

The Estimation of Age-specific Breeding Probabilities from Capture-Recapture data

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SUMMARY

We provide a new method to estimate the age-specific breeding probabilities from recaptures or resightings of animals marked as young. Our method is more direct than previous methods, and allows the modeler to fit and compare models where the age specific breeding proportions are equal over different cohorts or are a function of external covariates.

1. Introduction

In many species, animals do not commence breeding simultaneously but rather a certain proportion of the animals start to breed each year over a number of years. Furthermore, it is often the case that animals are essentially uncatchable prior to becoming breeders because they fail to return to breeding areas where observers are located. How then can the age-specific breeding probabilities, i.e. the probability that a specific aged animal will breed for the first time, be estimated?

Clobert et al. (1994) presented a method to estimate these age-specific breeding probabilities from a longitudinal capture-recapture study of animals marked as young. In this study design, successive cohorts of animals are marked as young at a known age.

Key words: capture-recapture; Jolly-Seber; local recruitment; mark-recapture

Prior to age k at which the youngest individual breeds, animals cannot be observed. Once an animal starts to breed, it may be recaptured or resighted. Consequently, a capture-recapture history vector can be recorded for each animal initially marked as young.

The difficulty in fitting a standard Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly, 1965; Seber, 1965) to this data is that the marked animals in a cohort after age k but before all animals have become breeders consists of two subgroups - those who are non-breeders which cannot be observed and those who are breeders which can be recaptured. This heterogeneity in the capture probabilities violates a key assumption of the CJS model that all animals alive have the same probability of recapture at a sampling occasion. Clobert et al. (1994) was forced to introduce a number of capture-parameters representing the overall, average, probability of capture during the progression to full breeding status, and it was the changes in these values that allowed them to estimate the breeding probabilities.

Recently, Pradel (1996) and Pradel et al. (1997) showed that age-specific breeding proportions can be estimated by reading the capture history vectors backwards in time. In his method, the survival rates from the reversed capture histories (what he calls the seniority probabilities) correspond to the probability that an animal alive and in the breeding population in year j was alive and in the breeding population in year $j - 1$. A simple function of these seniority probabilities leads to estimates of the age-specific breeding proportions.

Lebreton, Almeras, and Pradel (in press) and Pradel and Lebreton (in press) also show how a multi-state model could be used to model the movement of birds from non-breeding to breeding status.

In this paper, we demonstrate that age-specific breeding proportions can be estimated directly by fitting a Jolly-Seber model for an open-population with recruitment and death to the capture histories ignoring the first capture of the young animal. Prior parameterizations of the Jolly-Seber model made this difficult because the total recruitment between sampling occasions was modelled, and it was impossible to constrain

these to be non-negative or to simultaneously model several cohorts with common recapture, survival, or recruitment parameters. However, in the parameterization adopted by Schwarz and Arnason (1996), the birth parameters represent new entrants to the breeding population, i.e. they are directly representations of the age-specific breeding proportions. This is a natural parameterization that avoids many of the nasty model fitting complications of Clobert et al. (1994) and lends itself to direct model selection and testing. Furthermore, the Schwarz and Arnason (1996) formulation also naturally leads to multiple-cohort settings. Lastly, we will show that in Pradel's (1996) and Pradel et al.'s (1997) method, the parameters are conditional upon an animal surviving until all animals have become breeders while in our model, parameters are conditional merely upon the animal surviving until it starts to breed. For long-lived animals, the two sets of parameters should be similar - however, for shorter lived animals, they can be considerably different.

We start by outlining the model development and discuss what assumptions must be made to obtain full identifiability of the age-specific breeding proportions. We then analyze a subset of the black-headed gull (*Larus ridibundus*) data of Clobert et al. (1994) and compare our estimates with those previously published.

2. Notation

In this study, there are G cohorts of animals marked as young (for simplicity at age 0). For convenience we assume that animals start to breed at age 1; that no further animals start to breed after age m [If not all animals have become breeders, then the remaining animals in the population are essentially invisible as non-breeders are non-observable. With out loss of generality, assume that all animals have become breeders by age m .] that each capture-occasion is one year apart ; and that observations on breeders start in calendar year 1 - the first year when the first cohort starts to breed. Observations continue until calendar year T with $T \geq m$.

