MODELS ALLOWING FOR AGE-DEPENDENT SURVIVAL RATES
FOR BAND-RETURN DATA

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Summary

Seber (1970) and Robson and Youngs (1971) developed a statistical model for a tag-recapture experiment on an exploited animal population in which banded or tagged individuals are released into a population each year, and the bands from harvested individuals are returned by hunters or fishermen in following years. Consideration of certain biological and ecological factors affecting bird populations has led to the proposal of new models for an experimental situation where data are recorded separately for birds released as adults and as young-of-the-year. In particular, the effect of different survival rates of young birds, and the effect of migration on reporting rates, are taken into account in the models presented in this study. Maximum likelihood estimators of parameters are derived under the different models, and procedures are developed to discriminate between alternative models as well as provide non-discriminant goodness of fit tests.

1. Introduction

In the type of banding experiment considered here, a known number of banded birds is released into the population each summer for a number of years. The population is harvested during the hunting season each year, bands from captured birds are returned by hunters, and a yearly record is kept of the number of returns from each batch released. Seber (1970) and Robson and Youngs (1971)
developed a stochastic model for this situation under the assumption that annual survival, exploitation and reporting rates are year specific but independent of age. This model, (which we shall refer to as the SRY model), is a special case of the more general tag-recapture model given by Jolly (1965), and the SRY estimators can be derived from the Jolly estimators. For reasons outlined below, the assumptions made under the SRY model, with respect to annual survival, exploitation and reporting rates are probably not realistic. This has lead to the development of new models, which are sufficiently different from the Jolly model to merit separate consideration.

The assumption that survival rates are independent of age, restricts application of the SRY model to data from birds banded as adults only since young and adult birds are thought to have different survival rates. However if records of releases and returns are kept separately for birds banded as adults and as young-of-the-year, then models can be employed which admit different survival and reported exploitation rates of young birds.

Another limitation of the SRY model is the assumption that reporting rates are constant for all birds in a given year. Reporting rates have been noted to be lower near the banding site, probably because hunters there are more accustomed to seeing bands and so return them at a lower rate. After migration birds do not necessarily return to the banding site, and hence the reporting rate for birds banded and released in a given year should be different from that for birds banded in previous years since the latter have undergone at least one migration. This leads to another modification of the SRY model.

The development of models reflecting the above considerations, corresponding estimation formulae, and certain tests of hypothesis follow.
2. The Model Under $H_1$

In general it is possible to distinguish only two age-groups of birds, namely young-of-the-year birds and adults (i.e., birds more than one year old). Thus consider a banding experiment where known numbers of adults and young birds are released into the population each year before the hunting season, and yearly records of band returns are kept separately for birds banded and released as adults and for birds banded and released as young-of-the-year.

Consider the $i^{th}$ year of the banding experiment to be the period between the $i^{th}$ and $(i+1)^{th}$ banding dates. Let $N_i$ and $M_i$ be the number of adult and young birds respectively which are banded and released into the population in year $i$, $i=1,\ldots,k$.

Let $R_{ij}$ be the number of bands returned in year $j$ from the batch of adults released in year $i$, $i=1,\ldots,k$, $j=1,\ldots,k$.

Let $Q_{ij}$ be the number of bands returned in year $j$ from the batch of young birds released in year $i$, $i=1,\ldots,k$, $j=1,\ldots,k$.

Let $\{R_{ij}\}$ be the triangular array of random variables $R_{ij}$, i.e.,

$$
\{R_{ij}\} = \begin{pmatrix}
R_{11} & R_{12} & \cdots & R_{1k} \\
R_{21} & R_{22} & \cdots & R_{2k} \\
\vdots & \vdots & \ddots & \vdots \\
R_{k1} & R_{k2} & \cdots & R_{kk}
\end{pmatrix}
$$

Similarly let $\{Q_{ij}\}$ be the triangular array of random variables $Q_{ij}$.

For any banded adult alive at the start of year $i$, we define the following conditional probabilities:

$$
S_i = P \text{ [survives year } i] = \text{ survival rate.}
$$

$$
u_i = P \text{ [killed by hunter in year } i] = \text{ exploitation rate.}
$$
\[ \lambda_i = P \text{[band returned given banded adult killed by hunter in year } i\text{]} = \text{reporting rate.} \]

\[ f_i = \lambda_i u_i = P \text{[killed by hunter and band returned in year } i\text{]} = \text{reported exploitation rate.} \]

Similarly, for any young bird banded and released at the start of year \( i \), let

\[ S_i' = P \text{[survives year } i\text{].} \]

\[ f_i' = P \text{[killed by hunter and band returned in year } i\text{].} \]

Thus, as in the SRY model, survival, exploitation and reporting rates are assumed to be year specific, but in addition it is assumed that survival and exploitation rates are different for young-of-the-year and adult birds, and we define \( H_1 \) to be the hypothesis that this last assumption is true. \( H_1 \) can be characterized by the following.

\[
E_{H_1}[[R_{ij}]] = \begin{pmatrix}
N_1 f_1' & N_1 S_1 f_2 & \cdots & N_1 S_1 \cdots S_{k-1} f_{k-1} \\
N_2 f_2' & \vdots & \ddots & \vdots \\
N_k f_k'
\end{pmatrix}
\]

\[
E_{H_1}[[Q_{ij}]] = \begin{pmatrix}
M_1 f_1' & M_1 S_1 f_2 & \cdots & M_1 S_1 \cdots S_{k-1} f_{k-1} \\
M_2 f_2' & \vdots & \ddots & \vdots \\
M_k f_k'
\end{pmatrix}
\]

Assuming that banded birds released into the population suffer statistically independent fates, the likelihood under \( H_1 \) of \( \{R_{ij}\} \) is the same as that derived by Robson and Youngs (1971), i.e.,

\[
P_{H_1}[[R_{ij}]] = \prod_{i=1}^{k} \left( \frac{N_i}{R_{i1}, \ldots, R_{ik}} \right)^{R_i} S_{i-1}^{T_i - R_i} (1 - \rho_i)^{A_i - R_i}.
\]
where $R_i, R_{..}$ are row and column totals respectively of the array $\{R_{ij}\}$, $T_1 = R_1, T_{i+1} = R_{i+1} + T_i - R_{..}$, $i=1, \ldots, k-1$, and

$$
\rho_i = E[H_1 \left[ \begin{array}{c} R_{..} \\ N_1 \end{array} \right]] = \begin{cases} f_i + S_i f_{i+1} + \ldots + S_i S_{i+1} \ldots S_{k-1} f_k & i=1, \ldots, k-1 \\ f_k & i=k \end{cases}
$$

and $f_i, S_i, \rho_i$ correspond respectively to Seber's $\alpha_i, \beta_i, \theta_i$.

