A MODIFICATION OF THE SRY MODEL FOR BAND-RETURN DATA, ALLOWING FOR DIFFERENCES IN REPORTING RATES NEAR BANDING SITES*

by

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Summary

The Seber-Robson-Youngs (SRY) model for band-return data from exploited populations, and the experimental situation to which it applies, are described by Seber (1970) and Robson and Youngs (1971) and further discussed by Brownie and Robson (1974). Reasons for suspecting the validity of the assumptions made with respect to reporting rates under this model are discussed, and a new model proposed. Maximum likelihood estimators of population parameters are obtained under the new model, and a test to distinguish between the new model and the SRY model is discussed.

1. Introduction

The Seber-Robson-Youngs (SRY) model for band return data from exploited populations, and the experimental situation to which it applies, are described by Seber (1970) and Robson and Youngs (1971) and further described by Brownie and Robson (1974). The important assumptions of this model are that annual survival, exploitation and reporting rates are year-specific but independent of age or year of release. Use of this model is restricted to data from birds banded as adults only, by the "age-independence" assumption. We now consider a modification of this model which is appropriate for data from adults only, but which takes into account factors affecting reporting rates near banding sites. The model discussed here is analogous to that developed under similar

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considerations for data obtained by combining records of returns from birds banded as adults and as young-of-the-year (see the model under $H_2$, Brownie and Robson (1974)).

The reasons for suspecting the validity of the assumptions made with respect to annual reporting rates under the SRY model are as follows. In many areas reporting rates tend to be lower near banding sites, probably because hunters there are more used to seeing bands and so return them at a lower rate. In other areas where banding sites are close to restricted hunting preserves, reporting rates may be higher because game wardens or other officials tend to actively solicit bands from hunters leaving the grounds. Thus the reporting rate for newly released birds, which are clustered around banding sites may be different from that for birds which have been banded and released in previous years and are more widely dispersed, since they have undergone at least one migration.

Details for the model proposed to allow for this difference in reporting rates now follow.

2. The model under $H_0^*$

Using notation similar to that of Robson and Youngs, we make the following definitions:

\[
N_i = \text{number of banded adults released in year } i, \quad i=1,\ldots,k.
\]

\[
R_{ij} = \text{number of bands returned in year } j \text{ from the batch released in year } i, \quad i=1,\ldots,k, \quad j=i,\ldots,k+s, \quad s \geq 0.
\]

Let \( \{R_{ij}\} \) denote the array of random variables \( R_{ij} \), and let \( R_{i.} \), \( R_{.j} \) be the row and column totals respectively of the array \( \{R_{ij}\} \).
Define \( T_i = R_i \).

\[ T_i = R_i + T_{i-1} - R_{i-1}, \quad i = 2, \ldots, k. \]

As in the SRY model, the \( i^{th} \) year of the experiment is the period (of about one year) between the \( i^{th} \) and \((i+1)^{th}\) bandings, \( i = 1, \ldots, k-1 \), and the year following the \( k^{th} \) banding for \( i = k \). Commonly, records of band returns are kept for several years after the year following the \( k^{th} \) or last banding so that data collection may continue for \((k+s)\) years, \( s > 0 \). Reporting rates and exploitation rates are not separately identifiable, but their product, "the reported exploitation rate", is identifiable for the first \( k \) years. If \( s > 0 \), neither survival rates nor reported exploitation rates are separately identifiable in the last \( s \) years.

Thus, let \( f_i^* = P \) [adult banded and released in year \( i \) is shot and reported in year \( i \)], \( i = 1, \ldots, k \),

\[ f_i = P \] [banded adult alive at start of year \( i \), but released before year \( i \), is shot and reported in year \( i \)], \( i = 2, \ldots, k+s \),

\[ S_i = P \] [banded adult alive at start of year \( i \) survives year \( i \)], \( i = 1, \ldots, k+s-1 \).

