2nd shortcoming of the numerically derived estimates is that the small sample bias of the estimators currently cannot be corrected as is done with analytical estimates (cf. Brownie et al. 1978:16). However, Monte Carlo simulation results (see Discussion) suggest that constraining the range of the estimate to its admissible range may partially offset the bias of the estimators.

A 3rd drawback of the numerically derived estimates is that the program may occasionally fail to converge on the global maximum of the likelihood function. Such failures of the method may be due to small data sets relative to the number of parameters being estimated, low numerical precision of the computer relative to the number of parameters being estimated, and finally lack of parameter identifiability. In the 1st 2 circumstances, failure to converge theoretically should not occur, but does due to the physical limitations of the machine. However, in the 3rd case, estimates should not be obtained. Due to the limit of numerical precision of digital computers, the program will attempt to find a solution, even though none exists. Generally such solutions are obviously wrong, because some parameters were not changed from their initial values and/or the variance–covariance matrix is not positive definite.

HYPOTHESIS TESTING VIA NUMERICAL PROCEDURES

Numerical maximization of the likelihood function produces ML estimates of the unknown parameters. Generally, the researcher also wants to test hypotheses from the data. Likelihood-ratio tests provide the means of testing elaborate hypotheses about complex data sets.

The appropriateness of estimating common parameter values can be easily determined with numerical methods because likelihood-ratio tests can be constructed from the values of the likelihood functions evaluated at the ML estimates. Thus, if the null hypothesis of H_0: $S_1 = S_2$ and $S_3 = S_4$ is to be tested, the likelihood function is first maximized with all 4 parameters individually estimated and then maximized again with $S_1 = S_2$ and $S_3 = S_4$. Then a likelihood-ratio test with the 2 likelihood values is constructed. Because the computer programs described by Brownie et al. (1978) use specific models, all hypothesis tests are for specific situations. The numerical optimization procedure allows a more general approach.

Likelihood-ratio tests are specific tests between 2 particular models where the null hypothesis is H_0: Model A is equivalent to Model B when Model B is a special case (nested) of Model A. The alternative hypothesis is H_a: Model A is not equivalent to Model B. Likelihood-ratio tests are constructed from the values of the likelihood functions for each of the models to be compared. By likelihood-ratio theory, the quantity

$$\chi^2 = -2 \ln \frac{L(\theta_0 | X)}{L(\theta | X)}$$

is known to be asymptotically chi-squared distributed with degrees of freedom equal to the number of parameters removed from the parameter space for the reduced model (model in the numerator with parameter vector θ_0) (Mood et al. 1974:440). Thus, to test the hypothesis that 2 survival rates are equivalent, the likelihood value for the general model with S_i and S_{i+1} both estimated is obtained. Then S_i is set equivalent to S_{i+1} (i.e., the parameter space of the reduced model is made smaller by 1 parameter) and the likelihood for this reduced model is obtained. The resulting chi-square statistic is distributed with 1 degree of freedom. Additional parameters can be equated to obtain more general hypotheses (i.e., $S_i = S_{i+1} = S_{i+2} \ldots$, or $S_i = S_j$, $S_{i+1} = S_{j+1}, \ldots$) to obtain a chi-square statistic with more than 1 degree of freedom.

Chi-square goodness-of-fit tests can also be constructed for any particular model by summing the (observed − expected)^2/expected values for each of the cells of the model (Mitra 1958). Generally, cells with expected values less than 2.0 are pooled with neighboring cells (Roscoe and Byars 1971) to obtain a chi-square statistic.

PROGRAM SURVIV

The practical application of the numerical optimization approach requires that a user-oriented computer program is available. That is, the chore of constructing the matrix of expected cell probabilities is difficult in itself and additional complications due to complex input for a computer program make the task nearly insurmountable. Program SURVIV has been developed to handle the numerical optimization task with straightforward and simple input to SURVIV. The advantages to numerical estimation would be offset by requiring a complex coding of model specifications and observed data. The simplicity of this input is demonstrated by a simple example for biotelemetry data.