Similarly defining $Q_i, Q_{..}$ to be the row and column totals respectively of the array $\{Q_{ij}\}$, and $U_i = Q_{..}, U_{i+1} = Q_{i+1} + U_i - Q_{..}, i=1, \ldots, k-1$, and

$$
\rho'_i = E[H_1 \left[ \begin{array}{c} Q_{..} \\ M_1 \end{array} \right]] = \begin{cases} f'_i + S'_i f_{i+1} + \ldots + S'_i S_{i+1} \ldots S_{k-1} f_k & i=1, \ldots, k-1 \\ f_k & i=k \end{cases}
$$

we have

$$
P_{H_1}[[Q_{ij}]] = \prod_{i=1}^k \left( Q_{1i}, \ldots, Q_{ik} \right) f'_i S_i Q_i - Q_{ii} f_i S_{i-1} Q_i - Q_{ii} U_i Q_i - Q_{ii} + Q_{i-1}, i-1 (1-\rho'_i) M_i Q_i.
$$

where $Q_{0,i} = 0$. Hence

$$
P_{H_1}[[R_{ij}], [Q_{ij}]] = \prod_{i=1}^k \left( R_{1i}, \ldots, R_{ik} \right) f_i S_i Q_i - Q_{ii} f_i S_{i-1} Q_i - Q_{ii} U_i Q_i - Q_{ii} + Q_{i-1}, i-1 (1-\rho_i) N_i R_i. (1-\rho'_i) M_i Q_i.
$$

where $W_i = R_{..} Q_{..} - Q_{ii} i=1, \ldots, k$

$$
Z_i = \begin{cases} T_i + U_i - R_{..} - Q_{ii} + Q_{i-1}, i-1 & i=2, \ldots, k \\ 0 & i=k+1 \end{cases}
$$
By expressing the likelihood in this form, and noting that \( T_{i+1} + U_{i+1} = R_{i+1} + Q_{i+1} + T_i + U_i - W_i - Q_{ii}, \) \( i=2, \ldots, k-1, \) we can identify a minimal sufficient statistic \( \mathcal{J}_1 \) under \( H_1 \) as

\[
\mathcal{J}_1 = \{R_1, \ldots, R_k, q_1, \ldots, q_k, q_{11}, \ldots, q_{k-1,k-1}, T_2 + U_2, \ldots, T_k + U_k \}
\]

Now note that the likelihood can be expressed as the product

\[
P_{H_1}([R_{ij}], [Q_{ij}]) = P_{H_1}([\mathcal{J}_1]) P_{H_1}([R_{ij}], [Q_{ij}] | \mathcal{J}_1)
\]

\[
= \prod_{i=1}^{k-1} P_{H_1}([R_i], [N_i]) P_{H_1}([Q_i], [M_i]) P_{H_1}([Q_{ii}] | Q_{i})
\]

\[
P_{H_1}([W_i], [W_i + Z_{i+1}]) P_{H_1}([R_k], [N_k])
\]

\[
P_{H_1}([Q_k], [M_k]) P_{H_1}([R_{ij}], [Q_{ij}] | \mathcal{J}_1)
\]

where the residual distribution given by \( P_{H_1}([R_{ij}], [Q_{ij}] | \mathcal{J}_1) \) is independent of the unknown parameters, and

\( R_i \sim \text{Bin} (N_i, \rho_i), \quad i=1, \ldots, k \)

\( Q_i \sim \text{Bin} (M_i, \rho_i'), \quad i=1, \ldots, k \)

\( Q_{ii} \text{ given } Q_i \sim \text{Bin} (Q_{i}, f_i / \rho_i'), \quad i=1, \ldots, k-1 \)

\( W_i \text{ given } W_i + Z_{i+1} \sim \text{Bin} (W_i + Z_{i+1}, f_i / \rho_i), \quad i=1, \ldots, k-1 \)

and \( \text{Bin} (N, \rho) \) represents the Binomial distribution with parameters \( N, \rho. \)

Therefore, the maximum likelihood estimators of the parameters \( \rho_i, \rho_i', \) \( f_i / \rho_i, f_i' / \rho_i' \) are:

\[
\hat{\rho}_i = \frac{R_i}{N_i}, \quad \hat{\rho}_i' = \frac{Q_i}{M_i}, \quad i=1, \ldots, k,
\]

\[
\frac{\hat{f}_i}{\rho_i} = \frac{W_i}{W_i + Z_{i+1}}, \quad \frac{\hat{f}_i'}{\rho_i'} = \frac{Q_{ii}}{Q_i}, \quad i=1, \ldots, k-1,
\]
and using the relationships \( \rho_i = f_i + S_i \rho_{i+1} \), \( \rho_i' = f_i' + S_i' \rho_{i+1} \), gives the maximum likelihood estimators of the parameters \( f_i, S_i, f_i', S_i' \):

\[
\hat{f}_i = \frac{R_i - N_i}{W_i + Z_i + 1}, \quad \hat{f}'_i = \frac{Q_{ii}}{M_i}, \quad i = 1, \ldots, k
\]

\[
\hat{S}_i = \frac{R_i - \hat{f}_i}{N_i}, \quad \hat{S}'_i = \frac{Q_{ii} - R_i - Q_{ii} + N_i + 1}{M_i} \quad i = 1, \ldots, k - 1.
\]

The estimators \( \hat{f}_i \) can be shown to be unbiased, and the estimators \( \hat{S}_i, \hat{S}'_i \) are consistent.

Variances and covariances of maximum likelihood estimators under \( H_1 \)

\[
\text{Var} (\hat{f}_i') = \frac{f_i(1-f_i)}{M_i}, \quad i = 1, \ldots, k
\]

Using conventional Taylor series methods, the following asymptotic variances and covariances are obtained:

\[
\text{Var} (\hat{f}_i) \approx \frac{f_i^2}{E(R_i)} \left[ \frac{1}{N_i} - \frac{1}{E(W_i)} + \frac{1}{E(W_i + Z_i + 1)} \right], \quad i = 1, \ldots, k,
\]

\[
\text{Var} (\hat{S}_i) \approx \frac{S_i^2}{E(R_i)} \left[ \frac{1}{N_i} - \frac{1}{E(R_{i+1})} + \frac{1}{E(Z_{i+1})} + \frac{1}{E(W_{i+1})} - \frac{1}{E(Z_{i+1} + Z_{i+1})} \right],
\]

\[
\text{Cov} (\hat{f}_i, \hat{S}_i) \approx \frac{f_i S_i}{E(R_i)} \left[ \frac{1}{N_i} - \frac{1}{E(W_i + Z_i + 1)} \right], \quad i = 1, \ldots, k - 1,
\]

\[
\text{Cov} (\hat{f}_{i+1}, \hat{S}_i) \approx -S_i f_{i+1} \left[ \frac{1}{E(R_{i+1})} - \frac{1}{N_{i+1}} \right], \quad i = 1, \ldots, k - 1,
\]
\[
\text{Cov}(\hat{S}_{i}^{l}, \hat{S}_{i+1}^{l}) = -S_{i}^{l}S_{i+1}^{l+1} \left[ \frac{1}{E(R_{i+1}^{l})} - \frac{1}{N_{i+1}} \right], \quad i=1, \ldots, k-2,
\]

\[
\text{Cov}(\hat{S}_{i}^{l}, \hat{S}_{i+1}^{l+1}) = S_{i}^{l}S_{i+1}^{l+1} \left[ \frac{1}{E(R_{i+1}^{l+1})} - \frac{1}{N_{i+1}} \right], \quad i=1, \ldots, k-1,
\]

\[
\text{Cov}(\hat{S}_{i}^{l}, \hat{S}_{i+1}^{l+1}) = -S_{i}^{l+1}S_{i+1}^{l+1} \left[ \frac{1}{E(R_{i+1}^{l+1})} - \frac{1}{N_{i+1}} \right], \quad i=1, \ldots, k-2,
\]

\[
\text{Cov}(\hat{S}_{i}^{l}, \hat{f}_{i+1}^{l+1}) = -S_{i}^{l}f_{i+1}^{l} \left[ \frac{1}{E(R_{i+1}^{l+1})} - \frac{1}{N_{i+1}} \right], \quad i=1, \ldots, k-1,
\]

\[
\text{Cov}(\hat{f}_{i}^{l}, \hat{S}_{i}^{l+1}) = \frac{f_{i}^{l}S_{i}^{l+1}}{M_{i}} \quad i=1, \ldots, k-1,
\]

where expectations are with respect to the model under \( H_{1} \).

All other covariances are exactly or approximately zero. Estimators of variances and covariances are obtained in an obvious way by replacing expected values by observed values in the above formulae.