In other words, the relevant population parameters for the \( i^{th} \) year of the experiment are:

\( f_i^* \) = reported exploitation rate for adults released in year \( i \),

\( f_i \) = reported exploitation rate for surviving adults released before year \( i \),

\( S_i \) = survival rate.
For convenience we denote the model with this parameterization as the model under $H^*_i$, and refer to the SRY model as the model under $H_0$. Thus

$$E_{H^*_i}(R_{ij}) = \frac{N_i f^*_i}{j}, \quad E_{H_0}(R_{ij}) = \frac{N_i f_i}{j}, \quad i=1, \ldots, k$$

$$E_{H^*_i}(R_{ij}) = E_{H_0}(R_{ij}) = \frac{N_i S_i \cdots S_{j-1} f_j}{j}, \quad i = \begin{cases} i, \ldots, k-1 & \text{if } s = 0 \\ i, \ldots, k & \text{if } s > 0 \end{cases}, \quad j = i+1, \ldots, k+s.$$  

Results concerning identifiability and estimability are slightly different for the two cases $s > 0$ and $s = 0$, and so where necessary formulae are given separately for these two cases.

Assuming banded birds in the population suffer statistically independent fates the likelihood under $H^*_i$ of the array $[R_{ij}]$ is given by

$$P_{H^*_i}([R_{ij}]) = \begin{cases} \prod_{i=1}^{k} \left( R_{ii}^{N_i} \cdots R_{i,k+s}^{N_i-R_i} \right) f_{i-1}^{(1-\rho^*_i)} f_i^{(1-\rho^*_i)} & \text{if } s = 0 \\ \prod_{i=1}^{k} \left( R_{ii}^{N_i} \cdots R_{i,k+s}^{N_i-R_i} \right) f_{i-1}^{(1-\rho^*_i)} f_i^{(1-\rho^*_i)} & \text{if } s > 0 \end{cases}$$

where

$$\rho^*_i = E_{H^*_i} \left[ \frac{R_{ii}}{N_i} \right], \quad i=1, \ldots, k$$

$$= f^*_i + S_i f_{i+1} + S_i S_{i+1} f_{i+2} + \cdots + S_i \cdots S_{k+s-1} f_{k+s}$$

for $i=1, \ldots, k$, if $s > 0$

and for $i=1, \ldots, k-1$, with $\rho^*_k = f^*_k$, if $s = 0$;
\[ \rho_i = f_i^* S_i \rho_{i+1} \]

or

\[ \rho_i = f_i^* + S_i \rho_{i+1} \]

\[ i = \begin{cases} 1, \ldots, k & \text{if } s > 0 \\ 1, \ldots, k-1 & \text{if } s = 0 \end{cases} \]

where

\[ \rho_i = f_i + S_i f_{i+1} + \cdots + S_{i+k-1} f_{k+s-1} + f_{k+s} \]

\[ i = 1, \ldots, k+s-1 \]

\[ i = k+s \]

A minimal sufficient statistic is easily obtained from the likelihood as

\[ \Theta = \begin{cases} (R_1, \ldots, R_k, R_{k+1}, \ldots, R_{k+s}) & \text{if } s > 0 \\ (R_1, \ldots, R_k, R_{k+1}, \ldots, R_{k+s-1}) & \text{if } s = 0 \end{cases} \]

**Maximum likelihood estimators**

Maximum likelihood estimators, obtained directly from the distribution of \( \Theta^* \), are:

\[ \hat{\rho}_i = \frac{R_i}{N_i} \]

\[ \left( \frac{f_i^*/\rho_i}{\rho_i} \right) = \frac{R_1 - R_{i+1}}{T_i - R_i} \]

\[ \left( \frac{f_{i+1}/\rho_{i+1}}{\rho_{i+1}} \right) = \frac{R_{i+1}}{s} \sum_{j=i} R_{k+j} \]

\[ i = 1, \ldots, k \]

\[ i = 2, \ldots, k \]

\[ i = 1, \ldots, s \text{ if } s > 0 \]

or

\[ \hat{\rho}_i = \frac{R_{i+1}}{N_i} \]

