Estimation of age-specific probabilities of first return and annual survival rates for the male Grey Seal (*Halichoerus grypus*) on Sable Island from capture-recapture data

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ABSTRACT

We used a longitudinal capture-recapture study to estimate the age-specific probabilities of first return to the breeding colony and annual survival rates for male grey seals (*Halichoerus grypus*) based on resightings of seals branded as young on Sable Island. We estimated that the average age of first returns for seals born in 1969-1970 to be 9.1 (se 0.4) years; for seals born in 1973-1974 it is estimated to be 9.8 (se 0.2) years. The estimated annual survival rate of these males was estimated to be 0.976 (se 0.003).

Keywords: breeding rates; capture-recapture; mark-recapture; mark-resight; Jolly-Seber; local recruitment; return rates.
Grey seals (*Halichoerus grypus*), like many large vertebrates, do not commence breeding simultaneously, but rather a proportion of the population starts to breed each year over a number of years. We estimated the probability of first return to the breeding colony at a specific age based on resightings of previously branded pups.

‘First return’ must be carefully defined for male grey seals. Although males reach sexual maturity as young as 4 years old (Hewer, 1961; Mansfield, 1978), they are not able to copulate with females until they are large enough to attain social dominance on the breeding ground. Subordinate males (i.e. younger or non-aggressive individuals) are relegated to the periphery of the breeding areas. This usually means on the beach or the water’s edge. Occasionally, they enter deeper into the breeding colony and are successful in copulating with a receptive female, but are quickly relegated to peripheral locations. For the most part, these subordinate males lie near the water facing inshore and flee into the water at the approach of the observers. As such, the age of ‘first return’ is defined as the age when a male is sufficiently mature to be readily visible on the breeding colony. This may be closely related to the age of first breeding, but there are few data to confirm this. Nevertheless, the age of first return does provide some information about the ontogeny of breeding behaviour in males.

Also, the probability of first return at a specified age is not the same as the probability that a seal of a specific age will return unless survival rates are 100%. For example, consider the very simplified hypothetical cohort in Table 1. The proportion of
animals that return for the first time at age 5, 6 and 7 are 33\%=30.0/90.7, 44\%=40.0/90.7, and 23\%=20.7/90.7 respectively. The proportion of seals aged 5, 6 and 7 that return for the first time are 30\%=30/100, 44\%=40/90, and 26\%=20.7/81 respectively. If the survival rates are 100\%, then a similar table shows that the two ways of computing the percentages are identical. Fortunately in this study, the estimated survival rates were very close to 100\% so that the two views of the population dynamics should be very similar.

Many methods exist to estimate age-specific breeding (or return) probabilities from a longitudinal capture-recapture study of animals marked at birth (Clobert et al., 1994; Schwarz and Arnason, 2000; Schwarz and Stobo, 2000) however, until now none have been applied to male grey seals.

In this paper, we estimated the age-specific probabilities of first return for male grey seals to the Sable Island breeding grounds. The study is analogous to the estimation of female grey seal breeding proportions presented in Schwarz and Stobo (2000).

METHODS

Details of the experimental design and an analogous analysis of female grey seal data are presented in Schwarz and Stobo (2000). In 1969, 1970, 1973, 1974, 1985, 1986, 1987 and 1989 samples of pups born on Sable Island were sexed and branded with unique numbers. In subsequent years up to 1994, surveys were conducted and resighting vectors were created for all seals. Only the data from cohorts branded in 1969, 1970,
1973 and 1974 extended long enough to be used in the study. Summary statistics for the study are shown in Table 2.

The method we used is that proposed by Schwarz and Arnason (2000). In this approach the first instance of resighting on the breeding colony is treated as an initial mark in a Jolly-Seber mark-recapture model (Jolly, 1965; Seber, 1965; Schwarz and Arnason, 1996). The goodness-of-fit tests described by Pollock et al. (1990) were used to assess if the Jolly-Seber model provided an adequate fit to each cohort. The Jolly-Seber model provides estimates of resighting rates, annual survival rates, and ‘recruitment’ to the population. Here the population is defined as the previously branded seals that successfully survive to return to the breeding colony. Yearly ‘recruitment’ is then the number of branded seals that first return to the breeding colony each year. Finally, using the parameterization of Schwarz and Arnason (1996), the numbers of ‘recruits’ is used to estimate the proportion of the population that return for the first time at each age - the age-specific return probabilities.