The above derivations apply to the case where the data arrays \( \{R_{ij}\}, \{Q_{ij}\} \) are triangular, but the extension to the case where the data arrays have \( k \) rows and \( k+s \) columns, \( s > 0 \), is straightforward. In this case the minimal sufficient statistic is \( \mathcal{P}_{1} = \{R_{1}, \ldots, R_{k}, Q_{1}, \ldots, Q_{k}, Q_{11}, \ldots, Q_{kk}, T_{2} + U_{2}, \ldots, T_{k} + U_{k}, R_{k+1} + Q_{k+1}, \ldots, R_{k+s} + Q_{k+s} \} \) and the formulae for the estimators \( \hat{f}_{i}^{l}, \hat{f}_{i}^{l+1}, \hat{S}_{i}, \hat{S}_{i+1}^{l}, i=1, \ldots, k \), are the same if \( R_{i}, R_{i}, Q_{i}, Q_{i} \) are defined in the obvious way. As indicated by Seber (1970), the parameters \( S_{k-1+j}, f_{k+j} \) are not separately identifiable for \( j=1, \ldots, s \).
3. A Test of $H_0$ vs $H_1$

We now define a test of the assumption that young-of-the-year and adult birds have the same survival and reported exploitation rates. If we let $H_0$ be the hypothesis that this assumption is true, then the model under $H_0$ is characterized by

$$E_{H_0}\left[\frac{R_{ij}}{N_i}\right] = E_{H_0}\left[\frac{Q_{ij}}{M_i}\right] = \begin{cases} f_i & \text{i=j, i=1, \ldots, k} \\ S_i \ldots S_{j-1} f_j & \text{j=i+1, \ldots, k} \\ i=1, \ldots, k-1. \end{cases}$$

Under $H_0$, the model is analogous to the SRY model and the minimal sufficient statistic, derived by Robson and Youngs (1971), is

$\mathcal{J}_0 = \{R_1, Q_1, \ldots, R_k, Q_k, T_2 + U_2, \ldots, T_k + U_k\}$.

The conditional distribution under $H_0$ of $\mathcal{J}_1$ given $\mathcal{J}_0$ can now be used to derive a conditional test $\phi(\mathcal{J}_0, \mathcal{J}_1)$ of $H_0$ vs $H_1$ with the property

$$E_{H_0}[\phi(\mathcal{J}_0, \mathcal{J}_1)|\mathcal{J}_0] = \alpha.$$

In order to obtain $P_{H_0}(\mathcal{J}_1|\mathcal{J}_0)$ we need $P_{H_0}(Q_1, \ldots, Q_k, Q_{i1}, \ldots, Q_{k-1,k-1}|\mathcal{J}_0)$. Note that

$$P_{H_0}(Q_1, Q_{i1}|\mathcal{J}_0) = P_{H_0}(Q_1, R_1 + Q_1) P_{H_0}(Q_{i1}|Q_1, \mathcal{J}_0)$$

$$= \frac{\binom{M_i}{Q_1} \binom{N_i}{R_1}}{\binom{M_i + N_i}{R_1 + Q_1}} \frac{Q_{i1}}{T_1 + U_1 - Q_i} \frac{W_i}{T_1 + U_1}$$

since under $H_0$, $Q_i \sim \text{Bin} (M_i, \rho_i)$

$R_1 \sim \text{Bin} (N_i, \rho_i)$

and $Q_{i1}$ given $Q_i \sim \text{Bin} (Q_i, f_i/\rho_i)$

$W_i$ given $T_1 + U_i - Q_i \sim \text{Bin} (T_1 + U_i - Q_i, f_i/\rho_i)$
The conditional distribution $P_{H_0}[\mathcal{A} | \mathcal{O}]$ can therefore be represented as a product of hypergeometric distributions, and a chi-square test can be applied in the usual way to the $2 \times 2$ table corresponding to each hypergeometric term in the product. Thus a single degree of freedom chi-square statistic is obtained from each of the contingency tables.

$$
\begin{array}{ccc}
Q_{ii} & Q_{i} - Q_{i} \\
M_{i} - Q_{i} & R_{i} - N_{i} \\
\end{array} \quad \text{i=1, \ldots, k,} \quad \text{and} \quad \begin{array}{ccc}
Q_{ii} & Q_{i} - Q_{i} \\
T_{i} + U_{i} - Q_{i} & W_{i} \\
\end{array} \quad \text{i=1, \ldots, k-1.}
$$

These chi-square statistics are asymptotically independent and may be added to give a single test statistic which is asymptotically chi-square under $H_0$ with $2k-1$ degrees of freedom.

When the data arrays have $k$ rows and $k+s$ columns, $s > 0$, the sufficient statistic under $H_0$ is $\mathcal{A}_0^k = \{R_{1} + Q_{1}, \ldots, R_{k} + Q_{k}, T_{2} + U_{2}, \ldots, T_{k} + U_{k}, R_{k+1} + Q_{k+1}, \ldots, R_{k+s} + Q_{k+s}\}$, and the corresponding test is based on the distribution given by

$$
P_{H_0}[\mathcal{A} | \mathcal{O}] = \prod_{i=1}^{k} \frac{M_{i}}{Q_{i}} \frac{N_{i}}{R_{i}} \prod_{i=1}^{k-1} \frac{Q_{ii}}{W_{i}} \frac{T_{i} + U_{i} - Q_{i}}{R_{i} + Q_{i}}$$
4. The Model Under $H_2$

For reasons discussed in the introduction, another model which is of interest is one under which the assumptions about survival and exploitation rates are the same as under $H_1$, but in addition it is assumed that in any given year, the reporting rate for birds banded and released in that year is different from that for birds banded and released in previous years. We let $H_2$ be the hypothesis that these assumptions hold.

Let $f''''_i = P[\text{adult released in year } i \text{ is killed by hunter and its band returned in year } i], \ i=1,\ldots,k$

and

$$\rho''''_i = \mathbb{E}_{H_2}[R_{i\cdot}] = \begin{pmatrix} f''''_1 + S_1 \rho''''_{i+1} \\ \vdots \\ f''''_k \end{pmatrix} \quad i=1,\ldots,k-1$$

Then

$$\mathbb{E}_{H_2}[[R_{ij}]] = \begin{pmatrix} N_1 f''''_1 & N_1 S_1 f''''_2 & \cdots & N_1 S_1 \cdots S_{k-1} f''''_k \\ N_2 f''''_2 & \cdots & \cdots & \cdots \\ \vdots & \vdots & \vdots & \vdots \\ N_k f''''_k \\ \end{pmatrix}$$

and

$$\mathbb{E}_{H_2}[[Q_{ij}]] = \mathbb{E}_{H_2}[[Q_{ij}]] .$$

The likelihood under $H_2$ is given by

$$P_{H_2}[[R_{ij}],[Q_{ij}]] = \prod_{i=1}^{k} \begin{pmatrix} N_i \\ R_{i\cdot} \end{pmatrix} \begin{pmatrix} M_i \\ Q_{i\cdot} \end{pmatrix} f''''_i$$

$$Z_{i+1} f''''_i f''''_{Q_i} f''''_{Q_i - Q_{ii}}$$

$$S_i f''''_i f''''_{Q_i} f''''_{Q_i - Q_{ii}}$$

$$(1-\rho''''_i) \cdot (l-\rho''''_i) \cdot (1-\rho''''_i) .$$
Variances and covariances of maximum likelihood estimators under $H_0$

