ESTIMATION OF SURVIVAL RATES FROM A JOLLY-SEBER MODEL WITH TAG LOSS

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ABSTRACT

A stochastic model is described for a tag-recapture study based upon multiple sightings of non-permanent collars and multiple captures and identification by permanent bands. Survival, capture, and sighting probabilities are assumed to depend on year. Collar retention probabilities are assumed to depend on the age of the collar. Maximum likelihood estimates for the model do not exist in closed form but can be obtained by the EM algorithm. Estimates are compared with corresponding estimates from alternate models based upon conditioning arguments or partial data.

1. INTRODUCTION

In the field of biology the problem of estimation of population sizes and survival rates is of frequent interest for which there are many different approaches (Seber,1982). One model which has gained in favor is the Jolly-Seber model of Jolly (1965) and Seber (1965), for which the capture, tagging, and release of animals is followed by the possible reobservation of animals. Jolly and Seber derscribed reobservations as recaptures but in practice reobservations may be by sighting or other types of observation. Similarly, more than one type of reobservation can be included though until recently (Mardekian and McDonald,1981;Brownie and Robson,1983) there has been little done to combine different types of reobservation in a single model.

Another shortcoming of the present theory is that tags are assumed to be permanent though in reality tags may be lost. Animals often fight with tags until habituated to the presence of tags. Similarly tags age and may be more likely lost after a critical age. Arnason and Mills (1981) recognize and describe the effects of tag-loss where tag-loss is allowed to depend on year but not on the age of the tag. Nelson *et.al.* (1980) describe the effects of tag-loss where tag loss is allowed to depend on age of the tag. Nelson *et.al.* found when only adult animals are tagged, survival estimates or coverage probabilities of confidence intervals were not severely affected. For populations with separate survival rates for different age classes, tag-loss had a greater effect on estimation. Their results, however, apply only if tag loss and survival rates, which are unknown to the investigator, are small.

In practice, biological interest may center on not only survival rates for the single years, but also the probability of an animal surviving a sequence of years. Therefore, even if the probabilities of survival for the individual years are biased only slightly by tag loss, the estimation of the probability of an animal surviving a sequence of years may be severely biased, suggesting false qualitative as well as quantitative conclusions to the biologist. Hence, tag loss cannot be discounted as unimportant and its effects should be included in the estimation of survival rates or other population parameters.

With the objective of estimating survival rates in the presence of tag loss we obtain the likelihood for a model based upon two types of observations and two types of tags. The first type of observation, "capture", is based on the identification of animals by permanent tags, or "bands", as in the Jolly-Seber model. The second type of observation, "resighting", is based on an original capture followed by the identification of animals by non-peranent tags, or "collars". Special cases of this model include the Jolly-Seber model with one type of tag, which can be assumed to be either permanent or subject to loss.

Closed form Maximum Likelihood Estimates (MLEs) do not exist for the parameters of the model proposed here, but MLEs can be obtained by use of the EM algorithm (Dempster *et.al.*,1977). If reobservations are restricted to sightings, we find that even though survival rates are not identifiable, changes in survival rates between years are estimable (without any double tagging). Variances and covariances of the MLEs can be estimated from an estimate of the information matrix.

Estimates from this modified Jolly-Seber model are compared with corresponding estimates based on the hypergeometric model (Robson,1969; Pollock,1981) and the multinomial model (Seber,1970;Robson,and Youngs,1971; Brownie *et.al.*,1978).

2. TAG LOSS

Nelson, *et.al.* (1980) assume tag-loss probabilities to depend on age of the tag but not time period. Arnason and Mills (1981) assume tag-loss to depend on time but make clear that their approach does not account for dependence of tag-loss on age, thus recognizing the likely dependence of tag-loss rates on age. For example, tags may be applied incorrectly and thus be lost shortly after the release of an animal, or tags may become brittle and more easily lost after a certain age. To assume tag-loss is dependent on age of the tag and not time period we must ensure that time periods between observations are nearly constant throughout the sampling.

To minimize the effect of time period on tag loss the investigator can ensure that time periods between samples are of the same length and that the conditions the animals face are similar between the different sampling periods. For most animals, this is reasonable if samples are taken once a year, as animals should encounter similar environmental conditions and should exhibit similar behaviors such as annual migration and establishment of territories, which could effect the retention and loss of the tags. Therefore, in our model we will allow collar-loss to depend on age of the collar but not time period.