\[ \hat{\rho}_i = \frac{R_1 - R_{i+1}}{T_i - R_i} \]

\[ \hat{\rho}_i = \frac{R_1 - R_{i+1}}{T_i - R_i} \]

\[ i = 2, \ldots, k-1 \text{ if } s = 0 \]

\[ i = 2, \ldots, k \text{ if } s > 0 \]

\[ \hat{\rho}_i = \frac{N_{i+1}}{R_{i+1} - R_{i+1,i+1}} \left( 1 - \frac{R_{i+1} - R_{i+1,i+1}}{T_{i+1} - R_{i+1}} \right) \]

\[ i = 1, \ldots, k-2 \text{ if } s = 0 \]

\[ i = 1, \ldots, k-1 \text{ if } s > 0 \]
and
\[
\begin{aligned}
S_{k-1} f_{k} &= \frac{R_{k-1} - R_{k-1, k-1}}{N_{k-1}}, \\
S_{1} \cdots S_{k-1} f_{k+1} &= \frac{R_{k} - R_{k,k}}{N_{k}} \frac{R_{k+1}}{s} \sum_{j=1}^{s} R_{k+j}, \\
&\text{if } s = 0, \\
&i=1,\ldots,s, \text{ if } s > 0.
\end{aligned}
\]

Variance and covariance of maximum likelihood estimators

Exact variances of the estimators $\hat{\pi}_{i}$ are
\[
\text{Var}(\hat{\pi}_{i}) = E(1_{i} - \hat{\pi}_{i})^2 / N_{i}, \quad i=1,\ldots,k,
\]
and if $s = 0$,
\[
\text{Var}(\hat{S}_{k-1} f_{k}) = S_{k-1} f_{k} (1 - S_{k-1} f_{k}) / N_{k-1}.
\]

Asymptotic variances of the other estimators are:
\[
\text{Var}(\hat{\pi}_{i}) = E(1_{i} - \hat{\pi}_{i})^2 \sum_{j=1}^{s} \frac{1}{N_{j}} + E(1_{i} - \hat{\pi}_{i}) \sum_{j=1}^{s} \frac{1}{N_{j} + 1},
\]
i = \begin{cases} 2,\ldots,k-1, \text{ if } s = 0 \\ 2,\ldots,k, \text{ if } s > 0 \end{cases}
\]

\[
\text{Var}(\hat{S}_{i}) = S_{1}^2 \left[ \frac{1}{E(R_{1} - R_{i1})} - \frac{1}{N_{1}} + \frac{1}{E(T_{1} - R_{i1} + R_{i1})} \right]
\]
i = \begin{cases} 1,\ldots,k-2, \text{ if } s = 0 \\ 1,\ldots,k-1, \text{ if } s > 0 \end{cases}
\]

and if $s > 0$,
\[
\text{Var}(\hat{S}_{k} \cdots \hat{S}_{k+i-1} f_{k+1}) = (\hat{S}_{k} \cdots \hat{S}_{k+i-1} f_{k+1})^2 \left[ \frac{1}{E(R_{k} - R_{k,k})} - \frac{1}{N_{k}} \\
+ \frac{1}{E(R_{k+1})} - \frac{1}{E(\sum_{j=1}^{s} R_{k+j})} \right], \quad i=1,\ldots,s.
\]
Non-zero asymptotic covariances are:

\[ \text{Cov}(\hat{r}_{i_1}, \hat{r}_{i_1}) = -r_{i_1} f_{i_1} / N_i \]

\[ \text{Cov}(\hat{r}_{i_1}, \hat{s}_{i_1}) = -r_{i_1} \hat{s}_{i_1} / N_i \]

\[ \text{Cov}(\hat{r}_{i_1+1}, \hat{s}_{i_1}) = -s_i f_{i_1+1} / N_i \]

\[ \text{Cov}(\hat{r}_{i_1+1}, \hat{s}_{i_1}) = \hat{f}_{i_1} s_i / N_{i+1} \]

\[ \text{Cov}(\hat{s}_{i_1}, \hat{s}_{i_1+1}) = -s_i s_{i_1+1} \text{ for } i = \{2, \ldots, k-1\} \text{ if } s = 0 \]

\[ \text{Cov}(\hat{s}_{i_1}, \hat{s}_{i_1+1}) = s_i s_{i_1+1} \text{ for } i = \{2, \ldots, k-2\} \text{ if } s > 0 \]

where expectations are with respect to \( H^* \).