Exact variances of $\hat{f}_1^{'}, \hat{f}_1^{'}, S_{k-k-1}^{'}, S_{k-k-1}^{'}, f_k^{'}, S_{k-k-1}^{'}, f_k^{'}$ are the appropriate binomial variances. Asymptotic variances of the other estimators are:

$$\text{Var}(\hat{f}_1^{'}) = \frac{f_1^{'}}{1 - \frac{1}{N_i} - \frac{1}{E(Z_{i+1} - R_{i+1} + R_{i+1}) + \frac{1}{E(W_{i+1} - R_{i+1})}}$$

$$\text{Var}(\hat{S}_1^{'}) = \frac{S_1^{'}}{1 - \frac{1}{N_i} + \frac{1}{E(R_{i+1} - R_{i+1} + R_{i+1})} + \frac{1}{N_{i+1}}$$

$$\text{Var}(\hat{S}_1^{'}) = \frac{S_1^{'}}{1 - \frac{1}{N_i} + \frac{1}{E(Q_{i+1} - Q_{i+1})} + \frac{1}{N_{i+1}}$$

Non-zero asymptotic covariances are:

$$\text{Cov}(\hat{f}_1^{'},\hat{f}_1^{'}) = -\frac{f_1^{'}}{N_i}$$

$$\text{Cov}(\hat{f}_1^{'},\hat{S}_1^{'}) = -\frac{f_1^{'}}{S_1^{'}/N_i}$$

$$\text{Cov}(\hat{f}_1^{'},\hat{S}_1^{'}) = \frac{f_1^{'}}{S_1^{'}/N_{i+1}}$$

$$\text{Cov}(\hat{f}_1^{'},\hat{S}_1^{'}) = \frac{f_1^{'}}{S_1^{'}/M_i}$$

$$\text{Cov}(\hat{f}_1^{'},\hat{S}_1^{'}) = \frac{f_1^{'}}{S_1^{'}} \left[ \frac{1}{E(R_{i+1} - R_{i+1})} - \frac{1}{N_i} \right]$$
cov (\(\hat{f}_{i+1}, \hat{s}_{i+1}\)) = -f_{i+1} s_{i+1} \left[ \frac{1}{E(R_{i+1}, -R_{i+1}, i+1)} - \frac{1}{N_{i+1}} \right]

cov (\(\hat{f}_{i+1}, \hat{s}'_{i+1}\)) = -s_{i+1} f_{i+1} \left[ \frac{1}{E(R_{i+1}, -R_{i+1}, i+1)} - \frac{1}{N_{i+1}} \right]

cov (\(\hat{s}_{i}, \hat{s}_{i+1}\)) = -s_{i} s_{i+1} \left[ \frac{1}{E(R_{i+1}, -R_{i+1}, i+1)} - \frac{1}{N_{i+1}} \right]

cov (\(\hat{s}_{i}, \hat{s}'_{i}\)) = s_{i} s'_{i+1} \left[ \frac{1}{E(R_{i+1}, -R_{i+1}, i+1)} - \frac{1}{N_{i+1}} \right]

+ \frac{1}{E(Z_{i+2}, -R_{i+1}, +R_{i+1}, i+1)} - \frac{1}{E(W_{i+1}, Z_{i+2}, -R_{i+1}, i+1)}

cov (\(\hat{s}_{i+1}, \hat{s}'_{i}\)) = -s_{i+1} s'_{i} \left[ \frac{1}{E(R_{i+1}, -R_{i+1}, i+1)} - \frac{1}{N_{i+1}} \right].

All expectations are with respect to the model under \(H_2\).

5. The Model Under \(H_3\)

Under the hypotheses \(H_1\) and \(H_2\) it is assumed that survival rates are age-specific for birds less than one year old, but independent of age for all other birds. It may be, however, that survival rates are also age-dependent for yearlings, and independent of age only for birds more than two years old. This leads to a third modification of the basic model, and to the hypothesis \(H_3\), which assumes that survival rates are age-specific for young-of-the-year birds and yearlings only.
In most cases it is possible to distinguish between young-of-the-year birds and adults only, so that the experimental situation remains the same, with data collected for these two classes of birds only. Each batch of adults released will include yearlings and older birds in unknown proportions. So in a given year the survival rate for a newly released batch of adults will be different from that of birds released in previous years. Therefore, new parameters $f''', S'''$ are defined by:

\[
f'''_i = P \text{ [adult released in year } i \text{ is captured and reported in year } i], \quad i=1,\ldots,k
\]

\[
S'''_i = P \text{ [adult released in year } i \text{ survives year } i], \quad i=1,\ldots,k-1.
\]

Also

\[
f''_i = P \text{ [yearling released as young-of-the-year in year } i-1 \text{ is captured and reported in year } i \text{ given it survived year } i-1], \quad i=2,\ldots,k
\]

\[
S''_i = P \text{ [yearling released as young-of-the-year in year } i-1 \text{ survives year } i \text{ given it survived year } i-1], \quad i=2,\ldots,k-1.
\]

\[
E \frac{Q_i}{M_i} = \rho_i' = \begin{cases} 
\frac{f''_i + S''_i}{N} & i=k-1 \\
\frac{f''_{k-1} + S''_{k-1}}{N} & i=k \end{cases}
\]

\[
E \frac{R_i}{N_i} = \rho_i''' = \begin{cases} 
\frac{f'''_i + S'''}{N} & i=k-1 \\
f'''_k & i=k \end{cases}
\]

where $f_i, S_i, f'_i, S'_i$ are as defined under $H_2$. 
Then the hypothesis \( H_3 \) can be characterized by:

\[
E_{H_3}[\{R_{ij}\}] = \begin{pmatrix}
N_1^{f'''} & N_1^{f''} & N_1^{f'} & N_1 f \\
N_2^{f'''} & N_2^{f''} & N_2^{f'} & N_2 f \\
N_3^{f'''} & N_3^{f''} & N_3^{f'} & N_3 f \\
\vdots & \vdots & \vdots & \vdots \\
N_k^{f'''} & N_k^{f''} & N_k^{f'} & N_k f
\end{pmatrix}
\]

\[
E_{H_3}[\{Q_{ij}\}] = \begin{pmatrix}
M_1^{f'''} & M_1^{f''} & M_1^{f'} & M_1 f \\
M_2^{f'''} & M_2^{f''} & M_2^{f'} & M_2 f \\
M_3^{f'''} & M_3^{f''} & M_3^{f'} & M_3 f \\
\vdots & \vdots & \vdots & \vdots \\
M_k^{f'''} & M_k^{f''} & M_k^{f'} & M_k f
\end{pmatrix}
\]

Again assuming that banded birds released into the population suffer independent fates, we obtain:

\[
P_{H_3}[\{R_{ij}\},\{Q_{ij}\}] = \prod_{i=1}^{k} \left( \frac{N_i^{f'''} M_i^{f'''} R_{ii}^{f'''} R_{ii}^{f'} R_{ii}^{f}}{N_i R_{ii}^{f'''} R_{ii}^{f'} R_{ii}^{f}} - \frac{Q_i^{f'''} Q_i^{f''} Q_i^{f'} Q_i f}{Q_i R_{ii}^{f''} Q_i^{f'} Q_i^{f}} \right) \left( \frac{N_i^{f'''} M_i^{f'''} (1-\rho_1^{f'''})(1-\rho_1^{f''})}{N_i R_{ii}^{f''} (1-\rho_1^{f'''}) (1-\rho_1^{f''})} \right) \left( \prod_{i=2}^{k} \frac{Q_i^{f'''} Q_i^{f''} Q_i^{f'} Q_i f}{Q_i^{f'''} Q_i^{f''} Q_i^{f'} Q_i f} \right) \left( \prod_{i=2}^{k} \frac{N_i^{f'''} M_i^{f'''} W_i R_{ii}^{f'''} Q_i^{f'} Q_i f}{N_i R_{ii}^{f'''} Q_i^{f'} Q_i f} \right) \left( \prod_{i=2}^{k} \frac{Z_i^{f'''} R_{ii}^{f'''} Q_i^{f'} Q_i f}{Z_i^{f'''} R_{ii}^{f'''} Q_i^{f'} Q_i f} \right)
\]

The minimal sufficient statistic is \( \mathcal{J}_3 = \{R_1, \ldots, R_k, Q_1, \ldots, Q_k\} \)
Under $H_3$, parameters of interest are not identifiable and hence not estimable. However, the assumptions of the hypothesis $H_3$ are of interest and so tests related to $H_3$ are developed in the next sections. In other words, tests between $H_1$ and $H_3$ and between $H_2$ and $H_3$ are of interest because rejection of $H_1$ and $H_2$ in favor of $H_3$ would imply that survival and reported exploitation rates are age-specific for at least the first two years of life.

