CONSTANT PARAMETER CAPTURE-RECAPTURE MODELS

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SUMMARY

Jolly (1982, **Biometrics** 38, 301-321) presented modifications of the Jolly-Seber Model for capture-recapture data, which assume constant survival and/or capture rates. Where appropriate, because of the reduced number of parameters, these models lead to more efficient estimators than the Jolly-Seber model. The tests to compare models given by Jolly do not make complete use of the data, and we present here the appropriate modifications, and also indicate how to carry out goodness-of-fit tests which utilize individual capture history information. We also describe analogous models for the case where young and adult animals are tagged. The availability of computer programs to perform the analysis is noted, and examples are given using output from these programs.

Key words: Age-dependent survival, Capture-recapture models, Constant survival rate, Constant probability of capture, Jolly-Seber model.

1. Introduction

The Jolly-Seber model (Jolly, 1965; Seber, 1965) is now widely used in the analysis of multiple capture-recapture data, from populations open to both birth or immigration and death or emigration. This model allows for time-specific survival and capture rates, requiring estimation of a relatively large number of parameters. Recently, there has been interest in developing more parsimonious models, with parameters constant in time, with the motivation that, where they are appropriate, these models provide estimators with greater precision. That this is a worthwhile endeavor is evident from the success and widespread use of analogous constant-parameter models (Brownie et al., 1985; Conroy and Williams, 1984) in the analysis of band-recovery data (recapture data with 100 percent losses on capture).

Jolly (1982) presented a series of models with survival and/or capture rates assumed constant over time, and Jolly and Dickson (1980) developed a computer program to implement the analyses which involve solving likelihood equations using numerical techniques. Crosbie and Manly (1985) also described a series of parsimonious or reduced-parameter models which differ from those in Jolly (1982) in that they include modelling of the "birth" or immigration process. The Crosbie and Manly models, which do not allow for losses on capture, are heavily dependent on a complex computer program, which is not yet available for general use (Crosbie and Manly, 1985). Another approach to parsimonious modelling of multiple recapture data is the log-linear approach of Cormack (1981). However, there are practical difficulties associated with implementing these log-linear models except with small data sets.

In developing a likelihood for their models, Jolly (1982), Cormack (1981), Sandland and Cormack (1984) and Crosbie and Manly (1985) envisage a superpopulation containing all animals to be present in, or born into, the study population. Jolly and Cormack use this notion to motivate a Poisson likelihood with independent counts for each capture history while Crosbie and Manly develop a multinomial likelihood. Sandland and Cormack (1984) discuss the relationship between the Poisson and multinomial models. Comparing these approaches, we feel that Jolly's series of models has biological appeal, appears to be the most fully developed (e.g., explicit formulae for developing variance estimators are given), and is most readily extended to cope with additional complexities such as age-dependent survival.

In this article, we therefore focus on Jolly's (1982) models, and address the following points. Jolly's results can be obtained using a likelihood based on a more intuitive approach, which avoids assuming a superpopulation and independent counts. On the basis of this likelihood, we suggest that the tests given by Jolly to compare models are inefficient, and present appropriate modifications. We also indicate how to construct goodness-of-fit tests which utilize individual capture history information. The extension of Jolly's models to allow for age-dependent survival and capture rates is described, and the availability of supporting computer routines is noted. Examples based on output from these programs are given, followed by a short discussion.

2. Models for one-age class

The experimental situation is the open-population capture-recapture study, to which the Jolly-Seber model is applied (see Section 5.1, Seber, 1982).

2.1 Notation

To avoid unnecessary repetition, we assume that the reader is familiar with material in Jolly (1982); however, it is useful to present below the notation used by Jolly.

- s is the number of sampling occasions.
- t_i is the time between samples i and $i+1$.
- φ_i is the probability that an individual, present just after the ith release, survives to sample $i+1$.
- φ is the survival rate per unit of time when this is assumed constant, so that $\varphi_i = \varphi^{t_i}$.
- $p_i = 1-q_i$ is the probability of being captured in sample i for individuals present at the time of sample i.
- $1-\chi_i$ is the probability of being recaptured after sample i for individuals present just after the ith release.

  $[\chi_s = 1 \;,\quad 1-\chi_i = \varphi_i(1-q_{i+1}\,\chi_{i+1}) \;,\quad i=1,\ldots,s-1]$
- η_i , η_i' are the probabilities of being in the ith release for marked and, respectively, unmarked individuals caught in sample i.
- n_i is the total number caught in sample i.
- m_i is the number of marked individuals caught in sample i.

m_{ij} is the number caught in sample j that were last caught in sample i .

$u_i = n_i - m_i$ is the number of unmarked individuals caught in sample i .

d_i , d'_i are the numbers of m_i , and of u_i , respectively, that are "lost on capture" (i.e., caught in sample i but not released).

R_i is the number in the i<u>th</u> release.

r_i is the number of the R_i which are subsequently recaptured.

z_i is the number of marked individuals present at the time of sample i , not caught in sample i , but subsequently recaptured. $[z_1 = m_1 = 0$, $z_i = r_{i-1} + z_{i-1} - m_i$, $i = 2, \ldots, s]$.

N_i is the total number in the population at the time of sample i .

M_i is the number of marked individuals in the population at the time of sample i .

$U_i = N_i - M_i$ is the number of unmarked individuals in the population at the time of sample i .

B_i is the number of new individuals joining the population between samples i and i+1 , and present at the time of sample i+1 .

2.2 Model assumptions

The four models considered by Jolly (1982) are summarized below.

Model A, commonly called the Jolly-Seber model, assumes time-specific survival rates φ_i and capture rates p_i .

Model B assumes survival constant per unit of time $\left(\varphi_i = \varphi^{t_i}\right.$, $\left.i=1,\ldots,s-1\right)$ and time-specific capture rates p_i .

Model C assumes time-specific survival rates φ_i , and constant capture rates $\left(p_i = p ,\quad i=2,\ldots,s\right)$.

Model D assumes constant survival $\left(\varphi_i = \varphi^{t_i} ,\quad i=1,\ldots,s-1\right)$ and constant capture rates $\left(p_i = p ,\quad i=2,\ldots,s\right)$.

In addition, all models make the usual assumptions that there is no mark loss or temporary emigration, and that the sampled population is homogeneous with respect to probabilities of survival and capture. The usual assumption concerning the probability of being lost on capture is relaxed to allow this to be different for marked individuals ($=1-\eta_i$) and for unmarked individuals ($=1-\eta'_i$) in any sample.

Note that D, B, A and D, C, A form two series of increasingly general models. In some of the development below, we concentrate on the series D, B, A, partly because experience with band-recovery data suggests that B, rather than C, will often be the more useful intermediate model.