If we were to capture an animal which had lost its tag we would have the option of retagging the animal. Should we place a tag on an animal after the animal was found to have lost its first tag, we would have to assume that the retentions of the two tags were independent. This is biologically unreasonable when the animals are aware of and fight with the tags until habituated to the presence of the tags. However, by not placing a tag on an animal twice we may allow tag-loss probabilities to depend on both the behavior of an animal and the state of the tag. Therefore we will consider the sampling scheme where each animal is collared only once.

3. MODEL AND ESTIMATION

Animals are captured and released, and sighted once a year for s years, beginning with year 1. We will refer to the period during which captures and sightings are made as the beginning of the year. All animals captured for the first time are marked by a "band" which cannot be lost by the animal and a "collar" which can be lost. The probability of survival from the beginning of one year until the beginning of the next year is assumed to be the same for all banded animals alive at the beginning of the year, and is allowed to depend on the year. If an animal survives from one year to the next we assume the probability of collar retention to depend on age of the collar, but not on the year. We assume that for every year, each animal is captured with the same probability, and each collared animal is sighted with the same probability, and that a capture of an animal precludes the possibility of sighting for that animal in the same year.

We make no assumption about the catchability of each animal prior to or including its first capture. Hence, all estimates can be interpreted as either being conditional on the number of animals captured for the first time in each year, or being the MLEs for a model where the likelihood factors into two pieces, the first of which describes the first capture of each animal and involves none of the parameters governing survival, capture, or sighting probabilities, and the second of which describes all reobservations of animals.

The reason for restricting the population of inference to previously captured animals is to avoid making undue assumptions about the likeness of marked and unmarked animals. If we do assume marked and unmarked animals to behave alike, however, we can include first capture data for each animal as in Seber (1965). Should we include first observations as in the Jolly-Seber model, closed form MLEs do not exist for the model despite Seber's claim of solutions, though it appears his estimates are the proper estimates to use (Kremers,1984b). We avoid the confusion of whether to use the MLEs or Seber's estimates, in the present model, by restricting our population of inference to those animals previously captured.

Therefore the parameters of the model are the following.

S_i = probability that an animal survives until year (i+1) given it is alive at the beginning of year i.

P_i = probability that a collar is retained i years given the animal bearing the collar has retained its collar i-1 years since its first capture, and survived i years since its first capture.

f_i = probability that a banded animal is captured in the i'th year given it is alive at the beginning of the year.

g_i = probability that a banded bird is sighted in the i'th year given it is alive and has its collar at the beginning of the year, and was not captured in the i'th year.

ϕ = a reparameterization of the model, that is there is a one-to-one mapping between ϕ and the S_i, P_i, f_i, and g_i.

Φ = the parameter space for the possible ϕ.

Further, to construct and maximize the likelihood we consider the following definitions.

h denotes a history observable to the investigator. Specifically for each year i, i=1,...,s, h specifies whether an animal was captured with or without a collar, if an animal was sighted with a collar, or not observed at all.

h^* is a "complete" history. For each year i, $i=1,\ldots,s$, h^* specifies whether an animal was sighted or captured, with or without the collar, or not captured at all. h^* also specifies whether or not an animal possessed its collar at the beginning of the year, for each year preceeding and including the last year the animal was observed.

ho denotes the null history, that is, the history of no captures.

H is the set of all histories h, except ho, describing captures of an animal with and without its collar, and sightings of the animals with its collar.

H^* is the set of all histories h^*, except ho, describing collar retention for each year preceeding and including the last year that animal was observed, and the capture or sighting for each year.

y_h = number of animals in the study with history h for $h \varepsilon H$.

x_{h^*} = number of animals in the study with history h^* for $h^* \varepsilon H^*$.

$\{y_h\} = \{y_h : h \varepsilon H\}$

$\{x_{h^*}\} = \{x_{h^*} : h^* \varepsilon H^*\}$

H is the set of all histories observable to the investigator. The investigator can only identify an animal by a sighting if the animal possesses its collar. We say the investigator "unknowingly" observes an animal if the investigator sights an animal which has lost its collar. We say the investigator "knowingly" observes an animal if the investigator captures an animal or sights an animal with its collar. H^* is the set of all possible histories based upon collar retention until the time of last observation, and captures and sightings of animals with and without their collars. $\{x_{h^*}\}$ is only indirectly observable to the investigator through

$\{y_h\}$. In this context $\{y_h\}$ can be considered as partial data based on the incomplete knowledge of the observer. $\{x_h\}$ can be considered as complete data based on all sightings and recaptures, and also collar retention by each animal until each animal's last observation.