2.1 Parameters

- b_{ij} probability that an animal in cohort i that survives until it starts to breed will start breeding at age $j + 1$.
 $i = 1, \dots, G; j = 0, \dots, m - 1; \sum_{j=0}^{m-1} b_{ij} = 1$.
- ϕ_{ij} probability that an animal in cohort i that is alive and a breeder in year j will be alive in year $j + 1$.
 $i = 1, \dots, G; j = i, \dots, T - 1$.
- ϕ_{i0} probability that an animal in cohort i marked at age 0 will be alive at the first age of breeding. [This parameter is equivalent to the ‘local immature survival probability’ of Clobert et al. (1993).]
 $i = 1, \dots, G$.
- p_{ij} probability that an animal in cohort i that is a breeder in year j will be recaptured in year j . Animals which are not breeders have a 0 probability of being recaptured.
 $i = 1, \dots, G; j = i, \dots, T$.

2.2 Statistics

- n_{i0} number of animals in cohort i marked at age 0
 $i = 1, \dots, G$.
- n_{ij} number of animals in cohort i , marked at age 0, that are recaptured in calendar year j .
 $n_{ij} = m_{ij} + u_{ij}$.
 $i = 1, \dots, G; j = i, \dots, T$.
- m_{ij} number of animals in cohort i , marked at age 0, that are captured in year j and were previously recaptured prior to year j . [Note that this notation differs from another common usage of m_{ij} to represent the animals released at year i and next recovered in year j]
 $i = 1, \dots, G; j = i, \dots, T$.

- u_{ij} number of animals in cohort i , marked at age 0, that are captured in year j and were not previously recaptured prior to year j .
 $i = 1, \dots, G; j = i, \dots, T$.
- R_{ij} number of animals in cohort i , marked at age 0, recaptured in year j and released in year j . R_{ij} may differ from n_{ij} because of losses on capture or injections.
 $i = 1, \dots, G; j = i, \dots, T$.
- r_{ij} number of animals in cohort i , marked at age 0, from R_{ij} that are subsequently recaptured after release.
 $i = 1, \dots, G; j = i, \dots, T$.
- z_{ij} number of animals in cohort i , marked at age 0, recaptured before year j , not recaptured in year j , and recaptured after year j .
 $i = 1, \dots, G; j = i, \dots, T$.

3. Model Development and Fitting

As in Clobert et al. (1994), Pradel (1996), and Pradel et al. (1997) we make the following assumptions in addition to those commonly made in CJS models:

- all non-breeders have a 0 probability of recapture;
- all breeding animals, whether for the first time or not, have the same probability of recapture;
- once an animal has bred for the first time, it remains a breeder until the end of the study. [The models could be extended if a maximum age of breeding was known.]
- all animals, regardless of first time or a repeat breeder, have the same probability of survival in a year. [Note that a more general model could be developed that allowed for age-dependent survival among the cohorts.] We make no assumptions about the survival rate of non-breeders.
- no further animals from each cohort will commence to breed after the end of the study. Otherwise the age-specific estimates will be conditional upon animals breeding before the latest age in the study.

In our method, we use the mark applied at age 0 only to age the animals at subsequent recaptures, treat the first recapture as an initial mark, and treat the second and subsequent recaptures as recaptures after the initial mark. In this way, the population of animals who are breeders is treated as an open population in the Jolly-Seber framework. Animals that commence breeding are treated as new entrants into this population. Schwarz and Arnason (1996) parameterized births in the Jolly-Seber model by the proportion of the total entrants over the course of the study. This now corresponds directly to the age-specific breeding proportions of interest! [Note that in earlier parameterizations of the Jolly-Seber model, the absolute number of new entrants was the parameter - this is of limited interest in this study.] Capture-probabilities in this open model refer only to those animals now part of the population, i.e. only to breeders. There is no longer the heterogeneity caused by a mixture of breeders and non-breeders as found in Clobert et al. (1994). Survival probabilities refer only to breeders - it is not necessary to assume that non-breeders have the same survival rates as breeders as made by Clobert et al. (1994). Figure 1 illustrates the parameters as they would apply in a study with 2 cohorts over a span of 7 years.