2.3 Estimation of φ and p

Unlike Crosbie and Manly (1985), we make no restrictive assumptions concerning the birth process, i.e., concerning the parameters U_i . Thus, as in Seber (1982, p. 198), the distribution function for the observed variables $\{u_i\}$, $\{d_i , d'_i\}$, $\{m_{ij}\}$, can be factored into three components, giving

$$L\left[\{u_i\},\{d_i,d'_i\},\{m_{ij}\}\right] = L_1\left[\{u_i\}\middle|\{U_i,p_i\}\right]$$

$$\times\ L_2\left[\{d_i,d'_i\}\middle|\{u_i,m_i\},\{\eta_i,\eta'_i\}\right]$$

$$\times\ L_3\left[\{m_{ij}\}\middle|\{R_i\},\{\varphi_i,p_i\}\right] \quad .$$

More explicitly, L_1 is given by (5.4) in Seber (1982) and the terms in $L_2 \times L_3$ are obtained by successive conditioning as follows:

$$L_2{\times}L_3 = P\left[d'_1\middle|u_1\right]\ P\left[\{m_{1j}\}\middle|R_1 = u_1 - d'_1\right]\ P\left[d_2 \ , \ d'_2\middle|m_2 = m_{12} \ , \ u_2\right]$$

$$\times\ P\left[\{m_{2j}\}\middle|R_2 = m_2 + u_2 - d_2 - d'_2\right] \times \ . \ . \ .$$

$$= \prod_{i=1}^{s-1} P\left(d_i \ , \ d'_i\middle|m_i \ , \ u_i\right) \prod_{i=1}^{s-1} P\left(m_{i,i+1},\ldots,m_{i,s}\middle|R_i\right) \quad .$$

The only parameters that appear in L_2 are the nuisance parameters η_i , η'_i , so that L_2 can be ignored in estimating φ_i , p_i . Our approach is to obtain estimators of $\{\varphi_i , p_i\}$ from L_3 , which represents the distribution of the recapture data conditional on the releases $\{R_i\}$. These estimators are then used as in Jolly (1982) to obtain $\hat{M}_i = (m_i+z_i)/(1-\hat{q}_i\ \hat{\chi}_i)$, $\hat{U}_i = u_i/\hat{p}_i$, $\hat{N}_i = \hat{U}_i + \hat{M}_i$, and $\hat{B}_i = \hat{U}_{i+1} - \hat{\varphi}_i\hat{q}_i\hat{U}_i$.

The form of L_3 is easily obtained (e.g., see Brownie and Robson, 1983) by noting that, given the R_i , the vectors

$\left(m_{i,i+1},\ldots,m_{is}\right)$ are conditionally independent multinomials.

Thus,

$$L_3\left[\left\{m_{ij}\right\}\middle|\left\{R_i\right\},\left\{\varphi_i,p_i\right\}\right] = \prod_{i=1}^{s-1}\binom{R_i}{m_{i,i+1},\ldots,m_{is}}\left(\varphi_i\ p_{i+1}\right)^{m_{i,i+1}}$$

$$\ldots\left(\varphi_i\ q_{i+1}\cdots\varphi_{s-1}\ p_s\right)^{m_{is}} \times \chi_i^{R_i-r_i} \qquad \ldots (1)$$

Collapsing terms in L_3 leads to identifying $\mathcal{S} = \left\{r_1,\ldots,r_{s-1}\ ,\ m_2,\ldots,m_{s-1}\right\}$ as being minimally sufficient for L_3 (see also Seber, 1982), and estimation of φ_i , p_i is based on the distribution of $\mathcal{S}$. This is given by (e.g., see Brownie and Robson, 1983)

$$P\left[\mathcal{S}\middle|\left\{R_i\right\}\right] = \prod_{i=1}^{s-1}\binom{R_i}{r_i}\left(1-\chi_i\right)^{r_i}\chi_i^{R_i-r_i}$$

$$\prod_{i=2}^{s-1}\binom{m_i+z_i}{m_i}\left(\frac{p_i}{1-q_i\ \chi_i}\right)^{m_i}\left(1-\frac{p_i}{1-q_i\ \chi_i}\right)^{z_i} \qquad \ldots (2)$$

with corresponding log likelihood function

$$\mathcal{L} = \sum_{i=1}^{s-1}\left[r_i \ln\left(1-\chi_i\right) + \left(R_i-r_i\right)\ln \chi_i\right]$$

$$+\sum_{i=2}^{s-1}\left[m_i\ \ln\left(\frac{p_i}{1-q_i\ \chi_i}\right) + z_i\ \ln\left(1-\frac{p_i}{1-q_i\ \chi_i}\right)\right] \quad . \qquad \ldots (3)$$

Noting that $1-\chi_i = \varphi_i\left(1-q_{i+1}\ \chi_{i+1}\right)$, the Jolly-Seber or Model A estimators $\hat{\varphi}_i$, $\hat{p}_i$ are easily derived from (2) or from (3).

Estimators under Models B, C, and D are obtained by making the appropriate substitutions for constant φ or p in (3) and deriving the likelihood equations, which must be solved numerically. Resulting likelihood equations are identical to those in Jolly (1982), which is not surprising, given the discussion in Sandland and Cormack (1984). Similarly, elements in the corresponding information matrices in Jolly's Appendix 2 (with expectations suitably interpreted) can be obtained from (3) by deriving second order partials. A somewhat simpler approach is to note that, because of the Binomial structure of each term in (3), it is not necessary to obtain second order derivatives. For example, if θ_j , θ'_j are two parameters of interest, then

$$-E \frac{\partial^2}{\partial\theta_j \, \partial\theta'_j} \left[r_i \, \ln\left(1-\chi_i\right) + \left(R_i - r_i\right) \, \ln \, \chi_i\right]$$

$$= \frac{R_i}{\left(1-\chi_i\right)\chi_i} \left(\frac{\partial\chi_i}{\partial\theta_j}\right)\left(\frac{\partial\chi_i}{\partial\theta'_j}\right) \quad .$$

In duplicating Jolly's work, we found only one instance where our results differed from the detailed formulae in his Appendix 2. This concerned entries for $\mathrm{Cov}\left(\frac{m_j+z_j}{1-q \, \chi_j} - M_j \, , \, \frac{\partial L}{\partial\theta}\right)$ under Model D (page 319, Jolly, 1982) which seemed to us to lack certain terms, possibly because γ_i in Jolly's equations (41) and (42) had been viewed as constants, not variables.