Some confusion can results in interpreting the age of first return. The surveys were conducted in January of each year, approximately the same time of the year as the pups are born. Hence a seal born in early 1969, returning for the first time in 1977 is very close to age 8 (and depending upon the time of birth) could turn 8 years at the time of the survey. The Jolly-Seber model would refer to such event as occurring between ages 7 and 8, but we refer this even as an aged 8 seal returning for the first time.
Several assumptions were made in addition to those of the Jolly-Seber model:

- all male seals that have not matured enough to enter the breeding colony have a 0 probability of resightings. Just under 5% of all recorded sightings were of seals not physically in the breeding colony. These records were removed prior to the analysis.

- once having returned to the breeding colony, all seals have the same probability of resighting in a given year.

- once a male has returned once to the breeding colony, it returns for the rest of its life. This assumption is valid since our study involved only seals aged 23 and younger.

- all seals have the same probability of survival in a year. We make no assumptions about the survival rates of seals that have not returned to the breeding colony.

- all seals in each cohort who are mature enough to return to the colony have returned by the end of the study. If this assumption is false (e.g., the study is terminated before all seals have matured), then the estimated proportions are conditional upon those that returned as opposed to the entire population.

The parameters of the Jolly-Seber model were estimated using maximum likelihood estimation as described in Schwarz and Arnason (1996) using the computer package POPAN (Arnason, Schwarz and Boyer, 1998). Six models were fit to the data in which probabilities of recapture, survival rates and age-specific return proportions were constrained in various ways, e.g., equal survival over all cohort and years in the study and
equal sighting rates over cohorts. These models were selected after fitting the most
general models where the estimates showed that the survival rates could be equal, that
some of the cohorts may have equal resighting rates, and that the first return probabilities
were similar. These simpler models lead to more precise estimates of the parameters at
the possible expense of an increase in bias in the estimates.

No systematic surveys were conducted on Sable Island in 1979 and 1980. For these
years, and for years when no sightings were observed (e.g. for seals aged 1-4 for the 1973
and 1974 cohorts), the resighting rates were set to zero. The data gap in 1979 and 1980
implies that certain parameters are not separately estimable without further assumptions.
For example, the data gap implies that only the sum of the return probabilities for ages
10, 11 and 12 could be estimated for the 1969 cohort, i.e., the model estimates the
number (or proportion) of new returns in the 1981 sighting year, but can’t distinguish
between those that first returned in 1979, 1980, or 1981. Similarly, the data gap implies
that only the sum of the return probabilities for ages 9, 10 and 11 can be estimated for the
1970 cohort. However, if the age-specific return probabilities are assumed equal for the
1969 and 1970 cohorts, then the one-year age offset between the two cohorts would
enable the age 9 and age 12 return probabilities to be estimated, but only the sum of the
age 10 and 11 return probabilities could be estimated. In models where the annual
survival rate is assumed equal for all years, the same annual survival rate is assumed
during the data gap.
Model selection from those fitted to the data, was done using the Akaike Information Criterion corrected for small sample sizes (AIC-c) (Burnham and Anderson, 1998) where

\[
AIC-c = -2 \log \text{-likelihood} + 2K + 2K(K=1)/(n-K-1)
\]

where \(K\) is the number of parameters estimated in the model and \(n\) is the sample size. The sample size in capture-recapture models is equal to the total number of captures that occur. The AIC-c is a combined measure of goodness-of-fit and model complexity. The model with the smallest AIC-c is preferred. Models with AIC-c within 2 or 3 units of the best fitting model should also be considered as good descriptions of the data. In cases where several competing models all have similar AIC-c values, model averaging methods (Burnham and Anderson, 1998) can be used to combine the estimates from the competing models.

**RESULTS**

The goodness-of-fit tests of Pollock et al (1990) are summarized in Table 2. There was no evidence of lack-of-fit; some of the larger values for the second goodness-of-fit test were caused by 1 or 2 sub-tables (not shown) with very small counts which tended to inflate the test statistic.

The log-likelihood values, number of parameters, and AIC-c values for each model are shown in Table 3. Based on the AIC-c values, the model that best fit the data was the model in which age-specific return proportions were assumed equal for the 1969 and
1970 cohorts and for the 1973 and 1974 cohorts, the recapture rates were equal for the
were equal for all cohorts for all years (Model 6 of Table 3). The next best model based
on AIC-c was more than 10 units higher indicating that this single ‘best’ model was
preferred from the 6 considered and that model averaging (Burnham and Anderson,
1998) is not needed.

The estimated age-specific return proportions, the average age of first return, and
the annual survival estimates from this model are shown in Table 4. The estimated
sighting rates are shown in Fig. 1.

The distribution of first return proportions appears to be quite skewed. The average
age of first return for both sets of cohorts were about 9.3 years. The median ages of first
return was just under 6 years for the 1969/70 cohort, substantially smaller than the
estimated age of first return. The mean and median were similar for the 1973/74 cohorts.
The 95th percentiles for the two pooled cohorts were between 18 and 16 years
respectively. The estimated annual survival rate is 0.976 (SE 0.003).