The most general model shown in Figure 1 is not very useful as each cohort has its own set of parameters and there is confounding of parameters at the start and end of the study as listed in Schwarz et al. (1993). This implies that the age-specific probabilities are not estimable unless further assumptions are made. For example, in Figure 1, only the products $b_{10}p_{11}$ and $b_{20}p_{22}$ can be estimated which implies that b_{11} and b_{21} cannot be estimated. Also, because only the product $\phi_{16}p_{17}$ and $\phi_{26}p_{27}$ can be estimated, the parameter b_{25} cannot be estimated. [Note that the study in Figure 1 was long enough that b_{16} is known to be zero because all animals were fully recruited to breeders by age 5.]

The easiest way to resolve the confounding of the age-specific breeding probabilities at the end of the study is to ensure that the last capture occasion is sufficiently late so that all cohorts have fully entered breeding status, i.e. ensure that $b_{i,T-i} = 0$ for all cohorts.

Resolving the confounding at the start of the study can be done by assuming that certain parameters are equal across cohorts or by modeling the capture probabilities as functions of covariates.

For example, one may be willing to assume that the p_{ij} are cohort-independent, i.e. that $p_{1j} = p_{2j} = \dots = p_{Gj}$. This would imply that all breeders, regardless of cohort, have the same probability of being recaptured in year j . Referring to Figure 1, if the assumption that $p_{12} = p_{22}$ is acceptable, then b_{20} is now estimable because the capture histories from cohort 1 enable $p_{.2}$ to be estimated. However, b_{10} remains unestimable because there is no way to separately estimate p_{11} .

It is sometimes possible to have a separate cohort of known breeders that were marked prior to the start of the first recaptures of the new breeders. In this case, this additional cohort could be used to estimate the $p_{.j}$ (under the assumption of independence of recapture probabilities among cohorts) and this would fully resolve the confounding of $b_{10}p_{11}$ and $b_{21}p_{22}$.

Alternatively, the p_{ij} could be modeled as functions of covariates (as was done in Clobert et al. (1994)) or possibly it may be tenable to consider models where the p_{ij} are constant over time, i.e., where $p_{ij} = p_i$ for all j .

Once the confounding problem has been resolved, the Jolly-Seber model can be fit using the methods outlined in Schwarz and Arnason (1996) using the computer package POPAN (Arnason, Schwarz, Boyer 1998) based on the usual summary statistics.

Reduced models can also be investigated using likelihood ratio tests or AIC in the usual fashion.

Some of the more interesting sub-models are those where the last age of breeding is successively reduced as suggested by Clobert et al. (1994) and Clobert, Julliard, and McCleery (1993) who also developed a goodness-of-fit test specifically designed to test for the age at which full breeding status is obtained. For example, referring to Figure 1, the sequence of models with $\{b_{15} = 0\}$, $\{b_{14} = b_{15} = 0\}$, $\{b_{13} = b_{14} = b_{15} = 0\}$, etc. would be investigated.

Another interesting set of models is where the age-specific breeding proportions are stationary over time, i.e. $\{b_{1j} = b_{2j} = \dots = b_{Gj}\}$.

Following the model fit, derived parameters such as the average age of initiation of breeding can be easily found and their estimated standard errors can be found using a Taylor series expansion, e.g. $\widehat{average\ age}_i = \sum_{j=1}^m j \times \widehat{b}_{i,j-1}$.

Clobert et al. (1994) were also able to estimate the survival rate from the time of marking up to the age of first breeding (ϕ_{i0}). In our model, without making further assumptions about the survival rate of breeders and non-breeders after the age of first breeding, we can only estimate the probability of ever entering breeding status. Schwarz and Arnason (1996) showed how to estimate the actual number of new entrants in cohort i that entered between sampling times j and $j+1$ and survived to time j (the B_{ij} in their notation). The sum of these would estimate the total number of animals that became breeders in this cohort and then $(\sum B_{ij})/n_{i0}$ will estimate the fraction of animals from those initially marked that became breeders.