2.4 Tests to compare models

Tests to compare models in the hierarchial sequence D, B, A or D, C, A are based on the conditional likelihood L_3, and hence on the distribution of $\mathcal{S}$, as $\mathcal{S}$ is minimally sufficient for L_3 under the most general model A. Again, the simple product-form of (2) leads easily to a chi-square statistic for comparing two models in the sequence. For example, for testing Model B against the more general Model A, one such statistic has the form

$$X^2 = \Sigma\, n_i \left[\frac{(\hat{\Pi}_{iB}-\hat{\Pi}_{iA})^2}{\Pi_{iB}} + \frac{(1-\hat{\Pi}_{iB}-1+\hat{\Pi}_{iA})^2}{1-\Pi_{iB}} \right]$$

where summation is over the $(2s-3)$ Binomial terms in (2), n_i and Π_i represent the corresponding Binomial sample sizes and success probabilities, and $\hat{\Pi}_{iA}$, $\hat{\Pi}_{iB}$ are the maximum likelihood (ML) estimates under models A and B respectively. Degrees of freedom are given by the difference in the numbers of parameters estimated under models A and B.

Simplifying, and writing $\hat{\rho}_{iB} = \hat{p}_{iB}/(1-\hat{q}_{iB}\,\hat{\chi}_{iB})$, gives

$$X_I^2 = \sum_{i=1}^{s-1} \frac{[r_i-R_i(1-\hat{\chi}_{iB})]^2}{R_i\,\hat{\chi}_{iB}(1-\hat{\chi}_{iB})} +$$

$$\sum_{i=2}^{s-1} \frac{[m_i-(m_i+z_i)\hat{\rho}_{iB}]^2}{(m_i+z_i)\hat{\rho}_{iB}(1-\hat{\rho}_{iB})} = T_1 + T_2 \;, \qquad \ldots(4)$$

with s-3 degrees of freedom.

The test statistic given by Jolly (equation 47, Jolly, 1982) corresponds to the first component of X_I^2 above. That is, $X^2_{JOLLY} = T_1$, with s-3 degrees of freedom, which ignores part of the information in the data.

The likelihood ratio chi-square statistics proposed by Jolly for comparing two models have the same deficiency. Thus, from equation (48) of Jolly (1982), for comparing Model D against the alternative Model B,

$$X^2_{JOLLY(LR)} = -2 \sum_{i=1}^{s-1} \left\{ r_i \ \ln \left(\frac{1-\hat{\chi}_{iD}}{1-\hat{\chi}_{iB}} \right) + \left(R_i - r_i \right) \ln \frac{\hat{\chi}_{iD}}{\hat{\chi}_{iB}} \right\} ,$$

with s-2 degrees of freedom, while the more appropriate test statistic is

$$X^2_{II} = X^2_{JOLLY(LR)} - 2 \sum_{i=2}^{s-1} \left\{ m_i \ \ln \left(\frac{\hat{\rho}_{iD}}{\hat{\rho}_{iB}} \right) + z_i \ \ln \left(\frac{1-\hat{\rho}_{iD}}{1-\hat{\rho}_{iB}} \right) \right\} \qquad \ldots(5)$$

In fact, because the ML estimators $\hat{\chi}_i$ and $\hat{\rho}_i$ are based on $\mathcal{S} = \left(r_1 \ldots, r_{s-1} , \ m_2, \ldots, m_{s-1} \right)$ and not just on $\left(r_1, \ldots, r_{s-1} \right)$, $X^2_{JOLLY(LR)}$ can be negative.

2.5 Goodness of fit tests

Pollock, Hines and Nichols (1985) described non-discriminant goodness of fit tests for Model A which utilize individual capture history information. Their tests statistics (denoted here $X^2_{POLLOCK}$) can be combined with statistics for discriminating between models, of the form X_I^2 or X_{II}^2 [equations (4), (5) above], to provide goodness of fit tests to Models B, C, and D. The justification for this is outlined below, using notation from Pollock et al. (1985), where $\{a_w\}$ represents the array of all observable capture histories.

A non-discriminant test of fit to Model B can be based on the likelihood ratio $\lambda = \sup_{\{\theta_w\} \text{ in B}} P\left[\{a_w\}\right] \Big/ \sup_{\{\theta_w\}} P\left[\{a_w\}\right]$, where $\{\theta_w\}$ represents an array of outcome probabilities for all entries in $\{a_w\}$, and "$\{\theta_w\}$ in B" represents those $\{\theta_w\}$ for which the model B assumptions hold.

Multiplying numerator and denominator by $\sup_{\{\theta_w\} \text{ in A}} P\left[\{a_w\}\right]$, gives

$$\lambda = \frac{\sup_{\{\theta_w\} \text{ in B}} P\left[\{a_w\} \mid \mathcal{S}\right] P\left[\mathcal{S}\right]}{\sup_{\{\theta_w\} \text{ in A}} P\left[\{a_w\} \mid \mathcal{S}\right] P\left[\mathcal{S}\right]} \; \frac{\sup_{\{\theta_w\} \text{ in A}} P\left[\{a_w\}\right]}{\sup_{\{\theta_w\}} P\left[\{a_w\}\right]}$$

with $P[\mathcal{S}]$ given by (2)

$$= \frac{\sup_{\{\theta_w\} \text{ in B}} P\left[\mathcal{S}\right]}{\sup_{\{\theta_w\} \text{ in A}} P\left[\mathcal{S}\right]} \; \frac{\sup_{\{\theta_w\} \text{ in A}} P\left[\{a_w\}\right]}{\sup_{\{\theta_w\}} P\left[\{a_w\}\right]} \qquad \ldots(6)$$

by sufficiency of $\mathcal{S}$ for Models B and A.

Taking $-2 \ln \lambda$, the first term in the product (6) yields a statistic of the form X_{II}^2 [equation (5)] for testing Model B against Model A. The second component corresponds to a likelihood ratio chi-square for testing fit to Model A, which is asymptotically equivalent to $X^2_{POLLOCK}$ (constructed without the pooling suggested in Pollock et al., 1985). Also, under the null hypothesis that Model B holds, the statistics X^2_{II} and $X^2_{POLLOCK}$ are asymptotically independent, being based on $P[\mathcal{S}]$ and $P[\{a_w\}|\mathcal{S}]$ under Model B.

A test of fit to Model B which utilizes individual capture history information can therefore be based on

$$X^2_{III}(\text{for fit to B}) = X^2_{II}(\text{for B vs. A}) + X^2_{POLLOCK}(\text{for fit to A}) \qquad \ldots(7)$$

with degrees of freedom summed accordingly. Alternatively, X^2_I (for B vs. A) from (4) can be substituted for the likelihood ratio X^2_{II} in (7) as these are asymptotically equivalent (Jolly, 1982). Under the null hypothesis that Model B holds, (7) will have the appropriate large sample chi-square distribution.

Goodness of fit tests to Models C and D are obtained analogously. For example, for testing fit to D, use

$$X^2_{III}(\text{for fit to D}) = X^2_{II}(\text{for D vs. A}) + X^2_{POLLOCK}(\text{for fit to A}) \qquad \ldots(8)$$

In practice, implementing these tests often requires pooling, and the reader is referred to Pollock et al. (1985) for more detail.