Program SURVIV uses the procedures MODEL, ESTIMATE, and TEST to perform the numerical estimation calculations. PROC MODEL constructs the likelihood function from algebraic expressions describing the cell probabilities. The generality and ease of model specification are shown by the input in Fig. 1 for the simple example in Table 1. The PROC MODEL statement sets various options and alerts the program that the observed and expected cell probabilities are to follow. The COHORT card sets the number of animals for the 1st multinomial and is followed by the 3 multinomial cells with the observed value separated from the expected value by a colon. The entry of the expected cell probability is the feature of Program SURVIV that makes the numerical approach described feasible. The parameters to be estimated are denoted by the S(I) notation in the algebraic expression. This algebraic expression must be FORTRAN compatible, because the program manipulates this code to construct a FORTRAN subroutine to evaluate the likelihood function.

PROC MODEL continues to read COHORT, cell probability, and LABELS cards until the PROC ESTIMATE card is encountered. PROC ESTIMATE is called to make the actual parameter estimates. The INITIAL statement (Fig. 1) signifies that initial estimates of some parameters are provided (the default is S(I) = 0.5). The 1st time ESTIMATE is called in Fig. 1, only boundary constraints are provided (i.e., the admissible range of the parameter values are set). This call to PROC ESTIMATE evaluates the model with 4 individual values of S(1), S(2), S(3), and S(4).

The 2nd call (Fig. 1) to PROC ESTIMATE evaluates the model with S(1) = S(2) and S(3) = S(4) (i.e., the reduced model where 2 sets of parameters are assumed equal). The CONSTRAINTS statement is used to specify these equalities, and the degrees of freedom of the model are automatically reduced by 2. At this time, the constraints must be constants,

```
PROC TITLE SMALL BIOTELEMETRY EXAMPLE FOR JWM ARTICLE;
PROC MODEL NPAR=4 /* SIMPLE BIOTELEMETRY EXAMPLE */;
   COHORT = 40 /* NUMBER OF ANIMALS COLLARED IN YEAR 1*/;
    12:(1.-S(1));
     8:S(1)*(1.-S(2));
    13:S(1)*S(2)*(1.-S(3));
     7:S(1)*S(2)*S(3);
   COHORT = 50 /* NUMBER OF ANIMALS COLLARED IN YEAR 2*/;
    13:(1.-S(2));
    17:S(2)*(1.-S(3));
     7:S(2)*S(3)*(1.-S(4));
    13:S(2)*S(3)*S(4);
   LABELS;
     S(1)=SURVIVAL RATE IN YEAR 1;
     S(2)=SURVIVAL RATE IN YEAR 2;
     S(3)=SURVIVAL RATE IN YEAR 3;
     S(4)=SURVIVAL RATE IN YEAR 4;
PROC ESTIMATE NAME=GENERAL /* ALL PARAMETERS INDIVIDUALLY ESTIMATED */ ;
   INITIAL;   S(1)=0.6;   S(2)=0.7;   S(3)=0.5;   S(4)=0.6;
PROC ESTIMATE NAME=CONSTRAIN /* SETS OF 2 PARAMETERS CONSTRAINED */ ;
   INITIAL;   S(1)=0.6;   S(2)=0.7;   S(3)=0.5;   S(4)=0.6;
   CONSTRAINTS;   S(1)=S(2);   S(3)=S(4);
PROC TEST /* GENERATE LIKELIHOOD RATIO TEST OF ABOVE 2 MODELS */ ;
PROC STOP /* SIGNAL END OF ANALYSIS. */ ;
```

Fig. 1. Input to Program SURVIV to analyze the data and model in Table 1. Statements are separated by semicolons and observed recoveries are separated from the algebraic expression for the expected cell probabilities by colons.

hence they cannot be a function of the parameters.