**DISCUSSION**

Previous estimates of the age at which male grey seals first begin mating range
from 10-12 years (Boness and James, 1979; Mansfield, 1978; and Godsell, 1991). Until
now, however, there has not been enough collection of data on cohorts of known-age seals to estimate breeding proportions using longitudinal methods. Our estimates, the first obtained by a longitudinal capture-recapture study, place the average age of first return to the breeding colony between 9 and 10 years. The age of first return may be an underestimate of the age of first breeding as presence on the breeding colony does not necessarily imply that the seal will successfully compete with other males and mate.

Despite apparent differences in the distribution of the first return rates between the two sets of cohorts, the mean ages of first return appear to be equal. We are hesitant to over interpret the differences in the age distribution as these may be an artifact of the data gap in 1979/1980 which occurred just as the 1973/74 cohorts would be expected to start to return. This may have lead to the large difference in the return rates between the two groups of cohorts at ages 6 – notice that the SE for the 1973/74 cohort for age 6 is quite large indicating that this estimate is very imprecise. The effects of the data gap upon the data analysis may be quite subtle, and could be investigated in more detail using a simulation model.

The estimated precision for some estimates are also problematical. Because a logistic transform was used in the numerical optimization software, standard errors for estimates that are 0 or 1 cannot be reliably computed. The estimates ‘appear’ to have a 0 standard error, but this is an artifact of the estimation process. Unfortunately, there is no readily available way to estimate the true uncertainty in the estimates short of a large-scale simulation study.
One critical assumption upon which the accuracy of our estimates lies is that male seals that do not return to the colony have a 0 probability of resighting. We believe that after removing records of males sighted outside the colony that the remaining number of males observed in the colony but who were not yet mature enough to remain is small.

Heterogeneity in sighting rates is also known to cause bias in the estimates (Pollock et al, 1990). For example, some brands may be more difficult to read than other brands. The yearly sighting events are a ‘composite’ of multiple surveys conducted each year. Consequently, the pooling of sightings over several surveys into a single sighting event for the year reduces heterogeneity in the sighting rates (Pollock et al, 1990).

Another important consideration is that the study area must be surveyed consistently from year to year. If the study area is increased in a given year, seals that have returned in past years, but were not seen will be considered having first returned in that year. This would tend to increase the estimate of average age of first return. This was not a problem with our study, as Sable Island was surveyed each year in its entirety for breeding seals.

Gaps in the sighting records cause by intermittent and reduced survey effort in some years may have lead to a ‘artifactual’ separation between the two groups of cohorts. Unfortunately the study was terminated before enough information could be collected on additional cohorts branded between 1985 and 1987 – these cohorts were just starting to
return to the colony but were not fully ‘recruited’ before the study was terminated. The analysis presented above makes the assumption that all ‘recruitment’ has taken place by the end of the study which would have been severely violated for these later cohorts. These cohorts could have provided more precise estimates of the first return rates, unaffected by the missing study years had the study continued for several more years.

The estimate of the annual survival rate for males is much higher than that found for females (about 90%) found in Schwarz and Stobo (2000). Mansfield and Beck (1977) found that the survivorship curve for males and females were constant and similar (about 90%) up to about age 20, but males subsequently had a higher mortality rate. Harwood and Prime (1978) estimated that the male adult survival of British Grey Seals to be around 80%. Our estimate is substantially higher - but as our model focuses upon males that are sighted on the breeding colony, this may not be surprising. These males may be larger, stronger, and more aggressive than males not sighted in the colony which may be related to a higher subsequent yearly survival.

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References


Table 1: Hypothetical example to illustrate the difference between the first return at a specified age and the probability that a seal of a specified age will return. Refer to text for more details.

<table>
<thead>
<tr>
<th>Year</th>
<th>1973</th>
<th>1974</th>
<th>1975</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Animals alive on 1 January</td>
<td>100</td>
<td>90</td>
<td>81</td>
<td></td>
</tr>
<tr>
<td>Return for the first time</td>
<td>30.0</td>
<td>40.0</td>
<td>20.7</td>
<td>90.7</td>
</tr>
<tr>
<td>Survival rate</td>
<td>90%</td>
<td>90%</td>
<td>90%</td>
<td></td>
</tr>
<tr>
<td>Total Animals alive on 31 December</td>
<td>90.0</td>
<td>81.0</td>
<td>72.9</td>
<td></td>
</tr>
<tr>
<td>Animals alive on 31 December that have not yet returned</td>
<td>63.0</td>
<td>20.7</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>