3. Models for two age classes

We describe briefly how analogous procedures for models with survival and/or capture rates constant over time, are developed for the situation where releases of newly marked individuals contain young and adults. The experimental situation is described in more detail in Pollock (1981), with age classes 0 and 1 corresponding to young and adults. The period between successive releases and the time spent in age class 0 are required to be the same (usually one year), so that $t_i = 1$, $i=1,\dots,s-1$.

3.1 Notation

Additional notation is required. Superscripts "a" and "y" are used to distinguish between parameters or variables which relate to adults or young. Thus, φ_i^a and φ_i^y are adult and young survival rates respectively, and R_i^a and R_i^y are the numbers of marked adults and young in the i<u>th</u> release, and r_i^a and r_i^y denote the numbers of subsequent recoveries, etc.

Note that, by definition, $M_i^y = 0$ and $m_i^y = 0$ (since all recaptures are necessarily adults). Thus, p_i^y and U_i^y are not estimable (see also Pollock, 1981). Also, $1-\chi_i^a = \varphi_i^a\left(1-q_{i+1}^a\ \chi_{i+1}^a\right)$ and $1-\chi_i^y = \varphi_i^y\left(1-q_{i+1}^a\ \chi_{i+1}^a\right)$ represent the probability of being recaptured for, respectively, adults and young present just after the i<u>th</u> release. It seems superfluous to superscript m_i and z_i , thus $m_1 = z_1 = 0$, and

$$z_i = z_{i-1} + r^a_{i-1} + r^y_{i-1} - m_i \text{ , } \quad i=2,\ldots,s \text{ .}$$

3.2 Model assumptions

The models we consider are generalizations of Models B and D in Section 2, with assumptions concerning survival and capture rates outlined below.

Model A2 (cf Pollock, 1981, with ℓ=1) assumes time-specific adult and young survival rates $\{\varphi^a_i$ and $\varphi^y_i\}$ and time-specific (adult) capture rates p^a_i .

Model B2 assumes constant adult survival $\{\varphi^a_i = \varphi^a,\ i=1,\ldots,s-1\}$, constant young survival $\{\varphi^y_i = \varphi^y\ ,\ i=1,\ldots,s-1\}$, and time-specific capture rates p^a_i .

Model D2 assumes constant adult and young survival rates $\{\varphi^a$ and $\varphi^y\}$ and constant capture rates $\{p^a_i = p^a\ ,\ \ i=2,\ldots,s\}$.

3.3 ML Estimation

Under Model A2, the distribution of the recapture data conditional on the releases $\{R^a_i\}$, $\{R^y_i\}$ is obtained by a straightforward generalization of L_3 in (1) . A minimal sufficient statistic is found to be $\mathcal{S}_2 = \{r^a_1,\ldots,r^a_{s-1}\ ,\ r^y_1,\ldots,r^y_{s-1}\ ,\ m_2,\ldots,m_{s-1}\}$. Under A2, this has distribution, conditional on $\{R^a_i\}$, $\{R^y_i\}$ given by

$$P\left[\mathcal{S}_2\right] = \prod_{i=1}^{s-1} \binom{R_i^a}{r_i^a} \left(1-\chi_i^a\right)^{r_i^a} \left(\chi_i^a\right)^{\left(R_i^a-r_i^a\right)} \binom{R_i^y}{r_i^y} \left(1-\chi_i^y\right)^{r_i^y} \left(\chi_i^y\right)^{R_i^y-r_i^y}$$

$$\prod_{i=2}^{s-1} \binom{m_i+z_i}{m_i} \left(\rho_i^a\right)^{m_i} \left(1-\rho_i^a\right)^{z_i} \qquad \ldots (9)$$

where $\rho_i^a = p_i^a/\left(1-q_i^a \chi_i^a\right)$, $i=2,\ldots,s-1$

The log-likelihood function is

$$\ell = \sum_{i=1}^{s-1} r_i^a \ln\left(1-\chi_i^a\right) + \left(R_i^a-r_i^a\right) \ln \chi_i^a + r_i^y \ln \left(1-\chi_i^y\right) + \left(R_i^y-r_i^y\right) \ln \chi_i^y$$

$$+ \sum_{i=2}^{s-1} m_i \ln \rho_i^a + z_i \ln \left(1-\rho_i^a\right) \qquad \ldots (10)$$

For Model A2, explicit formulae for ML estimators of $\varphi_1^a,\ldots,\varphi_{s-2}^a$, $\varphi_1^y,\ldots,\varphi_{s-2}^y$, $p_2^a,\ldots,p_{s-1}^a$, and $\varphi_{s-1}^a p_s^a$, $\varphi_{s-1}^y p_s^a$ are obtained from (9) and (10) and agree with results in Pollock (1981). For Models B2 and D2, estimable parameters are $\left(\varphi^a , \varphi^y , p_2^a,\ldots,p_s^a\right)$ and $\left(\varphi^a , \varphi^y , p^a\right)$ respectively. Substituting constant φ or p where appropriate in (10) and differentiating leads to likelihood equations for Models B2 and D2 which must be solved numerically. Results are presented in the appendix for Models B2 and D2. Entries in the corresponding information matrices can be obtained using first-order partials only, as indicated in Section 2.3.

Population size estimates (for the adult segment of the population) are obtained as in Section 2. For example, Model D2 estimates $\hat{\phi}^a$, $\hat{\phi}^y$, $\hat{p}^a$ can be used to obtain

$\hat{M}_i^a = (m_i+z_i)/(1-\hat{q}^a\,\hat{\chi}_i^a)$, $\hat{U}_i^a = u_i^a/\hat{p}^a$, $\hat{N}_i^a = \hat{M}_i^a + \hat{U}_i^a$, and

$\hat{B}_i^a = \hat{U}_{i+1}^a - \hat{\phi}^a\,\hat{q}^a\,\hat{U}_i^a + \hat{\phi}^y\,R_i^y$. Corresponding variances and covariances are obtained as described by Jolly (1982) for Models B and D with obvious generalizations. Necessary formulae are given in detail in Brownie (1985).