Since only $\{y_h\}$ is observable to the investigator the likelihood is defined in terms of $\{y_h\}$, and not $\{x_h\}$. However, the likelihood, when given for $\{y_h\}$ is not of a form which readily suggests a maximizing solution. When the likelihood is written in terms of $\{x_h\}$ a closed form solution for ϕ is obtained by use of the usual Jolly-Seber estimates for survival and observation probabilities. Since $\{x_{h*}\}$ is not observable, but MLEs easily obtained if $\{x_{h*}\}$ were observable, we use the EM algorithm to find MLEs for this model. To this end let $f(\{x_{h*}\};\phi)$ be the probability mass function for $\{x_{h*}\}$, and define

$$Q(\phi'|\phi) = E[\ \log f(\{x_{h*}\};\phi')\ |\ \{y_h\},\phi\ ]$$

We begin the EM algorithm by giving an initial estimate of ϕ, $\phi^{(0)}$. We then begin an iterative procedure. Each iteration of the algorithm gives a new estimate of ϕ. Let $\phi^{(p)}$ be the estimate of ϕ after p iterations. The next iteration consists of evaluating $Q(\phi'|\phi^{(p)})$ and choosing $\phi^{(p+1)}$ such that $\phi^{(p+1)} \in \Phi$ and $\phi^{(p+1)}$ maximizes $Q(\phi'|\phi^{(p)})$ with respect to ϕ'. The iterations are stopped when a convergence criterion is reached and the last estimate of ϕ is interpreted as $\hat{\phi}$, where, in general $\hat{\theta}$ denotes the MLE of θ.

3.1 THE LIKELIHOOD

To derive MLEs we do not need to derive the likelihood. But to estimate the covariance matrix of $\hat{\phi}$ we consider the information matrix, and to this end we define the following random variables which are functions of $\{y_h\}$.

N(i) = number of animals first captured in year i.

R(i) = number of different animals which were first captured in year i which are knowingly reobserved during the entire study.

T(i) = number of animals first captured in or before year i which are known to have survived until at least year i+1.

Y(i,j,k)= number of animals first captured in year i, observed in year j with a collar, and observed knowingly, next in year k as a capture without a collar.

Cl(i,j) = number of animals first captured in year i, observed in year j with a collar, and not knowingly observed again.

Cc0(i) = number of animals captured in year i without their collars, and not knowingly observed again.

Cc(i) = number of animals captured in year i.

Csy(i,j) = number of animals first captured in year i, sighted in year j with a collar.

L(i) = number of animals first captured before year i, not observed in year i, and later knowingly observed.

L0(i) = number of animals first captured before year i, not observed in year i, and later observed with a collar.

Dy(i) = number of animals observed with collars of age at least i years.

For $i \leq j < k \leq s$ let

$\psi_{k,m,n}$ = probability that a bird is not knowingly observed from the (m+1)'th year to the (n-1)'th year and loses its collar between the beginning of the m'th and n'th year, given the bird is released in the k'th year, observed in the m'th year with a collar, and next captured in the n'th year.

$$\psi_{i,j,k} = \sum_{m=1}^{j-k} (1-P_{j-i+m}) \Pi_{n=1}^{m-1} P_{j-i+n}(1-g_{j+n}).$$

Further let $\psi 1_{i,j}$ be the probability that an animal is not knowingly observed after year j given the animal is first captured in year i and observed in year j with a collar . Let ψo_j be the probability that an animal is not captured after year j given the animal is caught in year j without a collar. $\psi 1_{i,j}$ and ψo_j are most easily expressed by the recursive relation

$$\psi o_j = (1-S_j) + S_j(1-f_{j+1})\psi o_{j+1}$$

$$\psi 1_{i,j} = (1-S_j) + S_j(1-f_{j+1}) \{ (1-P_{j-i+1})\psi o_j + P_{j-i+1}(1-g_{j+1})\psi_{i,j+1} \}$$