PROC TEST performs a likelihood-ratio test between all pairs of models called in PROC ESTIMATE, given that the degrees of freedom available for each model are not equal. In this simple example, only 1 test is performed because only 1 pair of models is available: the general model with 4 parameters and the reduced model with 2 parameters. The null hypothesis tested is H_0: $S_1 = S_2$ and $S_3 = S_4$ vs. the alternative hypothesis H_a of at least 1 of the equalities not true.

Other procedures in Program SURVIV useful for performing survival-rate estimation experiments are SIMULATE and SAMPLE SIZE. PROC SIMULATE performs Monte Carlo simulation of a model entered via PROC MODEL. Use of PROC SIMULATE allows the researcher to determine the power of hypothesis tests and to determine expected confidence-interval length of interval estimates based on numbers of marked animals and estimated survival rates. PROC SAMPLE SIZE performs sample-size estimation for banding experiments, as described by Brownie et al. (1978:186–193). Both of these procedures are designed to aid the researcher in performing an optimal analysis to estimate survival rates. PROC SIMULATE is also useful in studying the operating characteristics of a model and the associated estimates.

NUMERICAL ALGORITHMS IN PROGRAM SURVIV

Program SURVIV uses a quasi-Newton method (Fletcher 1972) to minimize the likelihood function constructed from the cell probability expressions. Neither 1st nor 2nd partial derivatives of the likelihood function with respect to the parameters is required.

Parameters are constrained to the interval (S_L, S_B) with the transformation (Box 1966)

$$S_i = (S_U - S_L)(0.5 \sin[P_i] + 0.5) + S_L,$$

where P_i varies in the interval $(-\infty, +\infty)$, but S_i is always $S_L \leq S_i \leq S_U$.

EFFECTS OF PARAMETER BOUNDARIES ON ESTIMATES

A Monte Carlo simulation using PROC SIMULATE was performed to assess whether constraining the parameter estimates to their admissible range caused the remaining estimates to exhibit poor properties. A banding-analysis model (Model 1 of Brownie et al. 1978:15–20 or Seber 1970) was chosen for the simulation because both bias-adjusted and exact maximum-likelihood estimators (Brownie et al. 1978:16) were known. Banding was assumed to occur for $k = 10$ years, with $N_i = 75$ birds banded each year (a small sample size ensuring some estimates >1). Recoveries were followed for $l = 10$ years, thus 9 survival rates and 10 recovery rates can be estimated. Recovery rates were all set to 0.075, but the 9 survival rates were varied by year as 0.3, 0.4, 0.5, 0.6, 0.7, 0.6, 0.5, 0.4, and 0.3, respectively. Estimation was replicated for 1,000 simulations. The 9 estimates of survival rates were constrained to the interval [0, 1].

Simulation results varied (Table 2). At least 1 of the bias-adjusted survival estimates was >1 for 37.6% of the simulations. The numerical estimates are biased (as expected), but not as much as the unadjusted analytical estimates. Thus, the trade-off between the numerical estimates and the bias-adjusted estimates is bias vs. up to 12% inadmissible values for $S_5 = 0.7$. This trade-off would favor the numerical estimates as the true parameter proceeds toward unity because the numerical procedure shows less bias. It would favor the bias-adjusted analytical estimates as the parameter value proceeds toward 0.5 because there is less chance of obtaining inadmissible values as S decreases and the bias increases for the numerical estimator. However, as S approaches zero, small observed values will lead to greater probability of failure of the analytical estimator (i.e., zero denominator). The numerical procedure handles the zero cells by constraining 1 or more estimates to 0 or 1.

EXAMPLE USING BIOTELEMETRY DATA

Elk were radiocollared by Los Alamos National Laboratory personnel from 1978 to 1980 with radio collars having a 3-year battery life. Animals were initially collared only in the eastern Jemez Mountains of New Mexico, but in 1980 a 2nd herd was studied in the western Jemez Mountains. The age and sex of the animals collared (by location and year) and the collar returns varied (Table 3).