3.4 Tests to compare models

Tests to discriminate between two models in the hierarchial series D2, B2 and A2 are straightforward generalizations of procedures in Section 2.4. Thus, to test Model B2 against the more general Model A2, either a generalization of X_I^2 or of the likelihood ratio X_{II}^2 may be used. Specific examples are

$$X_I^2\,(\text{for B2 vs A2}) = \sum_{i=1}^{s-1}\left\{\frac{\left[r_i^a-R_i^a(1-\hat{\chi}_{i,B2}^a)\right]^2}{R_i^a(1-\hat{\chi}_{i,B2}^a)\hat{\chi}_{i,B2}^a} + \frac{\left[r_i^y-R_i^y(1-\hat{\chi}_{i,B2}^y)\right]^2}{R_i^y(1-\hat{\chi}_{i,B2}^y)\hat{\chi}_{i,B2}^y}\right\}$$

$$+ \sum_{i=2}^{s-1}\frac{\left[m_i-(m_i+z_i)\hat{\rho}_{i,B2}^a\right]^2}{(m_i+z_i)\hat{\rho}_{i,B2}^a(1-\hat{\rho}_{i,B2}^a)} \quad ,$$

with 2s−5 degrees of freedom (11)

$$\chi^2_{II}\ \left[\text{for D2 vs B2}\right] = -2\sum_{i=1}^{s-1}\left\{r_i^a\ \ln\left[\frac{1-\hat{x}^a_{i,D2}}{1-\hat{x}^a_{i,B2}}\right] + \left[R_i^a - r_i^a\right]\ \ln\left[\frac{\hat{x}^a_{i,D2}}{\hat{x}^a_{i,B2}}\right]\right.$$

$$\left. + r_i^y\ \ln\left[\frac{1-\hat{x}^y_{i,D2}}{1-\hat{x}^y_{i,B2}}\right] + \left[R_i^y - r_i^y\right]\ln\left[\frac{\hat{x}^y_{i,D2}}{\hat{x}^y_{i,B2}}\right]\right\}$$

$$-2\sum_{i=2}^{s-1}\left\{m_i\ \ln\left[\frac{\hat{\rho}_{i,D2}}{\hat{\rho}_{i,B2}}\right] + z_i\ \ln\left[\frac{1-\hat{\rho}_{i,D2}}{1-\hat{\rho}_{i,B2}}\right]\right\}$$

with s-2 degrees of freedom. (12)

3.5 Goodness of fit tests

Pollock et al. (in preparation) describe a non-discriminant goodness of fit test for Model A2 which utilizes individual capture history information. This test statistic, denoted here $\chi^2_{POLLOCK}$ [for fit to A2] is combined with statistics used to compare Models B2 and D2 with A2 to provide goodness of fit tests to Models B2 and D2 respectively. For example,

$$\chi^2_{III}\ \left[\text{for fit to B2}\right] = \chi^2_{I}\ \left[\text{for B2 vs A2}\right] + \chi^2_{POLLOCK}\ \left[\text{for fit to A2}\right]$$

$$\chi^2_{III}\ \left[\text{for fit to D2}\right] = \chi^2_{I}\ \left[\text{for D2 vs A2}\right] + \chi^2_{POLLOCK}\ \left[\text{for fit to A2}\right]\ .$$

The large sample null distribution for X^2_{III} is again chi-square with degrees of freedom obtained by summing those for the corresponding X^2_I and $X^2_{POLLOCK}$ statistics.

4. Programs JOLLY and JOLLYAGE

FORTRAN programs have been developed for carrying out the estimation and test procedures described in Section 2 for Models A, B and D (program JOLLY), and in Section 3 for Models A2, B2 and D2 (program JOLLYAGE). Both programs also carry out additional analyses as described in Pollock et al. (in preparation). Programs JOLLY and JOLLYAGE were written on an HP/3000 minicomputer in FORTRAN/3000. However, specific HP extensions to standard FORTRAN were not used, so the programs are easily transported to other machines. They may be obtained (at no cost) from the second or third author (J. E. Hines or J. D. Nichols).

Program JOLLY should not be confused with the program developed by Jolly and Dickson (1980) which is being incorporated into POPAN-3 (Arnason and Schwarz, 1985). An advantage of program JOLLY relative to the Jolly-Dickson program is the superior array of tests for model assessment included in program JOLLY (see Section 2). Another difference between these two programs concerns computation of estimated variances and covariances. Jolly (1982, page 318) states that variance estimates should be obtained using the unconditional estimates $\left\{\widehat{EM}_i\right\}$ [see equation (5), Jolly, 1982], while program JOLLY uses the conditional $\hat{M}_i$ [equation (6), Jolly, 1982], because this seemed less sensitive to minor failures in the model assumptions (e.g., minor variations in survival).

POPAN-3 (Arnason and Schwarz, 1985) will also include parsimonious models based on the log-linear approach of Cormack (1981). However, these models cannot be implemented with data sets containing losses on capture or more than nine sampling occasions. Standard errors of parameter estimates are not provided.

5. Examples

5.1 Male Hypaurotis crysalus data from Jolly (1982)

The data in Jolly (1982) from a study on male butterflies (Hypaurotis crysalus) have been analyzed with program JOLLY and are used here to illustrate the difference between the tests given in Jolly (1982) and our equations (4) and (5). Model C estimates are not produced by program JOLLY, but estimates for Models B and D in Table 2 of Jolly (1982) agree to 2 or more significant digits with results from program JOLLY. Estimated standard errors for $\hat{\phi}$ differ by less than 2 percent but differ to a greater extent for $\hat{N}_i$ and $\hat{B}_i$ (see Section 4). The goodness of fit tests described in Section 2.5 were not carried out as individual capture histories were not available.

Results for tests comparing Models A, B and D are summarized in Table 1. Pooling to avoid small expectations (see Jolly, 1982) resulted in the loss of 3 degrees of freedom for each test. Jolly's statistic and our equation (4) give fairly similar results for comparing Model B against Model A. However, Model D is rejected convincingly in favor of Model B using our test statistic, while Jolly's fails to reject. Jolly concludes that ". . .any of the four models can be considered valid," while we conclude that p_i are not constant and Model D is not valid.

The result for Jolly's test of Model C against A is probably also misleading, because in analyzing various data sets, we have observed that the term omitted in Jolly's tests tends to be more important for detecting differences among the p_i and less sensitive to variation in the φ_i . This is not surprising in view of the definition of $\rho_i = p_i/(1-q_i \chi_i)$ and of $1-\chi_i = \varphi_i(1-q_{i+1} \chi_{i+1})$ [see equation (4)].

5.2 Esox lucius data, with two age classes, from Pollock and Mann (1983)

Data from a tag-recapture study on pike (Esox lucius L.) were analyzed by Pollock and Mann (1983) using Pollock's (1981) model which allows for age-dependent survival. Numbers of fish tagged were not large, so only two age classes were distinguished by Pollock and Mann (1983). In the terminology of Section 3, these are "young" or one year at tagging, and "adult" or two years and older at tagging. Numbers of recoveries r_i^a and r_i^y vary between 3 and 13 for the seven yearly releases, and 95 percent confidence intervals for annual survival rates in some cases are so wide as to be meaningless. It is therefore of interest to determine if a model with fewer parameters (such as B2 or D2) is appropriate for these data.