with $\psi o_s = \psi 1_{i,s} = 1$

Then the likelihood may be expressed as,

$$L[\phi;\{y_h\}] = (\Pi\, y_h!\,)^{-1} \{\Pi_{i=1}^{\ell} S_i^{T(i)} P_i^{D(i)} f_i^{Cc(i)} (1-f_i)^{L(i)+Csy(i)} g_i^{Csy(i)} (1-g_i)^{LO(i)} (1-\lambda_i)^{N(i)-R(i)}\}$$
$$\times\{\Pi_{i\le j\le k}\ \psi_{i,j,k}^{Y(i,j,k)}\}$$
$$\times\{\Pi_{i\le j}\ \psi 1_{i,j}^{\ C1(i,j)}\} \{\Pi_j\ \psi o_j^{\ Cc0(j)}\}$$

3.2 MAXIMIZATION OF THE LIKELIHOOD BY THE EM ALGORITHM

Recall that for the EM algorithm we must evaluate

$$Q(\phi'|\phi^{(p)}) = E[\ \log f(\{x_{h*}\};\phi')\ |\ \{y_h\},\phi^{(p)}\ ].$$

The evaluation of $Q(\phi'|\phi^{(p)})$ is simplified for each iteration if we consider the following conditional expectations.

a(i) = expected number of animals observed, knowingly or unknowingly, in sample i given $\{y_h\}$ if $\phi^{(p)}$ were the true parametrization of the model.

a(<i) = number of different animals captured before sample i, which is directly observable from the $\{y_h\}$.

a(>i) = expected number of different animals observed, knowingly or unknowingly, after sample i given $\{y_h\}$ and $\phi^{(p)}$.

$a(<i^{\cdot}i) = a(<i) + a(i) - a(i+1)$

$a(>i^{\cdot}i) = a(>i) + a(i) - a(>i-1)$

$b(i+1) = a(>i) + a(<i+2) - a(<s) - a(s) - a(i+1)$

$Cs(i) = a(i) - Cc(i)$

$D(i)$ = expected number of animals which have retained their collars i years and will be knowingly or unknowingly observed at or after i years after their release, given $\{y_h\}$ and $\phi^{(p)}$.

$E(i)$ = expected number of animals which have retained their collars i-1 years but not i years, which will be knowingly or unknowingly observed at or after i years after their release, given $\{y_h\}$ and $\phi^{(p)}$.

Properly, the above conditional expectations depend on $\phi^{(p)}$. This dependence on $\phi^{(p)}$ is implicit though not explicit in our notation. The evaluation of the conditional expectations is described in the Appendix, Section 6.1.

We also consider the following reparametrization.

$\rho_i = f_i + (1-f_i)g_i$,

$\alpha_i = \phi_i(1-\rho_{i+1})$,

$\beta_i = \phi_i\rho_{i+1}$,

$\nu_i = f_i/(f_i + (1-f_i)g_i)$,

Futher let χ_i be the probability that an animal is not, knowingly or unknowingly, observed after year i, given the animal is alive at the beginning of year i. χ_i is most easily given by the recursive relation

$\chi_i = (1-S_i) + S_i(1-\rho_{i+1})\chi_{i+1}$,

where $\chi_s = 1$.

From this reparametrization we find that $\exp[\ Q(\phi'|\phi^{(p)})\ ]$ is proportional to

$$\Pi \left\{ \chi_i^{a(i)-a(>i.i)} \beta_i^{a(<i+1.i+1)} \alpha_i^{b(i+1)} \nu_i^{Cc(i)} (1-\nu_i)^{Cs(i)} P_i^{D(i)} (1-P_i)^{E(i)} \right\}.$$

Hence to obtain $\phi^{(p+1)}$, our new estimate of ϕ, we use the Jolly-Seber estimates for the α_i and β_i, and the binomial MLEs for the ρ_i and ν_i. In particular we have

$$\alpha_i^{(p+1)} = a(>i.i)b(i+1)a(i+1)/(a(>i+1.i+1)a(i)(b(i+1) + a(<i+1.i+1)))$$

$$\beta_i^{(p+1)} = a(>i.i)a(<i+1.i+1)/(a(i)(b(i+1) + a(<i+1.i+1)))$$

$$\nu_i^{(p+1)} = Cc(i)/(Cc(i) + Cs(i))$$

$$P_i^{(p+1)} = D(i)/(D(i) + E(i))$$

The iterations are stopped when a convergence criterion is met and the last estimate of each parameter is taken as the MLE. To obtain MLEs of the original parameters observe,