Program SURVIV can be used to test the hypothesis of interest: was the survival of western Jemez elk different from that of eastern Jemez elk? This hypothesis involves testing the equality of the 1980 survival rates for the western and eastern animals. That is, the survival parameters for western Jemez elk are set equal to the corresponding parameters for the eastern Jemez elk in the CONSTRAINTS section of PROC ESTIMATE. The results of this model are tested against the general model where all parameters are estimated individually.

Some of the survival rates are not estimable for this data set (e.g., adult male survival for 1978) because no animals were captured. Program SURVIV can handle such data because either the parameter can be left out of the cell probability statements, or the parameter can be fixed to a particular value and not estimated. The latter choice is preferred because, as the parameters are constrained equally in the reduced models, estimates can be generated.

The sequence of 5 models was tested

Table 2. Simulation of Model 1 of Brownie et al. (1978:15–20) for 1,000 replications using 3 different estimators of survival rates.

Parameter	True parameter value	Percentage of estimates inadmissible[a]	Mean of estimates	Standard error of estimates	95% CI	Percent bias[b]
Estimates From Numerical Procedure						
1	0.3	0.0	0.32	0.0064	0.31–0.33	6.5
2	0.4	0.0	0.43	0.0063	0.42–0.44	8.0
3	0.5	0.0	0.52	0.0063	0.51–0.54	4.6
4	0.6	0.0	0.62	0.0066	0.60–0.63	2.8
5	0.7	0.0	0.72	0.0068	0.70–0.73	2.6
6	0.6	0.0	0.64	0.0070	0.62–0.65	6.2
7	0.5	0.0	0.54	0.0075	0.52–0.55	7.6
8	0.4	0.0	0.45	0.0077	0.44–0.47	13.7
9	0.3	0.0	0.35	0.0079	0.33–0.36	15.2
Bias-adjusted Analytical Estimates						
1	0.3	1.0	0.30	0.0060	0.28–0.31	−1.2
2	0.4	0.8	0.41	0.0062	0.39–0.42	1.4
3	0.5	1.8	0.50	0.0065	0.48–0.51	−0.9
4	0.6	5.9	0.59	0.0076	0.58–0.60	−1.7
5	0.7	12.7	0.70	0.0095	0.68–0.72	0.5
6	0.6	9.2	0.61	0.0105	0.59–0.63	1.8
7	0.5	4.9	0.50	0.0087	0.49–0.51	−0.9
8	0.4	3.2	0.41	0.0084	0.40–0.43	3.3
9	0.3	1.9	0.30	0.0075	0.28–0.31	−0.7
Unadjusted Analytical Estimates						
1	0.3	1.0	0.33	0.0070	0.31–0.34	8.7
2	0.4	1.7	0.44	0.0069	0.42–0.45	9.3
3	0.5	2.9	0.53	0.0073	0.52–0.54	5.9
4	0.6	8.4	0.63	0.0085	0.61–0.65	5.1
5	0.7	19.6	0.77	0.0113	0.74–0.79	9.5
6	0.6	13.4	0.69	0.0154	0.66–0.72	14.6
7	0.5	8.5	0.57	0.0117	0.54–0.59	13.2
8	0.4	6.1	0.49	0.0122	0.47–0.51	22.4
9	0.3	5.0	0.38	0.0118	0.36–0.40	26.1

[a] $S_i > 1.0$.
[b] Percent bias $= 100(\hat{\theta} - \theta)/\theta$.

from these data. The most general model allows individual survival rates for each age- and sex class, year, and geographic area, making a total of 24 parameters. Only 20 of these parameters are estimable from the data available (Table 3). The 1st reduced model was that survival was the same in geographic areas, and the null hypothesis was not rejected ($P = 0.25$). Then, the hypothesis of survival equal between years was tested ($P = 0.51$), and again was not rejected. The next hypothesis was that survival was the same for age- and sex classes within the categories of hunted and nonhunted. That is, male calves and all female age-classes are pooled as 1 survival rate, and adult and yearling males as 1 survival rate, giving only 2 survival parameters to estimate. This highly reduced model was not significantly different from the previous model ($P = 0.17$). The last model of all survival rates constant was rejected by the goodness-of-fit test ($P \leq 0.01$) as well as by the likelihood-ratio test against the previous model ($P \leq 0.01$).