These variances and covariances are estimated by replacing parameter values with estimates, and expectations with observed values, in the above formulae.

3. Conditional tests

We note that the parameterization in terms of \( \hat{r}_{i_1}, \hat{f}_{i_1}, \hat{s}_{i_1} \) under \( H^*_0 \) is not the only parameterization which yields a model with minimal sufficient statistic \( \omega^*_0 \). For example, a parameterization in terms of \( \hat{r}_{i_1}, \hat{f}_{i_1}, \hat{s}_{i_1}, \hat{s}_{i_1+1} \) defined by \( \text{E}(\frac{R_{i_1}}{N_i}) = \hat{f}_{i_1} + \hat{s}_{i_1} \hat{f}_{i_1+1} \) also yields a model for which \( \omega^*_0 \) is minimal sufficient. So, too, does the parameterization given by \( \text{E}(\frac{R_{i_1}}{N_i}) = \hat{f}_{i_1} + \hat{s}_{i_1} \hat{f}_{i_1+1} \).

Similar situations are discussed in Brownie and Robson (1974) in relation to the models developed there; and as pointed out there, the alternative parameterizations cannot be ignored since considerable use is made of the minimal sufficient statistics in the construction of tests. However, it was decided...
that the alternative parameterizations could be ruled out on biological grounds since no meaningful interpretation could be found for them. The present situation is not as simple, because more than one interpretation can be found for the alternative parameterization given by 

\[ E \left( \frac{R_1}{N_1} \right) = f^*_i + S^*_i \rho_{i+1}, \]

\( i = \begin{cases} 1, \ldots, k-1 & \text{if } s = 0 \\ 1, \ldots, k & \text{if } s > 0 \end{cases} \)

In fact, Robson and Youngs (1971) suggested the model with this parameterization as an alternative to the SRY model, to take into account an effect due to tagging on the recapture and survival rates of fish in the year immediately following tagging. There seems to be good reason to suspect an effect due to tagging on survival in fish, but a similar effect due to banding on the survival rate of birds seems far less likely.

A second way this parameterization could arise is if it is assumed that survival and recovery rates are age-dependent for the first two years of life. This is one of the assumptions of the hypothesis \( H_3 \) in Brownie and Robson (1974), and tests of this assumption have been developed and carried out on numerous data sets. So far, there is little evidence from the results of these tests to substantiate this assumption.

A third, and more probable way in which this parameterization could arise is if birds are mis-aged, so that each batch of "adults" banded and released actually contains a mixture of young and adults in unknown proportions. This could be a commonly occurring problem in some species.

Thus, provided there is no mis-aging of birds, the parameterization of \( H^*_0 \) seems more likely to apply to data from adult birds than the alternative one considered above. Tests based on \( \hat{\omega}_0^* \) are therefore constructed below and the use of these tests on data from banded adult birds is recommended provided some caution is exercised in interpreting the results. If the data in question are
from tagged fish then the alternative Robson-Youngs parameterization seems more appropriate than that of $H_0^*$, and the results of tests based on $\omega^*_0$ should be interpreted accordingly.

**Conditional goodness-of-fit-test of the model under $H_0^*$**

Using the method described in Robson and Youngs (1971), and Brownie and Robson (1974), a conditional goodness-of-fit-test of the model under $H_0^*$ is obtained from the residual distribution given by $P_{H_0^*}([R_{ij}]|\omega^*_0)$ as follows.