$$\hat{S}_i = \hat{\alpha}_i + \hat{\beta}_i,$$

$$\hat{\rho}_i = \hat{\beta}_i/(\hat{\alpha}_i + \hat{\beta}_i),$$

$$\hat{f}_i = \hat{\rho}_i\hat{\nu}_i,$$

$$\hat{g}_i = (\hat{\rho}_i - \hat{f}_i)/(1 - \hat{f}_i).$$

4. DISCUSSION OF MODIFIED JOLLY-SEBER, HYPERGEOMETRIC, AND MULTINOMIAL MODELS

A possible drawback of this modified Jolly-Seber model which accounts for collar loss is the calculations required to obtain the MLEs and the estimated covariance matrix. That is, there are not closed form MLEs. A disadvantage of the Jolly-Seber model, with or without collar loss, is the lack of (derived) closed form MLEs when we allow for different age classes to have different survival and capture probabilities. Hence if we are to allow heterogeneity by age class, we must numerically maximize $Q(\phi'|\phi^{(p)})$

with respect to the S_i and ρ_i for each iteration of the EM algorithm, thus significantly increasing computations and programming necessary to obtain MLEs.

A model allowing for separate survival and capture rates by age is given by Pollock (1981). Pollock's model is based on the hypergeometric approach of Robson (1969) for which the likelihood does not involve parameters for survival probabilities. Instead survival rates are defined in terms of changes in population sizes which are unknown parameters in the model. Similarly we might want to define collar retention rates in terms of animals which have retained or lost their collars. The hurdle, however, is to express the likelihood, given $\{y_h\}$, while allowing retention rates to depend on age of the collar but not the year.

The likelihood for a capture-recapture model allowing collar retention rates to depend on age class and year, and age of the collar can be described as in the Appendix, Section 6.2. However if collar retention is dependent on age of the collar and not year the model will be over fit with a loss of efficiency. And still there is the question of conditioning on sample sizes in the derivation of the hypergeometric likelihood. If sampling is binomial the likelihood should express this binomial property; if the sampling distribution is unknown it seems reasonable to condition on sample size but this must be done with some caution as estimates for the hypergeometric model are of the same basic form as in the Jolly-Seber model (Pollock,1981). If the binomial model gives inappropriate estimates so may the hypergeometric. Intuitively, conditioning on sample size is like estimating the nuisance parameters, the sampling probabilities. In the model the sampling and survival probabilities are not related but the random variables we observe are funtions of both types of probabilities, and their estimates are dependent. Hence to condition on sample sizes is to condition on a statistic providing information about survival and should be avoided if we can describe the likelihood while including the sampling scheme.

An alternate approach is to consider the likelihood using only the data describing the first and last observation of each animal. For this use of partial data a series of models developed by Brownie *et.al.* (1978) is applicable. Brownie's models are based on the multinomial approach of Seber (1970) and Robson and Youngs (1971). For these models either closed form MLEs or computer programs are available for the calculation of the MLEs (Brownie,1978). Properly Brownie's models are based on recoveries, that is recaptures of dead animals, however, the models are easily adapted to data involving both recoveries and resightings as in Mardekian and McDonald (1981) or recoveries and resightings of non-permanent collars as in Kremers (1984a). In a similar way Brownie's models may be adapted to (non-destructive) recaptures and resightings of animals. This simplifies the procedure of model selection and parameter estimation, though with the loss of information from the intermediate observations.

Thus we are left with three approaches when considering survival estimation in the presence of collar loss: the Jolly-Seber model, the hypergeometric model, and the multinomial model. To compare the three models we assume the probability distribution for sample sizes is binomial and that collar loss is dependent on age of the collar but not on the year. Statistically, the modified Jolly-Seber model has the strongest appeal as estimation is based on the asymptotically efficient MLEs. Should survival, observation, and collar retention rates depend on age class though, the programming and calculations become burdensome rendering the Jolly-Seber model less practical than if MLEs existed in closed form.