If it were reasonable to assume that survival rates of breeders and non-breeders were equal after the age of first breeding (as was made by Clobert et al. ,1994), then it is possible to estimate the survival rate from time of marking to age of first breeding. The \widehat{B}_{ij} must be inflated by the survival rates between the age of first breeding and their entrance to the breeding pool to account for intermediate mortality, giving $\widehat{\phi}_{i0} = \left(\sum_{k=0}^{m-1} \widehat{B}_{ik} / (\widehat{\phi}_{i1} \widehat{\phi}_{i2} \dots \widehat{\phi}_{ik}) \right) / n_{i0}$. Note that it would difficult to constrain the $\widehat{\phi}_{i0}$ to be equal over cohorts as this parameter does not explicitly enter into the modelling process, but a common average value can be estimated by pooling over cohorts.

The variances of both estimators above are found using a Taylor-series expansions.

Pradel (1996), Pradel et al. (1997), and Pradel and Lebreton (1997) used a different method to estimate the age-specific breeding proportions. These are based on *seniority probabilities*, defined as the probability of an animal present just before time j was already present just after time $j - 1$ and, in terms of parameters of a Jolly-Seber model (with the cohort subscript i dropped for convenience): $\gamma_j = \frac{N_{j-1}^+ \phi_{j-1}}{N_j^-}$ where N_j^- and N_j^+ are the number of animals alive in the population just before and just after sample time j .

For years greater than the maximum age of first breeding (m), $\gamma_j = 1$. The age-specific breeding proportions are found as: $b_{j,Pradel} = (1 - \gamma_{j+1})\gamma_{j+2} \dots \gamma_T$. Then, assuming no losses on capture, or injections of new animals, $b_{j,Pradel}$ can be written as: $b_{j,Pradel} = \frac{B_j \phi_{j+1} \phi_{j+2} \dots \phi_{T-1}}{N_T}$ where B_j is the actual number of new animals entering the breeding population. Now, $N_T = B_0 \phi_1 \phi_2 \dots \phi_{T-1} + B_1 \phi_2 \phi_3 \dots \phi_{T-1} + \dots + B_{T-1}$ and assuming that all animals have become breeders by age m implies that $B_{m+1} = \dots = B_{T-1} = 0$ and Pradel's age specific breeding proportions are conditional upon animals surviving until the age at which all animals have become breeders. For long lived animals, his estimates of the age-specific breeding proportions should be very similar to our estimates; however, for short lived animals, his method will tend to overestimate the proportion in the older age classes and underestimate the proportion in the younger age classes which will lead to a positive bias in the estimate of the average age of initiation of breeding. Note that this approach, like ours, conditions upon the set of animals ever seen as breeders and will also 'ignore' the marking occasion at age 0 which is used only to age the animals when recaptured.

4. Example

Clobert et al. (1994) describe a study of black-headed gulls (*Larus ridibundus*) in the Forez basin (Loire, France). Each spring from 1976 onwards, extensive number of chicks were marked in a large colony. Resightings of birds were made by screening accessible parts of the colony with a floating blind with an unequal number of visits in the various years (their Table 4).

In their analysis of the data, they selected a model where variations in capture-probabilities were satisfactorily explained as a linear function of the number of visits in each year, breeding commenced at age 2 and was completed by age 5, and survival was neither time nor cohort dependent.

We reanalyzed the first three years of their data to illustrate our method. The summary statistics are shown in Table 1. [These differ slightly from the data presented in Clobert et al., 1994, because of some minor corrections made during the data extraction.]

As in Clobert et al. (1994), we first fit a model where the capture probabilities were linear functions of the number of visits made to the colony, survival rates were constant over time, but allowed for different age specific breeding proportions among the cohorts. The estimates and estimated standard errors are shown in Table 2. Estimates of the survival rate and capture-probabilities (not shown) are similar to those of Clobert et al. (1994).

The estimate of the age specific breeding proportions are similar to those presented in Table 11 of Clobert et al. (1994) but now the estimated standard errors are readily available and the negative estimates in their table cannot occur. Precision is relatively poor, but the data are very sparse so this is not surprising.