The model under $H_3$ is the last in our sequence of models for the experimental situation where data are recorded separately for young-of-the-year and adult birds.

6. Tests to Discriminate Between $H_1$, $H_2$, $H_3$

The hypotheses $H_1$, $H_2$, $H_3$ are such that $H_1 \subset H_2 \subset H_3$ and there is also a relationship between the corresponding minimal sufficient statistics $\mathcal{J}_1$, $\mathcal{J}_2$, $\mathcal{J}_3$ given by $\mathcal{J}_2 = \{\mathcal{J}_1, R_{22}, \ldots, R_{k-1,k-1}\}$, $\mathcal{J}_3 = \{\mathcal{J}_2, Q_{12}, Q_{23}, \ldots, Q_{k-2,k-1}\}$. This suggests the construction of conditional tests $\phi(\mathcal{J}_1, \mathcal{J}_2)$ and $\phi(\mathcal{J}_2, \mathcal{J}_3)$ of $H_1$ vs $H_2$, and $H_2$ vs $H_3$ respectively, such that $E_{H_1}[\phi(\mathcal{J}_1, \mathcal{J}_2)|\mathcal{J}_1] = \alpha$, $E_{H_2}[\phi(\mathcal{J}_2, \mathcal{J}_3)|\mathcal{J}_2] = \alpha$. Actually $\phi(\mathcal{J}_2, \mathcal{J}_3)$ will be a test of $H_1 \cup H_2$ vs $H_3$ since $E_{H_1}[\phi(\mathcal{J}_2, \mathcal{J}_3)|\mathcal{J}_2] = E_{H_2}[\phi(\mathcal{J}_2, \mathcal{J}_3)|\mathcal{J}_2]$.

The tests $\phi(\mathcal{J}_1, \mathcal{J}_2)$, $\phi(\mathcal{J}_2, \mathcal{J}_3)$ are based on the conditional distributions given by $P_{H_1}[\mathcal{J}_2|\mathcal{J}_1]$, $P_{H_2}[\mathcal{J}_3|\mathcal{J}_2]$ respectively. The derivations of these distributions are analogous to the derivation of $P_{H_0}[\mathcal{J}_1|\mathcal{J}_0]$ outlined in section 3, and we obtain

$$P_{H_1}[\mathcal{J}_2|\mathcal{J}_1] = \prod_{i=2}^{k-1} \left( \frac{R_{ii}}{T_i+U_i-Q_i-R_i} \right) \left( \frac{T_i+U_i-Q_i-R_i}{W_i-R_{ii}} \right),$$
Both of the above expressions are in the form of a product of \( k-2 \) terms, each term being a hypergeometric probability, and the corresponding test statistics are obtained using the usual chi-square approximation as outlined in section 3. Thus the test of \( H_1 \) vs \( H_2 \) is based on a test statistic which is asymptotically chi-square on \( k-2 \) degrees of freedom under \( H_1 \), and similarly the test statistic for \( H_2 \) vs \( H_3 \) is asymptotically chi-square on \( k-2 \) degrees of freedom under \( H_2 \).

7. Non-Discriminant Goodness of Fit Tests of the Models Under \( H_1, H_2, H_3 \)

Robson and Youngs (1971) developed a size \( \alpha \) goodness of fit test of their model based on the conditional distribution of the data array given the minimal sufficient statistic. Analogous goodness of fit tests can be developed for the models under \( H_1, H_2, H_3 \), based on the residual distributions given by

\[
P_{H_1}[[R_{ij}],[Q_{ij}]|\mathcal{S}_1], \ P_{H_2}[[R_{ij}],[Q_{ij}]|\mathcal{S}_2], \ P_{H_3}[[R_{ij}],[Q_{ij}]|\mathcal{S}_3] \text{ respectively.}
\]

The derivation of each of these distributions is analogous to that given by Robson and Youngs (1971) and is omitted here.

Define

\[
R^*_{ij} = \begin{cases} R_{1j} & i=1 \\ R_{1j} + R_{2j} + \cdots + R_{ij} & i=2, \ldots, j, \end{cases}
\]

\[
Q^*_{ij} = \begin{cases} Q_{1j} & i=1 \\ Q_{1j} + Q_{2j} + \cdots + Q_{ij} & i=2, \ldots, j. \end{cases}
\]
Then $$P_{H_1}[[R_{ij}],[Q_{ij}]|\mathcal{F}_1] =$$

$$\prod_{i=2}^{k-1} \frac{Z_{i}}{R_{i-1,1}^{*} + Q_{i-2,1}^{*} + \cdots + R_{i-1,k}^{*} + Q_{i-2,k}^{*}} \left| \begin{array}{c} R_{i,1}, \ldots, R_{1,k} \\ Q_{1,1}, \ldots, Q_{1,k} \end{array} \right| \frac{Q_{i-1,1} - Q_{i-1,1,1 - 1}}{T_{1}^{*} + U_{1}^{*} - Q_{1}^{*}} \left( R_{1,1}^{*} + Q_{1,1}^{*} + \cdots + R_{1,k}^{*} + Q_{1,k}^{*} \right)$$

$$P_{H_2}[[R_{ij}],[Q_{ij}]|\mathcal{F}_2] = \frac{R_{1,1}^{*} - R_{11}^{*}}{R_{1,2}, \ldots, R_{1,k}} \left| \begin{array}{c} R_{1,1}, \ldots, R_{1,k} \\ Q_{1,1}, Q_{1,2}, \ldots, Q_{1,k} \end{array} \right| \frac{Q_{1,1}^{*} - Q_{11}^{*}}{T_{2}^{*} + U_{2}^{*} - Q_{2}^{*}} \left( R_{1,2}^{*} + Q_{1,2}^{*} + \cdots + R_{1,k}^{*} + Q_{1,k}^{*} \right)$$

$$\prod_{i=2}^{k-2} \frac{T_{i+1}^{*} + U_{i+1}^{*} - R_{i+1}^{*} - Q_{i+1}^{*} - R_{i1}^{*} + Q_{i1}^{*}}{R_{i-1,1}^{*} + Q_{i-2,1}^{*} + \cdots + R_{i-1,k}^{*} + Q_{i-2,k}^{*}} \left| \begin{array}{c} R_{i,1}, \ldots, R_{1,k} \\ Q_{1,1}, \ldots, Q_{1,k} \end{array} \right| \frac{Q_{i,1}^{*} - Q_{i,i+1}}{T_{i+1}^{*} + U_{i+1}^{*} - Q_{i+1}^{*}} \left( R_{i,1}^{*} + Q_{i,1}^{*} + \cdots + R_{i,k}^{*} + Q_{i,k}^{*} \right)$$