These results must be interpreted within the framework of statistical hypothesis testing, i.e., we "fail to reject" the null

Table 3. Return of radio collars from an elk biotelemetry study in the Jemez Mountains, New Mexico.

				Year returned				Battery failure or still alive
Year	Location	Sex	Age (yr)	*N*	1978	1979	1980	
1978	East Jemez	M	2½+	0	0	0	0	0
1979	East Jemez	M	2½+	1		0	1	0
1980	East Jemez	M	2½+	1			0	1
1980	West Jemez	M	2½+	1			1	0
1978	East Jemez	M	1½	1	1	0	0	0
1979	East Jemez	M	1½	1		1	0	0
1980	East Jemez	M	1½	2			1	1
1980	West Jemez	M	1½	5			0	5
1978	East Jemez	M	½	5	1	1	3	0
1979	East Jemez	M	½	2		0	1	1
1980	East Jemez	M	½	1			0	1
1980	West Jemez	M	½	0			0	0
1978	East Jemez	F	2½+	8	0	0	1	7
1979	East Jemez	F	2½+	3		2	0	1
1980	East Jemez	F	2½+	7			1	6
1980	West Jemez	F	2½+	5			0	5
1978	East Jemez	F	1½	0	0	0	0	0
1979	East Jemez	F	1½	0		0	0	0
1980	East Jemez	F	1½	4			0	4
1980	West Jemez	F	1½	0			0	0
1978	East Jemez	F	½	2	0	0	0	2
1979	East Jemez	F	½	4		0	0	4
1980	East Jemez	F	½	2			0	2
1980	West Jemez	F	½	2			0	2

hypothesis, but cannot accept it as true. The probability of a Type II error is high due to the small number of radio-collared animals relative to the number of years and age- and sex classes. Thus, the simple model with only 2 survival rates is probably not the true model for the elk population, but sufficient data are lacking to justify a more complex model. Therefore, this model is accepted as the model consistent with the observations taken. The estimated survival rates and their associated standard errors are 0.54 ± 0.10 and 0.93 ± 0.03 for the hunted and nonhunted segments of the radio-collared elk population, respectively.

However, a more extensive data set may indicate that survival rates do differ between age- and sex classes other than hunted and nonhunted. Certainly the small sample sizes in this example are not adequate for good estimates of survival, as indicated by the large estimated standard error of the 2 estimates.

Previous attempts to estimate survival rates in elk using tag recoveries (Kimball and Wolfe 1974, 1979) assumed that survival was constant from year to year. The advantage of the methods presented in this paper and those of Brownie et al. (1978) is that the estimates are less likely to be biased due to an incorrect model.

DISCUSSION

Instantaneous Survival Rates

Program SURVIV can also be used to estimate instantaneous survival rates. The finite survival rate (probability of survival for the time period between bandings) can be replaced with the appropriate algebraic expression containing the instantaneous survival rate. Rather than an estimate and standard error of a finite rate, the estimate and standard error of the instantaneous rate would be obtained. Boundary constraints on the instantaneous rate would differ from the default interval of [0, 1] appropriate for a finite rate.