We then fit a model where the age-specific breeding proportions were assumed to be constant over cohorts - results are also shown in Table 2. The simpler model could not be rejected relative to the previous model ($X^2 = 4.2$, 6 df, $p = .65$).

For both models, the average age of initiation of breeding and its estimated standard error was also readily computed and is shown in Table 2.

Estimates of the survival rate from the time of marking to the first age of breeding were also computed using n_{i0} of 1,275, 696, and 1,090 as reported in Table 3 of Clobert et al. (1994). Our estimates are comparable to the estimate in Clobert et al. (1994) [their 'local immature survival probability'].

Finally, we also estimated the age-specific breeding proportions using the method of Pradel et al. (1997) based upon the final model with constant breeding proportions among cohorts as shown in Table 2. In this case, the age specific breeding proportions are conditional upon the birds living to age 5 and hence overestimate the proportion in older age classes and underestimate the proportion in younger age classes leading to a positive bias in the estimate of the average age of initiation of breeding.

5. Discussion

Our proposed method has a number of advantages over that used by Clobert et al. (1994):

- Estimates of age-specific breeding proportions are a fundamental parameter of the model and are easily estimated using the methodology of Schwarz and Arnason (1996).
- It is easy to constrain the estimates to be within the admissible range of 0-1 and to model them as functions of covariates.
- It is straight forward to examine models where the breeding proportions are equal among cohorts.
- The confounding among the breeding proportions, capture probabilities, and survival rates at the beginning and end of the study are now readily apparent and the modeler is aware of the need to estimate some of the confounded parameters to ‘free up’ the estimates of the breeding proportions. Suggestions for alleviating this confounding were made earlier.

Our proposed method also has a number of advantages over that proposed by Pradel (1996) and Pradel et al. (1997):

- It is easy to constrain the breeding proportions to be within the admissible range of 0-1 and to model them as functions of covariates. In Pradel’s method, the estimates are found indirectly and cannot be constrained or modeled directly.

- Our estimates are not conditional upon animals being alive until the age when all have become breeders, but rather estimate the age-specific proportion conditional upon an animal breeding, even if the animal subsequently dies before the end of the study.
- Our method uses the capture histories directly - it is not necessary to analyze them ‘backwards’ in time as is done in Pradel et al. (1997).

Pradel’s method does have the advantage that if the study is designed so that all animals have entered breeding status by the end of the study (so that there is no confounding at the end of the study), it is still possible to estimate the age-specific breeding proportions for all but the first two age classes (where only their sum can be estimated) even if the confounding is not resolved at the start of the study.

Lastly, in all studies of this type, there are several issues that must be carefully considered during the design phase. First, the study must be long enough that all animals in at least one cohort enter breeding status before the end of the study. Otherwise, the estimates of the age specific breeding proportions will be conditional upon entering breeding status by the end of the study. Second, if the geographic area searched for breeders changes over time, and if breeders do not randomly locate themselves in the search area, then the estimates of the breeding proportions may be confounded with changes in the search area. [If animals randomly locate themselves in the search area, then changes in the search area will be reflected in changes in the capture-probabilities among occasions.] Third, because these estimates are directly related to estimates of ‘births’ in the ordinary Jolly-Seber method, all of the problems associated with heterogeneity in capture probabilities and bias in the estimate of ‘births’ will also be important here.

ACKNOWLEDGEMENTS

This work was supported by Natural Science and Engineering Research Council of Canada (NSERC) Research Grants. Funding for the development of POPAN was provided by Manitoba Hydro. The raw data for this study was extracted by Mr. Vladimir Grosbois and supplied by Dr. Jean-Dominique Lebreton of CEFÉ-CNRS.

RÉSUMÉ

To be added by editor.