and $$P_{H_3}[[R_{ij}],[Q_{ij}]|\mathcal{F}_3] =$$

$$\prod_{i=2}^{k-2} \frac{Z_{i+1}^{*} - R_{i,1}^{*} - Q_{i-1,1}^{*} + Q_{i-1,1,1}^{*} + Q_{i-1,1,1}^{*}}{R_{i-1,1}^{*} + Q_{i-2,1}^{*} + \cdots + R_{i-1,k}^{*} + Q_{i-2,k}^{*}} \left| \begin{array}{c} R_{i,1}, \ldots, R_{1,k} \\ Q_{1,1}, \ldots, Q_{1,k} \end{array} \right| \frac{Q_{i-1,1}^{*} - Q_{i-1,1,1}^{*} - Q_{i-1,1,1}^{*}}{Z_{i+1}^{*}} \left( R_{i,1}^{*} + Q_{i,1}^{*} + \cdots + R_{i,k}^{*} + Q_{i,k}^{*} \right)$$

where $$Q_{0,i} = 0.$$
each yielding a chi-square statistic on 2(k-1) degrees of freedom for 
i=2,\ldots,k-1. The chi-square statistics obtained in this way for a given dis-
tribution \( P_{m}[\{R_{ij}\},\{Q_{ij}\} | \theta_m] \) are asymptotically independent and may be added
to give a single statistic on which the goodness of fit test to \( H_m \) is based.

For example, the goodness of fit test to \( H_1 \) is based on a chi-square statistic
with degrees of freedom equal to \( \sum_{i=2}^{k-1} 2(k-i) = (k-2)(k-1) \).

8. Discussion of Tests Derived in Sections 3, 6, 7

8.1 Comments related to the statistics \( \mathcal{J}_1, \mathcal{J}_2, \mathcal{J}_3 \)

Considerable use is made of the sufficient statistics \( \mathcal{J}_1, \mathcal{J}_2, \mathcal{J}_3 \) in deriving
the tests above, and so it should be noted that there other models for which
the statistics \( \mathcal{J}_1, \mathcal{J}_2, \mathcal{J}_3 \) are minimal sufficient. For example, \( \mathcal{J}_1 \) is minimal
sufficient for models which are identical to the model under \( H_1 \) except that
\( \mathbb{E}[Q_{ij} | M_i] = \rho_1' \) is defined by \( \rho_1' = f_1 + S_1 \rho_{i+1} \) or by \( \rho_1' = f_1' + S_1 \rho_{i+1} \), for each \( i \)
in any subset of the index set \( \{1,2,\ldots,k-1\} \). The dimension of the natural
parameter space corresponding to the model under \( H_1 \) is unaffected if \( S_1' = S_1 \)
or if \( f_1' = f_1 \), \( i \neq k \), but the number of biologically meaningful parameters is
reduced.

In the context of this study, the model under \( H_1 \) has a meaningful biologi-
cal interpretation but the other models described above do not. This is because
a difference in the harvesting rate of young birds should be reflected by a
difference in their survival rate, and vice versa. Also young and adult birds released in the same year should have the same reporting rate.

The situation is more complex for the statistics $J_2, J_3$, since analogous changes in the definition of $\rho_1', \rho_2''$ also give rise to new models. Again it is difficult to find a meaningful biological interpretation for any of these models except the models under hypotheses $H_2, H_3$, and so all except these last two models have been largely ignored.

It should now be recognized that tests based on $J_1, J_2, J_3$ are in fact related to the composite hypotheses comprising the numerous alternative models described above. However, in view of the biological considerations outlined above, tests based on $J_1, J_2, J_3$ will be regarded as being related to just those models under hypotheses $H_1, H_2$ and $H_3$.

8.2 Some asymptotic considerations

Define $\chi^2([R_{ij}],[Q_{ij}]; J_m)$ to be the test statistic associated with $P_{H_m}([R_{ij}],[Q_{ij}]; J_m), m=1,2,3$, as described in section 7.

Similarly, define $\chi^2(J_{m+j}; J_m)$ to be the test statistic associated with $P_{H_m}(J_{m+j}; J_m), m=1,2, j=1, \ldots, (3-m)$.

We note the following

(i) Asymptotically, $\chi^2(X; J_m)$, (where $X = ([R_{ij}],[Q_{ij}])$ or $J_{m+j}$), is a sum of independent central chi-square variables under $H_\ell$ for $\ell \leq m$, and is a sum of independent non-central chi-square variables under $H_\ell$ for $\ell > m$.

Approximate power for the statistics $\chi^2(X; J_m)$ can be obtained using methods outlined by Meng and Chapman (1966). They obtained asymptotic power results, using alternatives of Pitman type, for chi-square tests for contingency tables. Evaluation of their formulae for non-centrality parameters
in the "comparative trials" situation involves making the correct substitution for their $Q_i = N_i/N$, where $N_i$ are the contingency table row totals, and $N$ the grand total. Row totals and the grand total for the contingency tables associated with the statistics $\chi^2(X; J_j)$ are components of the sufficient statistic $J_j$ and so $Q_i$ is replaced by the stochastic limit of the appropriate ratios of the components of $J_j$. Motivation for this can be found in results of Harkness and Katz (1964).

(ii) The order relationships between $J_1, J_2, J_3$ imply

(a) $P_{H_j} \{[R_{ij}], [Q_{ij}] | J_1 \} = P_{H_j} \{J_2 | J_1 \} P_{H_j} \{[R_{ij}], [Q_{ij}] | J_2 \}$,

(b) $P_{H_j} \{J_3 | J_1 \} = P_{H_j} \{J_2 | J_1 \} P_{H_j} \{J_3 | J_2 \}$, $j=1,2,3$

(iii) The degrees of freedom for the two statistics associated with the right-hand side of each of (a), (b) add to the degrees of freedom of the statistic associated with the corresponding left-hand side. For example, the statistics $\chi^2([R_{ij}],[Q_{ij}]; J_1), \chi^2(J_2; J_1), \chi^2([R_{ij}],[Q_{ij}]; J_2)$ have degrees of freedom $(k-2)(k-1), (k-2), (k-2)^2$ respectively and $k-2 + (k-2)^2 = (k-2)(k-1)$.

(iv) For $j=2,3$, if the non-centrality parameters for the statistics associated with each of (a), (b) are evaluated for Pitman type alternatives contained in $H_2$ or $H_3$, using the Meng and Chapman formulae as described above, then these non-centrality parameters satisfy the same additive relationship described in (iii) for the corresponding degrees of freedom.

(v) If $X_i$ is a non-central chi-square variable with degrees of freedom $v_i$ and non-centrality parameter $\lambda_i$, $i=1,2$, and $X_1,X_2$ are independent, then $X_1+X_2$ is a non-central chi-square variable with degrees of freedom $v_1+v_2$ and non-centrality parameter $\lambda_1+\lambda_2$.
These observations suggest (but do not prove) asymptotic equivalence of the statistics $\chi^2([R_{ij}, Q_{ij}]; J_1)$ and $\chi^2(J_2; J_1) + \chi^2([R_{ij}, Q_{ij}]; J_2)$ and also of the statistics $\chi^2(J_3; J_1)$ and $\chi^2(J_2; J_1) + \chi^2(J_3; J_2)$. This result would be useful both for practical reasons involved in the computation of the goodness of fit tests, and for the purpose of making power comparisons.

The statistics $\chi^2(J_{m+1}; J_m)$ are relatively easy to compute in comparison to the statistics $\chi^2([R_{ij}, Q_{ij}]; J_m)$. Thus, for large enough $N_1, M_1$, and if the above conjecture is true, the goodness of fit test to $H_2$ could be computed as the sum $\chi^2(J_3; J_2) + \chi^2([R_{ij}, Q_{ij}]; J_3)$ and the goodness of fit test to $H_1$ as $\chi^2(J_2; J_1) + \chi^2(J_3; J_2) + \chi^2([R_{ij}, Q_{ij}]; J_3)$, making it necessary to compute $\chi^2([R_{ij}, Q_{ij}]; J_m)$ for $m = 3$ only.