The hypergeometric model, as presented here, is practical in that estimates are easily described in closed form, but the use of the hypergeometric model results in loss of efficiency when compared to the Jolly-Seber model because of 1) the over fitting of the model and, 2) the conditioning on the binomial sample sizes. The multinomial model has the advantage of being computionially simpler than the Jolly-Seber model, but with the loss of information by the neglection of intermediate observations. An advantage of the multinomial approach over the hypergeometric is that it does not over fit.

Consider the circumstance where reobservations consist only of sightings of animals with non-permanent collars. This may occur if animals become trap shy or by design of the investigator. Survival rates are no longer identifiable. When investigating stresses placed on wildlife populations though, interest may concern not only absolute survival rates but also changes in survival rates between years. For the hypergeometric model the likelihood becomes indistinguishable in form from that of Pollock, and we are only able to estimate population sizes of collared animals. As collar loss is dependent on both age of the collar and year in this model, we are unable to estimate either survival rates or changes in survival rates. When observations consist only of sightings the multinomial model is overparameterized. Survival and collar retention probabilities are not identifiable but products of survival and capture probabilities, such as those in Table 1, are identifiable and thereby ratios of survival (or collar retention) probabilities are identifiable. Thus, in the absence of recaptures, changes in survival and collar retention probabilities can be estimated and tested for with the Jolly-Seber or multinomial models but not with the hypergeometrtic model.

The necessity of overfitting the hypergeometric model disallows the estimation of changes in survival rates when the data comprise of only resightings. Should the amount of recaptures in a study be small and the number of sightings large, we expect the overfitting to lead to instability of estimates of changes in survival rates and hence survival rates, for the hypergeometric model. For the multinomial model the captures allow the estimation of absolute survival rates while sightings allow accurate estimates of changes in survival rates between years.

The best way to account for collar loss in the planning of studies is to eliminate it. If, however, collar loss cannot be eliminated and is thought to depend on age of the collar, the study should be designed to minimize the effect of year, or time periods between samples, on collar loss. Collar loss can then be accounted for in the likelihood, thereby allowing asymptotic MLEs of survival rates, from a single study. For the case of binomial sampling model selection might be executed using the multinomial model as the calculations are less involved than for the Jolly-Seber model, and the multinomial model does not overfit collar retention probabilities as in the hypergeometric model. Efficient estimates for survival probabilities may then be derived using the Jolly-Seber model.

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6. APPENDIX

6.1 Evaluation of conditional expectations for the EM algorithm

From $\{y_h\}$ we may calculate

ay(i) = number of animals knowingly observed in year i,

ay(>i) = number of different animals knowingly observed after year i,

by(i) = number of animals captured without collars before year i, not captured in year i but later captured (without a collar, we hope).

We also define the following events.

Eva_i is the event where an animal is unknowingly sighted in year i.

Evb_i is the event where an animal is unknowingly sighted after year i

$Evc_{i,j,k}$ is the event where an animal is first captured in year i, observed in year j with a collar, captured in year k without a collar and not knowingly observed from year j+1 to k-1.

$Evl_{i,j}$ be the event where an animal is first captured in year i, observed in year j with a collar and not knowingly observed thereafter.

EvO_j be the event where a banded animal is caught in year j without a collar and not knowingly observed thereafter.

Writing probabilities in terms of these events we now calculate the conditional expectations for the EM algorithm from the newly defined random variables. We first evaluate a(i), observing

$$a(i) = ay(i) + aso(i),$$

where aso(i) is the expected number of animals unknowingly observed in year i. An animal can be considered when evaluating aso(i) only if the animal was captured before year i, not knowingly observed in year i, and later captured without a collar, or if the animal was last knowingly observed in year j, where j<i. Hence

$$\begin{aligned} a(i) &= ay(i) + aso(i) \\ &= ay(i) + by(i)g_i + \textstyle\sum_{m,n<i<\ell} Y(m,n,\ell) \Pr[\ Eva_i \mid Evc_{m,n,\ell}\ ] \\ &\quad + \textstyle\sum_{m,n<i} Cl(m,n) \Pr[\ Eva_i \mid Evl_{m,n}\ ] \\ &\quad + \textstyle\sum_{n<i} Cc0(n) \Pr[\ Eva_i \mid Evo_n\ ]\ ) \\ &= ay(i) + by(i)g_i \\ &\quad + \textstyle\sum Y(m,n,\ell)\ \psi_{m,n,i} g_i / \psi_{m,n,\ell} \\ &\quad + \textstyle\sum Cl(m,n)\ [\ \psi_{m,n,i}\ g_i\ \psi o_i\ \Pi_{\ell=1}^{i-n}\ s_{n-1+\ell}(1-f_{n+\ell})]/\psi l_{m,n} \\ &\quad + \textstyle\sum Cc0(n)\ [\ g_i\ \psi o_i\ \Pi_{\ell=1}^{i-n}\ s_{n-1+\ell}(1-f_{n+\ell})\ ]/\psi o_n, \end{aligned}$$