Results obtained with program JOLLYAGE are summarized in Tables 2 and 3, with Table 2 containing estimates and estimated standard errors and Table 3 containing results of the tests outlined in Sections 3.4 and 3.5.

The tests indicate no reason to reject Model B2, while the test of D2 against B2 is just significant at the 10 percent level. We conclude the Model B2 estimates may be used and compare precision for the B2 estimates $\hat{\varphi}^y$, $\hat{\varphi}^a$ and individual A2 estimates $\hat{\varphi}_i^y$, $\hat{\varphi}_i^a$ and their averages $\bar{\hat{\varphi}}^y = \Sigma\, \hat{\varphi}_i^y/6$, $\bar{\hat{\varphi}}^a = \Sigma\, \hat{\varphi}_i^a/6$. Note that confidence intervals for φ^y and φ^a based on the Model B2 estimates will average about two-thirds the length of intervals based on $\bar{\hat{\varphi}}^y$ and $\bar{\hat{\varphi}}^a$. For these data, the advantages of a reduced-parameter model are apparent.

6. Discussion

The conditional likelihood L_3 and the unconditional Poisson model in Jolly (1982) give the same results for point estimates and likelihood ratio tests concerning $\{\varphi_i, p_i\}$ (see Sandland and Cormack, 1984). However interpretation of expectations in variance formulae may differ. Apart from the simplicity of likelihoods in (2) and (9), there are other practical reasons for basing inferences on L_3. Non-informative losses on capture are handled easily and satisfactorily (in direct contrast to the models of Cormack, 1981 and Crosbie and Manly, 1985). Also the frequently more reliable information on the marked animals (contained in L_3) is dealt with separately from the $\{u_i\}$. This is certainly appropriate when the process of capturing animals for tagging may not provide useful information concerning population sizes.

A useful consequence of focusing on the conditional likelihood L_3 is that the relationship to models for band-recovery data is made apparent (see Section 8.2, Brownie et al., 1985). Computer algorithms (White, 1983; Conroy and Williams, 1984) already exist for implementing a much wider range of biologically interesting parsimonious models with band-recovery data, than the models considered here. For example, these programs allow modelling survival as a simple function of an environmental variable (Conroy and Williams, 1984). Using (1) and (9) it should be possible to modify White's program to allow application of such models to multiple recapture data. The chief forseeable difficulty will be obtaining variances for $\hat{N}_i$ and $\hat{B}_i$.

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REFERENCES

Aranson, A. N. and Schwarz, C. J. (1985). POPAN-3: extended analysis and testing features for POPAN-2. Charles Babbage Research Centre, St. Pierre, MB. Canada.

Brownie, C. (1985). Reduced-parameter models for analysis of capture-recapture data from one- and two-age class open populations. Institute of Statistics Mimeo Series 1675, North Carolina State University, Raleigh, NC.

Brownie, C., Anderson, D. R., Burnham, K. P. and Robson, D. S. (1985). Statistical Inference from Band-Recovery Data--A Handbook. Second Edition. Resource Publication No. 131. Washington, DC: Fish and Wildlife Service, U.S. Dept. of the Interior.

Brownie, C. and Robson, D.S. (1983). Estimation of time-specific survival rates from tag-resighting samples: A generalization of the Jolly-Seber model. Biometrics 39, 437-453.

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

Cormack, R. M. (1981). Loglinear models for capture-recapture experiments on open populations. In The Mathematical Theory of the Dynamics of Biological Populations, R. W. Hiorns and D. Cooke (eds), 217-235. London: Academic Press.

Crosbie, S. F. and Manly, B. F. J. (1985). A new approach for parsimonious modelling of capture-mark-recapture experiments. Biometrics 41, 385-398.

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration--stochastic model. Biometrika 52, 225-247.

Jolly, G. M. (1982). Mark-recapture models with parameters constant in time. Biometrics 38, 301-321.

Jolly, G. M. and Dickson, J. M. (1980). Mark-recapture suite of programs. In COMPSTAT 1980: Proceedings in Computational Statistics Vol. 4, M. M. Barritt and D. Wishart (eds.). 570-576. Vienna: Physica-Verlag (for International Association for Statistical Computing).

Pollock, K. H. (1981). Capture-recapture models allowing for age-dependent survival and capture rates. Biometrics 37, 521-529.

Pollock, K. H., Hines, J. E. and Nichols, J. D. (1985). Goodness of fit tests for open capture-recapture models. Biometrics 41, 399-410.

Pollock, K. H. and Mann, R. H. K. (1983). Use of an age-dependent mark-recapture model in fisheries research. Canadian Journal of Fisheries and Aquatic Sciences 40, 1449-1455.

Sandland, R. L. and Cormack, R. M. (1984). Statistical inference for Poisson and multinomial models for capture-recapture experiments. Biometrika 71, 27-33.

Seber, G. A. F. (1965). A note on the multiple-recapture census. Biometrika 52, 249-259.

Seber, G. A. F. (1982). Estimation of Animal Abundance and Related Parameters. London: Griffin.

White, G. C. (1983). Numerical estimation of survival rates from band-recovery and biotelemetry data. Journal of Wildlife Management 47, 716-728.

APPENDIX

Likelihood equations and information matrices for Models B2 and D2

Model B2

As for Model B in Jolly (1982), it is easier to derive likelihood equations for estimating φ^a , φ^y and χ_i^a , $i=1,\ldots,s-1$, and then to obtain $\hat{p}_i^a = \left(\frac{1-\hat{\chi}_i^a}{\hat{\varphi}^a} - 1 + \hat{\chi}_{i+1}^a\right) \Big/ \hat{\chi}_{i+1}^a$.

Thus, with $\mathcal{L}$ as in equation (10), after simplifying,

$$\frac{\partial\mathcal{L}}{\partial\varphi^a} = \frac{1}{\varphi^a}\sum_{i=2}^{s-1}\frac{1}{\chi_i^a}\left\{\frac{z_i}{q_i^a} - \frac{m_i\left(1-\chi_i^a\right)}{p_i^a}\right\} \tag{13}$$

$$\frac{\partial\mathcal{L}}{\partial\chi_i^a} = \frac{\varphi^y}{\varphi^a}\,\frac{R_i^y-r_i^y}{\chi_i} + \frac{1}{\chi_i^a}\left[\frac{m_i\, q_i^a}{p_i^a} - z_i + R_i^a - r_i^a\right]$$

$$- \frac{1}{\varphi^a\,\chi_{i+1}^a}\left[\frac{m_{i+1}}{p_{i+1}^a} - \frac{z_{i+1}}{q_{i+1}^a}\right] \qquad i=1,\ldots,s-1 \tag{14}$$

$$\frac{\partial\mathcal{L}}{\partial\varphi^y} = \frac{1}{\varphi^y}\sum_{i=1}^{s-1}\left\{R_i^y - \frac{\left(R_i^y-r_i^y\right)}{\chi_i^y}\right\} \tag{15}$$