Asymptotic equivalence of $\chi^2([R_{ij}, Q_{ij}]; J_1)$ and $\chi^2(J_2; J_1) + \chi^2([R_{ij}, Q_{ij}]; J_2)$, which depends on the asymptotic independence of $\chi^2(J_2; J_1), \chi^2([R_{ij}, Q_{ij}]; J_2)$, would imply that, asymptotically under $H_2$, the statistics $\chi^2([R_{ij}, Q_{ij}]; J_1), \chi^2(J_2; J_1)$ have the same non-centrality parameter. The difference in degrees of freedom of these two statistics would then suggest that for making tests about $H_1$, the statistic $\chi^2(J_2; J_1)$ would be more powerful against alternatives contained in $H_2$, than the statistic $\chi^2([R_{ij}, Q_{ij}]; J_1)$, or the (probably) asymptotically equivalent conventional chi-square goodness of fit statistic.

9. Applications and Extensions

So far we have discussed the application of the methods of this paper to band return data from exploited bird populations only. However there are data from other types of populations to which these methods can be applied. For example, blackbird populations, though not exploited, are subjected to yearly
banding operations and substantial numbers of banded birds are found dead each
year and reported to the banding office. Also models under $H_1, H_3$ are applicable
to other exploited animal populations, whenever there is a yearly banding pro-
gram in which young animals are distinguished from adults. Many fish popula-
tions are of this type.

The methods of this paper are easily extended to experimental situations
where data are recorded separately for more than two age groups. This is the
case in some tagging operations carried out in fish populations. If data for
more than two age groups are available, then models can be developed which
permit even greater flexibility in the assumptions about annual survival,
exploitation, and reporting rates. A sequence of models, estimation formulae
and tests have been derived for the situation where three age groups are
recognizable, namely young-of-the-year, yearlings, and animals more than two
years old. Details are given in Brownie (1973). These three age groups can
be distinguished in some species of geese.

In the derivations above, it has been assumed for simplicity that the data
arrays $[R_{ij}], [Q_{ij}]$ are triangular, i.e., that returns are recorded only for as
many years as banded birds are released. In practice it is common for returns
to be recorded for several years after the last batch is released, and in this
case the arrays $[R_{ij}], [Q_{ij}]$ have more columns than rows. This situation is
referred to briefly at the end of sections 2, 3 and details can be found in
Brownie (1973). A numerical example for data of this type follows.

10. Numerical Example

The above methods are illustrated using data for mallards banded in
southwestern Saskatchewan during 1956 to 1959. Estimates and tests are
presented in Tables 1 to 7 in the form of output from a fortran program developed by Mrs. E. Keokosky of the Computer Activities Group at Cornell University.

In Table 1 the "input matrices" for adults and young correspond to the \{R_{ij}\} and \{Q_{ij}\} arrays respectively. The first column gives the year of banding and the second column gives the number of birds banded. The "Basic parameters" correspond to the summary statistics \(R_i, R_i', Q_i, Q_i'\) etc., (reading from left to right).

Tables 2 and 4 contain estimates and confidence intervals for the models under hypotheses \(H_1\) and \(H_2\) respectively. In these tables \(\hat{F}\), \(\hat{F}'\) or \(\hat{F}''\) should be read as \(\hat{f}\), \(\hat{f}'\), \(\hat{f}''\) etc.

Tables 3 and 5 contain the estimated covariances under \(H_1\) and \(H_2\) respectively. Here \(\hat{F}HATP(I)\) should be read as \(\hat{f}_i\), \(\hat{F}HAT3P(I)\) as \(\hat{f}_i''\) etc.

Table 6 contains the tests of \(H_0\) vs \(H_1\), \(H_1\) vs \(H_2\) and \(H_2\) vs \(H_3\), and Table 7 contains the goodness of fit tests. In the goodness of fit tests some pooling across columns in the contingency tables may be necessary in order to justify applying a chi-square test. The fortran program uses an algorithm for pooling columns which is based on a procedure described by Robson (1971). Thus in the first contingency table in the goodness of fit test to \(H_3\) pooling has resulted in a table with 5 columns instead of 7 and the degrees of freedom are therefore 8 instead of 12. The goodness of fit tests to \(H_1\), \(H_2\) are computed using the approximate method described in section 8.2.

Table 6 shows that the test of \(H_0\) vs \(H_1\) is very significant and we conclude that young-of-the-year and adult birds have different survival and reported exploitation rates. None of the other tests are significant and we conclude that the model under \(H_1\) is appropriate for this data.
Availability of the FORTRAN Program

A source deck and brief documentation for the FORTRAN program, written for an IBM 360, are available from The Migratory Bird and Habitat Research Laboratory, Patuxent Wildlife Research Center, Laurel, Maryland 20810.

Acknowledgements

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Dr. J. B. Gollop deserves credit for banding most of the mallards in the banding experiment used in the example of section 10.

References


Key Words: Age-specific survival rates; Age-specific exploitation rates; Banding experiment; Band-return; Tag-recapture.
Table 1

MALLARDS BANDED IN SOUTHWESTERN SASKATCHEWAN, 1956 TO 1959.

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### Table 2

**Mallards Banded in Southwestern Saskatchewan, 1956 to 1959.**

**Estimates Under H1**

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<th>95% Confidence Interval</th>
<th><em>SHAT</em> Estimate</th>
<th>Standard Deviation</th>
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<td>0.0081</td>
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<td>0.0868 - 0.0984</td>
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<tr>
<td>5</td>
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<td>0.0012</td>
<td>0.0075 - 0.0122</td>
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Table 3

MALLARDS BANDED IN SOUTHWESTERN SASKATCHEWAN, 1956 TO 1959.

ESTIMATED NON-ZERO ASYMPTOTIC COVARIANCES UNDER H1

<table>
<thead>
<tr>
<th>YR</th>
<th>COVAR((\hat{F}(1), \hat{S}(1)))</th>
<th>CORR((\hat{F}(1), \hat{S}(1+1)))</th>
<th>COVAR((\hat{S}(1), \hat{S}(1+1)))</th>
<th>CORR((\hat{S}(1), \hat{S}(1+1)))</th>
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<tbody>
<tr>
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<td>-0.000206255</td>
<td>-0.071571609</td>
<td>0.001895337</td>
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<tr>
<td>2</td>
<td>1957</td>
<td>0.000115200</td>
<td>0.376951111</td>
<td>0.000009145</td>
</tr>
<tr>
<td>3</td>
<td>1958</td>
<td>-0.000086804</td>
<td>-0.557912343</td>
<td>0.00007836</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>YR</th>
<th>COVAR((\hat{S}(1), \hat{S}(1+1)))</th>
<th>CORR((\hat{S}(1+1), \hat{S}(1)))</th>
<th>COVAR((\hat{F}(1), \hat{S}(1+1)))</th>
<th>CORR((\hat{F}(1), \hat{S}(1+1)))</th>
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<td>0.301125332</td>
<td>0.351039515</td>
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<tr>
<td>2</td>
<td>1957</td>
<td>0.000779786</td>
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<td>0.000537698</td>
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<tr>
<td>3</td>
<td>1958</td>
<td>0.000346496</td>
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<th>CORR((\hat{S}(1+1), \hat{F}(1+1)))</th>
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<td>3</td>
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<td>-0.000061996</td>
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MALLARDS BANDED IN SOUTHWESTERN SASKATCHEWAN, 1956 TO 1959.
ESTIMATES UNDER H2