Similarly,

$$\begin{aligned} a(>i) &= ay(>i) + \textstyle\sum_{m,n\le i} Cl(m,n) \Pr[\ Evb_i \mid Evl_{m,n}\ ] \\ &\qquad + \textstyle\sum_{n\le i} Cc0(n) \Pr[\ Evb_i \mid Evo_n\ ] \\ &= ay(>i) + \textstyle\sum Cl(m,n)[\ \Sigma_{\ell=i+1}^{s}\ \psi_{m,n,\ell}\ g_\ell\ \Pi_{k=1}^{\ell-n} s_{n-1+k}\ (1-f_{n+k})\ \chi_\ell]/\psi l_{m,n} \\ &\qquad + \textstyle\sum Cc0(n)\ [\ \Sigma_{\ell=i+1}^{s}\ g_\ell\ \ \Pi_{k=1}^{\ell-n}\ s_{n-1+k}(1-f_{n+k})\ \chi_\ell]/\psi o_m \end{aligned}$$

$$D(i) = Dy(i) + \sum_{m,n\leq i<\ell} Y(m,n,\ell) \; [\; \psi_{m,i,\ell} \; \Pi_{k=1}^{i-n+m} \; P_{n-m+k} \; (1-g_{n+k})]/\psi_{m,n,\ell}$$

and,

$$E(i) = \sum_{m,n\leq i<\ell} Y(m,n,\ell) \; [\; (1-P_i) \; \Pi_{k=1}^{i-n+m-1} \; P_{n-m+k} \; (1-g_{n+k})]/\psi_{m,n,\ell}.$$

From the a(i), a(>i), D(i), and E(i) we may calculate all other conditional expectations which appear in $Q(\phi'|\phi^{(p)})$.

6.2 Liklihood for collar loss using the hypergeometric approach

To use the hypergeometric approach to collar loss we first allow collar loss to depnd on both age of the collar and year or time period. The notation we use is that of Pollock's (1981) with slight modifications. Here in year j, the year of collaring for animals still with their collars, or absence of a collar, defines j subpopulations for every one subpopulation of Pollock's. To distinguish the subpopulations we let $M1_{i,j}^{(\nu)}$ be the number of animals with collars in year j, banded in year i, of age class ν, and $M0_j^{(\nu)}$ be the number of animals without collars in year j of age class ν, Similarly let $z1_{i,j}^{(\nu)}$ be number of animals which are later observed with collars, of those which we enumerate to obtain $M1_{i,j}^{(\nu)}-m1_{i,j}^{(\nu)}$. Let $z10_{i,j}^{(\nu)}$ be the number of animals which are not later observed with a collar but are observed without a collar, of those which we enumerate to obtain $M1_{i,j}^{(\nu)}-m1_{i,j}^{(\nu)}$. Let $z00_{i,j}^{(\nu)}$ be the number of animals later observed (without collars), of those which we enumerate to obtain $M0_{i,j}^{(\nu)}-m0_{i,j}^{(\nu)}$. Similarly define $r1_{i,j}^{(\nu)}$, $r10_{i,j}^{(\nu)}$, $r00_{i,j}^{(\nu)}$, $T1_{i,j}^{(\nu)}$, $T10_{i,j}^{(\nu)}$, and $T00_{i,j}^{(\nu)}$. $z10_{i,j}^{(\nu)}$ is not observable but can be estimated by $z0_{i,j}^{(\nu)}\; r10_{i,j}^{(\nu)}/r0_{i,j}^{(\nu)})$, where $r0_{i,j}^{(\nu)}=r10_{i,j}^{(\nu)}+r00_j^{(\nu)}$ and analogously $z0_{i,j}^{(\nu)}=z10_{i,j}^{(\nu)}+z00_j^{(\nu)}$.