Elements of the corresponding information matrix follow:

$$-E\,\frac{\partial^2\mathcal{L}}{\left(\partial\varphi^a\right)^2} = \frac{1}{\left(\varphi^a\right)^2}\sum_{i=1}^{s-1}\left\{\frac{R_i^y\left(1-\chi_i^y\right)}{\chi_i^y} + \frac{E\left(m_i+z_i\right)\left(1-\chi_i^a\right)}{p_i^a\, q_i^a\left(\chi_i^a\right)^2}\right\} \tag{16}$$

$$-E\,\frac{\partial^2 \ell}{\left(\partial\chi_i^a\right)^2} = \frac{1}{1-\chi_i^a}\left\{\frac{R_i^a}{\chi_i^a} + \frac{\varphi^y}{\varphi^a}\,\frac{R_i^y}{\chi_i^y} + \frac{E\left(m_i+z_i\right)q_i^a}{p_i^a\left(\chi_i^a\right)^2}\right.$$

$$\left. + \frac{E\left(m_{i+1} + z_{i+1}\right)\left(1-\chi_{i+1}^a\right)}{p_{i+1}^a\; q_{i+1}^a\left(1-\chi_i^a\right)\left(\chi_{i+1}^a\right)^2}\right\} \qquad i=1,\ldots,s-1 \qquad (17)$$

$$-E\,\frac{\partial^2 \ell}{\partial\varphi^a\;\partial\chi_i^a} = \frac{1}{\varphi^a}\left\{\frac{\varphi^y}{\varphi^a}\,\frac{R_i^y}{\chi_i^y} - \frac{E\left(m_i+z_i\right)}{p_i^a\left(\chi_i^a\right)^2}\right.$$

$$\left. + \frac{E\left(m_{i+1} + z_{i+1}\right)\left(1-\chi_{i+1}^a\right)}{\left(1-\chi_i^a\right)p_{i+1}^a\; q_{i+1}^a\left(\chi_{i+1}^a\right)^2}\right\} \qquad i=1,\ldots,s-1 \qquad (18)$$

$$-E\,\frac{\partial^2 \ell}{\partial\varphi^a\;\partial\varphi^y} = -\,\frac{1}{\varphi^a\;\varphi^y}\sum_{i=1}^{s-1}\frac{R_i^y\left(1-\chi_i^y\right)}{\chi_i^y} \qquad (19)$$

$$-E\,\frac{\partial^2 \ell}{\partial\chi_i^a\;\partial\chi_{i+1}^a} = -\,\frac{E\left(m_{i+1}\right)}{\varphi^a\left(p_{i+1}^a\;\chi_{i+1}^a\right)^2} \qquad i,1,\ldots,s-2 \qquad (20)$$

$$-E\,\frac{\partial^2 \ell}{\partial\chi_i^a\;\partial\varphi^y} = -\,\frac{R_i^y}{\varphi^a\;\chi_i^y} \qquad i=1,\ldots,s-1 \qquad (21)$$

In equations (13) through (21) above, terms with m_1 , z_1 , and z_s vanish as $m_1 = z_1 = z_s = 0$. Variances and covariances for $\hat{\varphi}^a$, $\hat{\varphi}^y$, $\hat{\chi}_i^a$, $i=1,\ldots,s-1$ are obtained from this information matrix in the usual way. Then

$$
\begin{aligned}
\mathrm{Cov}\left(\hat{p}_i^a,\hat{p}_j^a\right) = \frac{1}{\chi_i^a\,\chi_j^a} \Bigg\{ & \frac{\left(1-q_i^a\,\chi_i^a\right)}{\varphi^a} \left[\frac{\left(1-q_j^a\,\chi_j^a\right)}{\varphi^a}\,\mathrm{Var}\left(\hat{\varphi}^a\right) + \frac{\mathrm{Cov}\left(\hat{\varphi}^a,\hat{\chi}_{j-1}^a\right)}{\varphi^a}\right. \\
& \left. - q_j^a\,\mathrm{Cov}\left(\hat{\varphi}^a,\,\hat{\chi}_j^a\right)\right] + \frac{1}{\varphi^a}\left[\frac{\left(1-q_j^a\,\chi_j^a\right)}{\varphi^a}\,\mathrm{Cov}\left(\hat{\varphi}^a,\hat{\chi}_{i-1}^a\right)\right. \\
& \left. + \frac{\mathrm{Cov}\left(\hat{\chi}_{i-1}^a,\,\hat{\chi}_{j-1}^a\right)}{\varphi^a} - q_j^a\,\mathrm{Cov}\left(\hat{\chi}_{i-1}^a\,,\,\hat{\chi}_j^a\right)\right] \\
& - q_i^a\left[\frac{\left(1-q_j^a\,\chi_j^a\right)}{\varphi^a}\,\mathrm{Cov}\left(\hat{\varphi}^a,\hat{\chi}_i^a\right) + \frac{\mathrm{Cov}\left(\hat{\chi}_i^a,\hat{\chi}_{j-1}^a\right)}{\varphi^a}\right. \\
& \left. - q_j^a\,\mathrm{Cov}\left(\hat{\chi}_i^a,\hat{\chi}_j^a\right)\right]\Bigg\} \qquad 2\le i,\ j\le s
\end{aligned} \tag{22}
$$

Model D2

The likelihood equations for obtaining $\hat{\varphi}^a$, $\hat{p}^a$ and $\hat{\varphi}^y$, are given below, where $\mathcal{L}$ is as in (10) with $\varphi_i^a = \varphi^a$, $\varphi_i^y = \varphi^y$ and $p_i^a = p^a$.

$$
\frac{\partial\mathcal{L}}{\partial\varphi^a} = \frac{1}{\varphi^a}\sum_{i=1}^{s-1}\left\{r_i^a + r_i^y + z_i - \delta_i\left(\frac{R_i^a-r_i^a}{\chi_i^a} + \frac{\varphi^a}{\varphi^a}\,\frac{R_i^y-r_i^y}{\chi_i^y}\right)\right\} \tag{23}
$$

$$
\frac{\partial\mathcal{L}}{\partial p^a} = \frac{1}{p^a q^a}\sum_{i=1}^{s-1}\left\{R_i^a - \frac{R_i^a-r_i^a}{\chi_i^a}\right\} \tag{24}
$$

$$
\frac{\partial\mathcal{L}}{\partial\varphi^y} = \frac{1}{\varphi^y}\sum_{i=1}^{s-1}\left\{R_i^y - \frac{R_i^y-r_i^y}{\chi_i^y}\right\} \tag{25}
$$

where $\delta_s \equiv 0$, $\delta_i = \left(1-\chi_i^a\right) + \varphi^a\,q^a\,\delta_{i+1}$, $i=1,\ldots,s-1$.