Radio Failure

The failure of biotelemetry transmitters attached to experimental animals is assumed to occur only at the predicted time of battery depletion. Although failure with modern, commercially available equipment is generally uncommon, failures do occur. How radio failures are handled in the analysis depends on the cause of failure. If the failure is truly a random event (i.e., failure was not caused by some factor attributable to the animal's survival characteristics), then the animal can be discarded from the study and the number of radio-marked animals reduced by 1. However, often the failure of a radio is due to the animal's mortality, such as when it is illegally killed and the radio destroyed. In this case, the time of radio failure should be taken as the time of the animal's death. Obviously the biologist is not always sure why the radio failed. A small percentage of radio failures will not greatly change the results. However, significant numbers of radio failures lead to subjective decisions and will invalidate the results. The only solution to this problem is to use high-quality equipment so that random failures occur infrequently and time of death can be taken as the time of radio failure. Reliability studies of radio transmitters might also be performed by double-radio-tagging animals. Radio failure is not the same problem as that of band loss (Nelson et al. 1980), because radio failure is known to occur, whereas the loss of a band is rarely identified. The failure of a radio can be placed in a specified time interval, and the problem is 1 of excluding the animal from the experiment or assuming that the radio failure time is also the animal's time of death.

Radio-marked animals that move great distances from the population being studied present an additional complication. If they are known to have moved off the area, their survival rates may not be representative of the population and hence should be discarded. If the animal is not located again (i.e., the fate of the animal is not known), the animal can be classified as a radio failure.

Heterogeneous Survival Rates

Pollock and Raveling (1982) discussed the problem of heterogeneous survival rates of the members of the population. They found that the band-recovery models of Brownie et al. (1978) provide unbiased estimates of the average annual survival rate and the average recovery rate if both year-to-year recovery and survival rates are independent. They conjecture that such is unlikely because an individual with a high survival rate 1 year will probably continue to have a high survival rate the next year.

Estimates of survival rates from biotelemetry data using the techniques described would also be the average rates for heterogeneous populations, with the degree of bias depending on the correlation of survival rates among years. The ability of the biologist to separate the population based on age, sex, or any other identifiable characteristics of the animals helps in examining the causes of heterogeneity. The example of survival-rate estimation for elk in New Mexico illustrates the procedure for testing for differences in survival rates based on the geographic area where the animal was radiocollared. Tests of differences in survival rates of radio-marked animals could also be constructed based on the geographic area of recovery or past areas used. For example, Pollock and Raveling (1982) mentioned the case of waterfowl banded at the same location using different migration corridors. Radio-marked birds could be followed during migration to determine a category for separating the marked animals, and a test of the equality of survival rates for migration corridors could be conducted. This approach will not apply to waterfowl that are only banded because the model requires both survival and recovery rates to be estimated. Recovery rates for radio-marked birds are known except if radio failures become significant.

Current ecological theory suggests that individuals in a population must have heterogeneous survival rates over their lifetime because selection of the fittest implies that some animals are more fit than others. Presumably, fitness may be associated with survival rates. However, the variability of survival rates could not be too large or the proportion of the population with low survival rates would already be extinct. Thus, survival rates are undoubtedly heterogeneous, but not drastically so. The results of Pollock and Raveling (1982) show that the variance of the distribution of population survival rates must be fairly large to cause substantial bias in survival estimates. I suspect that the innate variability of a population's annual survival-rate distribution is not large enough to bias survival estimates significantly.

Sparse Data

One of the advantages of Program SURVIV over current methods available to handle the estimation of survival rates from band-recovery data is its ability to handle small sample sizes and sparse recovery matrices. However, this ability may become a hindrance to biologists analyzing such data because incorrect conclusions may often be reached if the user is unaware of the dangers of the statistical procedures. Small samples usually lead to hypothesis tests that lack power, and thus Type II errors are made (i.e., the null hypothesis is accepted when it should have been rejected). When the null hypothesis is accepted, usually nothing has been learned. Statistical tests only reject hypotheses, they do not prove them true. Thus, accepting a null hypothesis may mean the hypothesis is actually correct, or it may mean that a Type II error has been made. The only correct conclusion that can be made is that further research is required. Use of Program SURVIV on sparse data sets may lead to increased understanding of the biological situation if the principles of statistical hypothesis testing are well understood. However, if the program is used without this understanding, greater confusion of the biological picture will result.