Hence we find the likelihood is proportional to

$$\prod_{j=2}^{k-1}\prod_{i=1}^{j-1}\prod_{\nu=1}^{\ell-1} \frac{\binom{M1_{i,j}^{(\nu)} - m1_{i,j}^{(\nu)}}{z1_{i,j}^{(\nu)} + z10_{i,j}^{(\nu)}}\binom{R1_{i,j}^{(\nu)}}{r1_{i,j}^{(\nu)}+r10_{i,j}^{(\nu)}}}{\binom{M1_{i,j}^{(\nu)} - m1_{i,j}^{(\nu)} + R1_{i,j}^{(\nu)}}{z1_{i,j}^{(\nu)}+r1_{i,j}^{(\nu)}+z10_{i,j}^{(\nu)}+r10_{i,j}^{(\nu)}}}$$

$$\times \frac{\binom{M1_{i,j}^{(\ell)}+M1_{i,j}^{(\ell+1)}-m1_{i,j}^{(\ell)}}{z1_{i,j}^{(\ell)}+z10_{i,j}^{(\ell)}}\binom{R1_{i,j}^{(\ell)}}{r1_i^{(\ell)}+r10_i^{(\ell)}}}{\binom{M1_{i,j}^{(\ell)}+M1_{i,j}^{(\ell)}-m1_{i,j}^{(\ell)}+R1_{i,j}^{(\ell)}}{z1_{i,j}^{(\ell)}+r1_{i,j}^{(\ell)}+z10_{i,}^{(\ell)}+r10_{i,j}^{(\ell)}}}$$

$$\times \frac{\binom{M1_{i,j}^{(\ell)}}{T1_{i,}^{(\ell)}+T10_{i,j}^{(\ell)}}\binom{M1_{i,j}^{(\ell+1)}}{T1_{i,j}^{(\ell+1)}+T10_{i,j}^{(\ell+1)}}}{\binom{M1_{i,j}^{(\ell)}+M1_{i,j}^{(\ell+1)}}{T1_{i,j}^{(\ell)}+T1_{i,j}^{(\ell+1)}+T10_{i,j}^{(\ell)}+T10_{i,j}^{(\ell+1)}}}$$

$$\times\prod_{j=2}^{k-1}\prod_{\nu=1}^{\ell-1}\frac{\binom{M0_j^{(\nu)}-m0_j^{(\nu)}}{z00_j^{(\nu)}}\binom{R0_j^{(\nu)}}{r00_j^{(\nu)}}}{\binom{M0_j^{(\nu)}-m0_j^{(\nu)}+R0_j^{(\nu)}}{z00_j^{(\nu)}+r00_j^{(\nu)}}}$$

$$\times\frac{\binom{M0_j^{(\ell)}+M0_j^{(\ell+1)}-m0_j^{(\ell)}}{z00_j^{(\ell)}}\binom{R0_j^{(\ell)}}{r00_j^{(\ell)}}\binom{M0_j^{(\ell)}}{T00_j^{(\ell)}}\binom{M0_j^{(\ell+1)}}{T00_j^{(\ell+1)}}}{\binom{M0_j^{(\ell)}+M0_j^{(\ell+1)}-m0_j^{(\ell)}+R0_j^{(\ell)}}{z00_j^{(\ell)}+r00_j^{(\ell)}}\binom{M0_j^{(\ell)}+M0_j^{(\ell+1)}}{T00_j^{(\ell)}+T00_j^{(\ell+1)}}}$$

By differencing we may obtain closed form estimates of the subpopulation sizes, from which we may give estimates of survival rates.

Table 1

SIGHTING PROBABILITIES WITH COLLARS

Sighting probabilities of animals with collars (with year of first capture given in the far left column).

	Year of Sighting			
	2	3	4	5
1	$S_1P_1(1-f_2)g_2$	$S_1S_2P_1P_2(1-f_2)g_2$	$S_1S_2S_3P_1P_2P_3(1-f_4)g_4$	$S_1S_2S_3P_1P_2P_3(1-f_4)g_4$
2		$S_2P_1(1-f_3)g_3$	$S_2S_3P_1P_2(1-f_4)g_4$	$S_2S_3S_4P_1P_2P_3(1-f_5)g_5$
3			$S_3P_1(1-f_4)g_4$	$S_3S_4P_1P_2(1-f_5)g_5$
4				$S_4P_1(1-f_5)g_5$