The information matrix has the following elements:

$$-E\,\frac{\partial^2 \ell}{(\partial\varphi^a)^2} = \frac{1}{(\varphi^a)^2}\sum_{i=1}^{s-1}\left[\frac{\delta_i^2}{1-\chi_i^a}\left\{\frac{R_i^a}{\chi_i^a} + \frac{E(m_i)\,q^a}{1-q^a\,\chi_i^a}\right\} + \left\{q^a\varphi^y\right\}^2 \frac{\delta_{i+1}^2\,R_i^y}{\chi_i^y(1-\chi_i^y)}\right] \tag{26}$$

$$-E\,\frac{\partial^2 \ell}{(\partial p^a)^2} = \sum_{i=1}^{s-1}\frac{1}{1-\chi_i^a}\left\{\left(\frac{\delta_i}{q^a} - \frac{(1-\chi_i^a)}{p^a q^a}\right)^2\left(\frac{R_i^a}{\chi_i^a} + \frac{\varphi^y}{\varphi^a}\,\frac{R_i^y}{\chi_i^y}\right) + \frac{\delta_i^2\,E(m_i)}{q^a(1-q^a\chi_i^a)}\right\} \tag{27}$$

$$-E\,\frac{\partial^2 \ell}{(\partial\varphi^y)^2} = \frac{1}{(\varphi^y)^2}\sum_{i=1}^{s-1}\frac{R_i^y(1-\chi_i^y)}{\chi_i^y} \tag{28}$$

$$-E\,\frac{\partial^2 \ell}{\partial\varphi^a\partial p^a} = -\frac{1}{\varphi^a}\sum_{i=1}^{s-1}\frac{1}{1-\chi_i^a}\left\{\left(\delta_i - \frac{(1-\chi_i^a)}{p^a}\right)\left[\frac{R_i^a}{\chi_i^a}\,\frac{\delta_i}{q^a} + \varphi^y\delta_{i+1}\,\frac{R_i^y}{\chi_i^y}\right] + \frac{E(m_i)\;\delta_i^2}{1-q^a\;\chi_i^a}\right\} \tag{29}$$

$$-E\,\frac{\partial^2 \ell}{\partial\varphi^a\partial\varphi^y} = \frac{q^a}{\varphi^a}\sum_{i=1}^{s-2}\frac{R_i^y}{\chi_i^y}\,\delta_{i+1} \tag{30}$$

$$-E\,\frac{\partial^2 \ell}{\partial p^a\partial\varphi^y} = -\frac{1}{q^a\varphi^a}\sum_{i=1}^{s-1}\frac{R_i^y}{\chi_i^y}\left(\delta_i - \frac{(1-\chi_i^a)}{p^a}\right) \tag{31}$$

Variances and covariances for $\hat{\varphi}^y$, $\hat{\varphi}^a$, $\hat{p}^a$ are obtained from the information matrix defined by equations (26) to (31) in the usual way. Additional formulae needed to obtain variances and covariances for $\hat{M}_i^a$, $\hat{N}_i^a$, $\hat{B}_i^a$ are in Brownie (1985).

Table 1

Results for tests comparing Models A, B and D for male *Hypaurotis crysalus* data taken from Table 2, Jolly (1982), and from program JOLLY using our equations (4) and (5)

Test of B vs A

	Jolly (1982)	Equation (4), Brownie et al.
Chi-square value with 13 df	15.20	15.23 + 3.79* = 19.02
P-value	>.25	.1224

Test of D vs B

	Jolly (1982)	Equation (5), Brownie et al.
Chi-square value with 14 df	10.94	10.97 + 30.71* = 41.68
P-value	>.25	.0001

Test of D vs A

		Equation (4), Brownie et al.
Chi-square value with 30 df		26.10 + 33.86* = 59.96
P-value		.0009

*Contribution due to term omitted in Jolly (1982).

Table 2

Estimates* (approximate standard errors) under Models A2, B2 and D2 for pike (Esox lucius L.) data (Pollock and Mann, 1983).

<u>Model A2 - time-specific survival and capture rates</u>

	$\hat{\phi}_i^y$	$\hat{\phi}_i^a$	$\hat{p}_i^a$	$\hat{N}_i^a$	$\hat{B}_i^a$
1971	.51(.234)	.59(.234)			
1972	.17(.082)	.28(.114)	.44(.172)	48(17.8)	25**
1973	.20(.119)	.55(.192)	.69(.171)	38(8.16)	16
1974	.19(.095)	.28(.125)	.63(.200)	37(11.3)	28
1975	.34(.178)	.40(.134)	.61(.199)	38(11.3)	28
1976	.46(.218)	.59(.281)	.67(.177)	44(10.7)	42
1977			.55(.228)	68(29.2)	
Average estimate	.31(.068)	.45(.078)	.60(.078)		

<u>Model B2 - constant adult and young survival rates</u>

	$\hat{\phi}^y$	$\hat{\phi}^a$	$\hat{p}_i^a$	$\hat{N}_i^a$	$\hat{B}_i^a$
1972			.57(.128)	41(7.23)	37(10.5)
1973			.54(.148)	50(11.6)	16(6.17)
1974	.31(.053)	.42(.044)	.64(.144)	37(6.71)	42(13.4)
1975			.45(.143)	53(14.6)	28(10.5)
1976			.61(.156)	50(11.4)	28(6.32)
1977			.73(.124)	53(7.74)	5(2.16)
1978			.34(.115)	27(10.7)	

(Continued on next page)

Table 2. Continued.

<u>Model D2 - constant survival and constant capture rates</u>

	$\hat{\phi}^y$	$\hat{\phi}^a$	$\hat{p}^a$	$\hat{N}_i^a$	$\hat{B}_i^a$
1972				40(6.04)	35(12.6)
1973				48(7.50)	19(4.34)
1974	.30(.052)	.40(.042)	.58(.073)	40(6.18)	33(5.41)
1975				43(7.05)	33(6.15)
1976				53(8.19)	33(5.08)
1977				62(8.77)	3(2.69)
1978				15(3.69)	

*Estimates have not been adjusted for tag-loss (see Pollock and Mann, 1983).

**Standard error not computed in program JOLLYAGE.

Table 3

Results for tests of fit and tests comparing models for pike data (Pollock and Mann, 1983).

	Goodness of fit tests				Tests between models		
	Chi-square value	df	P		Chi-square value	df	P
to Model A2	3.13	4	.54	B2 vs A2	9.83	10	.456
to Model B2	12.96	14	.53	D2 vs B2	7.87	4	.097
to Model D2	19.77	20	.47	D2 vs A2	16.64	16	.409