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</tr>
<tr>
<td></td>
<td>0.1123</td>
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<td>0.0764 - 0.1482</td>
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<tr>
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<td>0.0738</td>
<td>0.0079</td>
<td>0.0584 - 0.0892</td>
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<tr>
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<td>0.0480 - 0.0716</td>
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<td>STANDARD ERROR</td>
<td>95% CONFIDENCE INTERVAL</td>
</tr>
<tr>
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<td>0.0820</td>
<td>0.0069</td>
<td>0.0684 - 0.0956</td>
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<td>0.0703</td>
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<td>95% CONFIDENCE INTERVAL</td>
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<td>0.0926</td>
<td>0.0030</td>
<td>0.0684 - 0.0984</td>
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<table>
<thead>
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<td>STANDARD ERROR</td>
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<td>0.0660</td>
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<table>
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<td>95% CONFIDENCE INTERVAL</td>
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<td>0.3845</td>
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<td>95% CONFIDENCE INTERVAL</td>
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Table 4
### Table 5

**MALLARDS RANDED IN SOUTHWESTERN SASKATCHEWAN, 1956 TO 1959.**

**ESTIMATED NON-ZERO ASYMPTOTIC COVARIANCES UNDER H2**

<table>
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<tr>
<th>Year</th>
<th>Covariance ( FHAT3[I], SHAT[I] )</th>
<th>Correlation ( FHAT3[I], SHAT[I] )</th>
<th>Covariance ( FHAT3[I], SHAT[I+1] )</th>
<th>Correlation ( FHAT3[I], SHAT[I+1] )</th>
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<tr>
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<tr>
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<td>-0.00001961</td>
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<td>-0.00014500</td>
<td>-0.054110327</td>
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<tr>
<td>1958</td>
<td>-0.00001788</td>
<td>-0.056160593</td>
<td>-0.000037078</td>
<td>-0.059308664</td>
</tr>
<tr>
<td>1959</td>
<td>-0.000010924</td>
<td>-0.062700846</td>
<td>-0.000082075</td>
<td>-0.08414402</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Covariance ( FHAT[I], SHAT[I] )</th>
<th>Correlation ( FHAT[I], SHAT[I] )</th>
<th>Covariance ( FHAT[I+1], SHAT[I] )</th>
<th>Correlation ( FHAT[I+1], SHAT[I] )</th>
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<tbody>
<tr>
<td>1956</td>
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<td>0.096194816</td>
<td>0.000037078</td>
<td>0.07650967</td>
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<td>1957</td>
<td>0.00022408</td>
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<td>0.00016316</td>
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<td>0.05930864</td>
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<table>
<thead>
<tr>
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<th>Correlation ( FHAT[I+1], SHAT[I] )</th>
<th>Covariance ( FHAT[I], SHAT[I+1] )</th>
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<td>-0.000037078</td>
<td>-0.059308664</td>
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Table 6

MALLARDS BANDED IN SOUTHWESTERN SASKATCHEWAN, 1956 TO 1959.

CONTINGENCY CHI-SQUARE TEST OF H0 VS H1

<table>
<thead>
<tr>
<th>2 x 2 CONTINGENCY TABLE</th>
<th>CORRESPONDING CHI-SQUARE STATISTIC WITH 1 DEGREE OF FREEDOM</th>
</tr>
</thead>
<tbody>
<tr>
<td>R(i,1) N(i)-R(i,1) Q(i,1) M(i1)-Q(i,1)</td>
<td></td>
</tr>
<tr>
<td>I=1 89 489 398 1488</td>
<td>9.080</td>
</tr>
<tr>
<td>I=2 147 577 741 3856</td>
<td>7.878</td>
</tr>
<tr>
<td>I=3 405 2234 713 3919</td>
<td>0.003</td>
</tr>
<tr>
<td>I=4 315 1730 147 1204</td>
<td>14.158</td>
</tr>
</tbody>
</table>

TOTAL CHI-SQUARE WITH 8 DEGREES OF FREEDOM = 127.120

CONTINGENCY CHI-SQUARE TEST OF H1 VS H2

<table>
<thead>
<tr>
<th>2 x 2 CONTINGENCY TABLE</th>
<th>CORRESPONDING CHI-SQUARE STATISTIC WITH 1 DEGREE OF FREEDOM</th>
</tr>
</thead>
<tbody>
<tr>
<td>I=2 51 96 105 124</td>
<td>4.591</td>
</tr>
<tr>
<td>I=3 185 220 263 297</td>
<td>0.156</td>
</tr>
<tr>
<td>I=4 125 190 309 480</td>
<td>0.025</td>
</tr>
</tbody>
</table>

TOTAL CHI-SQUARE WITH 3 DEGREES OF FREEDOM = 4.773

CONTINGENCY CHI-SQUARE TEST OF H2 VS H3

<table>
<thead>
<tr>
<th>2 x 2 CONTINGENCY TABLE</th>
<th>CORRESPONDING CHI-SQUARE STATISTIC WITH 1 DEGREE OF FREEDOM</th>
</tr>
</thead>
<tbody>
<tr>
<td>I=1 81 95 24 29</td>
<td>0.009</td>
</tr>
<tr>
<td>I=2 167 173 96 124</td>
<td>1.611</td>
</tr>
<tr>
<td>I=3 120 152 189 328</td>
<td>4.276</td>
</tr>
<tr>
<td>I=4 22 30 318 352</td>
<td>0.515</td>
</tr>
</tbody>
</table>

TOTAL CHI-SQUARE WITH 4 DEGREES OF FREEDOM = 6.411
Table 7

MALLARDS BANDED IN SOUTHWESTERN SASKATCHEWAN, 1956 TO 1959.

CHI-SQUARE GOODNESS OF FIT TEST OF THE MODEL UNDER H3

<table>
<thead>
<tr>
<th>CONTINGENCY TABLES</th>
<th>CORRESPONDING CHI-SQUARE STATISTICS AND DEGREES OF FREEDOM</th>
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</tr>
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<tr>
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<td>8, 9, 10, 18, 44,</td>
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<td>4, 3, 5, 5, 12,</td>
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<td>4.04 WITH 8 D.F.</td>
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<tr>
<td>I = 3</td>
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<tr>
<td></td>
<td>19, 13, 17, 29, 62,</td>
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<tr>
<td></td>
<td>3, 12, 12, 26, 57, 63,</td>
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<tr>
<td></td>
<td>9, 7, 11, 13, 38, 46,</td>
</tr>
<tr>
<td></td>
<td>10.60 WITH 10 D.F.</td>
</tr>
<tr>
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<td></td>
</tr>
<tr>
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<td>22, 21, 20, 38, 89,</td>
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<tr>
<td></td>
<td>13, 11, 21, 35, 72,</td>
</tr>
<tr>
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<td>31, 40, 32, 68, 157,</td>
</tr>
<tr>
<td></td>
<td>5.32 WITH 8 D.F.</td>
</tr>
<tr>
<td>I = 5</td>
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<tr>
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<td>2, 4, 5, 19,</td>
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<tr>
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<td>66, 72, 73, 141,</td>
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<td>6.77 WITH 3 D.F.</td>
</tr>
<tr>
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<td>TOTAL CHI-SQUARE 27.32 WITH 29 D.F.</td>
</tr>
</tbody>
</table>

CHI-SQUARE GOODNESS OF FIT TEST OF THE MODEL UNDER H1

| TOTAL CHI-SQUARE 38.51 WITH 36 D.F. |

CHI-SQUARE GOODNESS OF FIT TEST OF THE MODEL UNDER H2

| TOTAL CHI-SQUARE 33.73 WITH 33 D.F. |