Define

$$R^*_{ij} = R_{lj}, \quad j = 1, \ldots, k+s$$

$$R^*_{ij} = R_{lj} + R_{2j} + \cdots + R_{ij}, \quad j = i, \ldots, k+s$$

Then

$$P_{H_0^*}([R_{ij}]|\omega^*_0) = \prod_{i=2}^{\min(k,k+s-2)} \frac{R_{i-1, i+1} \cdots R_{i, k+s}}{(R_{i, i+1} \cdots R_{i, k+s})} \frac{T_{1-R_{i-1}} \cdots T_{1-R_{i-1, k+s}}}{(R_{1, i+1} \cdots R_{1, k+s})}$$

Corresponding to each multihypergeometric term in the above product is a contingency table from which the usual chi-square statistic can be obtained. These chi-square statistics are asymptotically independent under $H_0^*$ and may be added to give a single chi-square statistic on which the goodness-of-fit-test is based. Thus the table

<table>
<thead>
<tr>
<th>$R^*_{i-1, i+1}$</th>
<th>$R^*_{i-1, i+2}$</th>
<th>$R^*_{i-1, k+s}$</th>
<th>$T_{1-R_{i-1}}$</th>
<th>$T_{1-R_{i-1} + R_{ii}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{i, i+1}$</td>
<td>$R_{i, i+2}$</td>
<td>$R_{i, k+s}$</td>
<td>$R_{i-1, i}$</td>
<td>$R_{i-1}$</td>
</tr>
</tbody>
</table>
yields a chi-square statistic on \((k+s-3)(k+s-2)/2\) degrees of freedom.

Let \(H_{0}^{**}\) represent the Robson-Youngs alternative to the SRY model discussed above. We emphasize that the goodness-of-fit test derived above based on
\[ P_{H_{0}^{**}}[R_{ij}|\theta_{0}] = P_{H_{0}^{**}}[R_{ij}|\theta_{0}] \]

The conjecture in section 8.2 of Brownie and Robson (1974) would imply that this conditional test is asymptotically equivalent to the more conventional goodness-of-fit test based on the statistic
\[ \sum_{i=1}^{k} \sum_{j=1}^{k+s} \frac{[R_{ij} - E_{H_{0}^{**}}(R_{ij})]^2}{E_{H_{0}^{**}}(R_{ij})} \]

To avoid confusion we note that this statistic also does not distinguish between the alternative parameterizations of \(H_{0}^{**}\), \(H_{0}^{**}\) since
\[ E_{H_{0}^{**}}(R_{ij}) = E_{H_{0}^{**}}(R_{ij}) \]

\(E_{H_{0}^{**}}(R_{ij})\) is to be interpreted as the maximum likelihood estimator under the model \(H_{0}^{**}\) of the parameter denoted by \(E_{H_{0}^{**}}(R_{ij})\), and similarly for \(H_{0}^{**}\).

A test to distinguish between the SRY model and \(H_{0}^{**}\)

A test of \(H_{0}^{**}\) vs \(H_{0}^{**}\) (i.e., a test of the SRY model vs the model under \(H_{0}^{**}\)), is constructed in an analogous manner using the conditional distribution given by \(P_{H_{0}^{**}}[\theta_{0}|\theta_{0}]\).
Thus

$$\Pr_0[\omega|\omega_0] = \prod_{i=2}^{\min(k+s-1,k)} \frac{R_{ii}}{R_i} \left( \frac{T_i - R_{ii}}{R_i - R_{ii}} \right)$$

with corresponding contingency tables

<table>
<thead>
<tr>
<th></th>
<th>$R_{ii}$</th>
<th>$R_{i} - R_{ii}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{i} - R_{ii}$</td>
<td>$T_i - R_{i} - R_{ii} + R_{ii}$</td>
<td>$T_i - R_{i}$</td>
</tr>
<tr>
<td>$R_{i}$</td>
<td>$T_i$</td>
<td></td>
</tr>
</tbody>
</table>

each yielding a single degree of freedom chi-square statistic. Summing these individual chi-squares gives a test statistic with degrees of freedom = $\begin{cases} \frac{k-2}{s=0} & \frac{k-1}{s>0} \end{cases}$

Again we emphasize that the results of this test which is in fact a test of $H_0$ vs $(H^*_0$ and/or $H^{**}_0$), must be interpreted with care, unless one of the alternatives $H^*_0$, $H^{**}_0$ can be ruled out on biological grounds.