Plant or Bird-nest Survivorship

The problem of estimating survival rates of sessile organisms such as plants or bird nestlings has been considered by Mayfield (1961, 1975), Johnson (1979), Hensler and Nichols (1981), and Bart and Robson (1982). The survival-rate estimation problem considered by Bart and Robson (1982) can be handled by SURVIV because maximum-likelihood estimates can be obtained from the cell probability expressions for the fates of the organisms under observation. Generally, for nest studies, the object is to estimate the daily survival rate (DSR) from which the survivorship during any interval of length l can be estimated as $(\mathrm{DSR})^l$.

Bart and Robson (1982) used mourning dove (*Zenaida macroura*) nest-success data from the North American Nest Record Card Program (NRCP). They estimated the daily nest-survival rate for doves from the center and periphery of the doves' North American range, and tested whether the daily nest-survival rate was constant for the 2 areas.

Nests are initially located then checked at a later time to determine if the nest is still active (i.e., has not been destroyed by predators or abandoned). The time between the initial location of the nest and the follow-up check will vary. Thus, the cell probability expression for nests that are observed L days apart in Program SURVIV would be S(1)**L, where S(1) is the daily survival rate. Suppose that 30 nests are located on day 3, and 15 are checked on day 6 with 13 still surviving, and the remaining 15 are checked on day 8 with 12 still surviving. Then the cell probability and cohort cards to estimate the daily survival rate [S(1)] for Program SURVIV would be

```
COHORT = 15;
  13: S(1)**3;
COHORT = 15;
  12: S(1)**5;
```

Program SURVIV would automatically supply the additional cell probability for each cohort by subtracting the above expressions from unity.

Reanalysis of the Bart and Robson (1982) data with Program SURVIV gives exactly the same estimates of daily nest survival for the 2 areas because they derive the maximum-likelihood estimates. However, the variances of the estimators are derived with slightly different assumptions about the number of nests located (cf. Bart and Robson 1982:1080–1081) and an ML estimator of the variance was not obtained. The variances calculated with Program SURVIV assume that the number of nests located is fixed (i.e., a predetermined number of nests is located). Thus, the standard errors of the estimates and the probability level of the test of differences between the center and peripheral areas from Program SURVIV do not agree with those of Bart and Robson (1982).

Bart and Robson (1982) also suggested extensions to the basic model they presented, such as a visitor-impact factor and changes in the daily survival rate through time. Such extensions are relatively easy to incorporate into models analyzed with program SURVIV. For example, the visitor-impact model they suggested does not fit the dove data significantly better than the standard model.

PROGRAM AVAILABILITY

Program SURVIV has been written in ANSI FORTRAN 77 (ANSI 1978) and is portable between machines having a FORTRAN 77 compiler. Conversion to any machine with a FORTRAN 77 compiler should not be difficult. However, conversion to a non-FORTRAN 77 compiler may be difficult because of the CHARACTER constructs used in Program SURVIV. A magnetic tape of the source code, example input, and a user's manual for the program are available upon request from the author.

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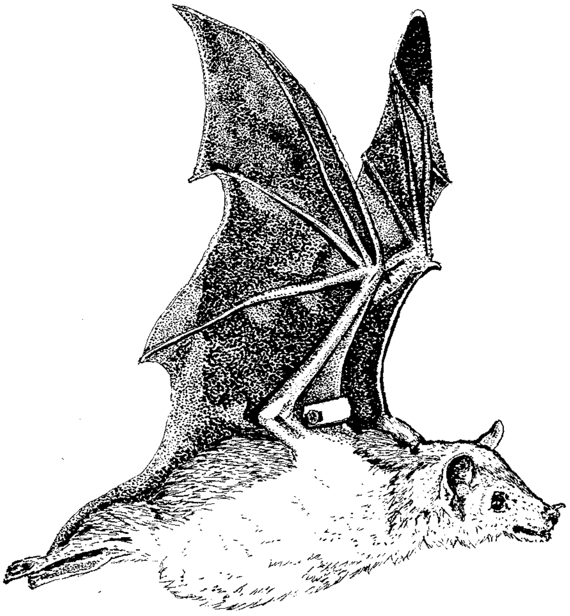

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