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Figure 1*Relationship of parameters to sampling occasions*

Cohort	Year						
	1	2	3	4	5	6	7
1	$\xrightarrow{b_{10}}$	$\xrightarrow{b_{11}}$	$\xrightarrow{b_{12}}$	$\xrightarrow{b_{13}}$	$\xrightarrow{b_{14}}$	$\xrightarrow{b_{15}}$	$\xrightarrow{0}$
		$\xleftarrow{\phi_{11}}$	$\xleftarrow{\phi_{12}}$	$\xleftarrow{\phi_{13}}$	$\xleftarrow{\phi_{14}}$	$\xleftarrow{\phi_{15}}$	$\xleftarrow{\phi_{16}}$
	p_{11}	p_{12}	p_{13}	p_{14}	p_{15}	p_{16}	p_{17}
2		$\xrightarrow{b_{20}}$	$\xrightarrow{b_{21}}$	$\xrightarrow{b_{22}}$	$\xrightarrow{b_{23}}$	$\xrightarrow{b_{24}}$	$\xrightarrow{b_{25}}$
			$\xleftarrow{\phi_{22}}$	$\xleftarrow{\phi_{23}}$	$\xleftarrow{\phi_{24}}$	$\xleftarrow{\phi_{25}}$	$\xleftarrow{\phi_{26}}$
		p_{22}	p_{23}	p_{24}	p_{25}	p_{26}	p_{27}

This is a two cohort study with a large number of animals originally marked when young. Animals in cohort 1 start to breed at age 1; those from cohort 2 also start to breed at age 1 which is in calendar year 2. Animals are fully recruited to breeding status by age 6. The parameters b_{ij} measure the age-specific breeding proportion for cohort i at age $j + 1$. The parameters p_{ij} are the year specific capture probabilities for cohort i in year j . The parameters ϕ_{ij} are the probability of survival from year j to year $j + 1$ for animals in cohort i .

Table 1

*Summary statistics for three years of data of black-headed
gulls *Larus ridibundus* from Clobert et al. (1994)*

<i>Year</i> (<i>j</i>)	n_{ij}	m_{ij}	R_{ij}	r_{ij}	z_{ij}
Banded as young in 1976 (cohort $i=1$)					
78	2	0	2	0	0
79	3	0	3	0	0
80	4	0	4	1	0
81	7	0	7	3	1
82	5	2	5	2	2
83	4	1	4	1	3
84	4	2	4	2	2
85	8	4	8	0	0
Banded as young in 1977 (cohort $i=2$)					
78	0	0	0	0	0
79	0	0	0	0	0
80	5	0	5	3	0
81	8	2	8	5	1
82	7	4	7	2	2
83	5	1	5	1	3
84	4	1	4	1	3
85	6	4	6	0	0
Banded as young in 1978 (cohort $i=3$)					
78	0	0	0	0	0
79	0	0	0	0	0
80	5	0	5	1	0
81	8	1	8	1	0
82	3	1	3	0	0
83	6	0	6	1	0
84	8	1	8	0	0
85	3	0	3	0	0

Table 2

Estimates of age-specific breeding proportions from fitting two models with capture-probabilities a linear function of the number of visits of Table 4 of Clobert et al. (1994), breeding restricted to ages 2-5, and survival is constant over time and among cohorts.

Age	Each cohort allowed its own breeding proportions						Common breeding proportions for all cohorts		Common breeding proportions using Pradel's γ	
	Chort 1		Chort 2		Chort 3		<i>Est</i>	<i>se</i>	<i>Est</i>	<i>se</i>
2	.240	.169	.000	-	.401	.181	.299	.124	.214	.113
3	.339	.219	.553	.249	.214	.201	.356	.173	.316	.165
4	.000	-	.293	.314	.000	-	.001	.161	.001	.177
5	.422	.179	.155	.269	.385	.151	.344	.120	.470	.162
Average	3.604	.426	3.602	.413	3.370	.393	3.390	.296	3.727	.378
$\hat{\phi}^a$.808	.064	.808	.064	.808	.064	.806	.064	.806	.064
$\hat{\phi}_0^b$.076	.024	.109	.035	.094	.027	.091	.024		
log-likelihood			-185.1				-187.2			

^a Survival probability for breeders

^b Survival probability from the time of marking at age 0 to the first age of breeding.

^c Standard errors are not available when estimates of age-specific breeding proportions fall on the boundary of the parameter space - refer to Schwarz and Arnason (1996) for details.