The above test was proposed by Robson and Youngs (1971) as a test against their model $H^{**}_0$. They show how the contingency tables required for testing $H_0$ vs $H^*_0 \cup H^{**}_0$ and goodness-of-fit to $H^*_0 \cup H^{**}_0$ can be obtained by partitioning the contingency tables for the analogous goodness-of-fit test to $H_0$. We repeat their observation here because it can be used to simplify computations. Specifically, the tables

<table>
<thead>
<tr>
<th></th>
<th>$R_{i} - R_{ii}$</th>
<th>$T_i - R_{i} - R_{ii} + R_{ii}$</th>
<th>$T_i - R_{i}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{ii}$</td>
<td>$R_{i} - R_{ii}$</td>
<td>$R_{i}$</td>
<td>$- \chi^2_1$,</td>
</tr>
<tr>
<td>$R_{i}$</td>
<td>$T_i - R_{i}$</td>
<td>$T_i$</td>
<td></td>
</tr>
</tbody>
</table>
are obtained by partitioning the table

\[
\begin{array}{c|c|c}
R_{i-1,i+1} & \cdots & R_{i-1,k+s} \\
R_{i,i+1} & \cdots & R_{i,k+s} \\
T_i - R_i & & T_i - R_i \\
\end{array}
\]

\[\chi^2_{k+s-1} \rightarrow \chi^2_{k+s-1}, \text{ a component in the goodness-of-fit test to } H_0.\]

One-sided tests about \(r_i^*, f_i\)

When the alternative is known to be \(H_0^*\) and not \(H_0^{**}\), the test based on

\[P_{H_0}[f_i^* | f_i] \provides a test of \(f_i^* = f_i, i = \{2, \ldots, k-1\} \text{ if } s = 0\]

against the \(2, \ldots, k \text{ if } s > 0\)

"two-sided" alternative \(r_i^* \neq f_i, i = \{2, \ldots, k-1 \text{ if } s = 0\}

\(2, \ldots, k \text{ if } s > 0\).

However, in a given experimental situation it may be desired to make one-sided tests about the \(r_i^*\) and \(f_i\). For example, if it is believed that reporting rates are lower near banding sites for reasons described in the introduction, then the alternative of interest is \(r_i^* < f_i, i = \{2, \ldots, k-1 \text{ if } s = 0\}

\(2, \ldots, k \text{ if } s > 0\). For a given \(i\), the corresponding one-sided test is based on the statistic

\[Z_i = \left(\frac{R_{ii}}{R_i} - \frac{R_{i.}}{T_i}\right) \sqrt{\frac{R_i(T_i - R_i)(T_i - R_i)}{R_{i.}^2(T_i - 1)}}\]

which is approximately distributed as a standard normal variable. These statistics are asymptotically independent under \(H_0\) and may be combined to give a single size \(\alpha\) test of \(H_0\) against \(r_i^* < f_i, i = \{2, \ldots, k-1 \text{ if } s = 0\}

\(2, \ldots, k \text{ if } s > 0\), based on the statistic
\[
Z = \frac{1}{\sqrt{\min(k+s-2,k-l)}} \sum_{i=2}^{\min(k+s-1,k)} Z_i,
\]

the critical region being \( Z < z_\alpha \), where \( z_\alpha \) is the \( \alpha \) per cent point of the standard normal distribution. Similarly, the critical region for the size \( \alpha \) test of \( H_0 \) vs \( f_i^* > f_i \), \( i = 2, \ldots, k-1 \) if \( s = 0 \) would be given by \( Z > z_{1-\alpha} \).

References

