

Pitfalls in the estimation of age-dependent survival rates of birds from ringing and recovery data

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1. Introduction

Considerable progress has been made during the last decade in the calculation of survival probabilities using the recoveries of dead birds by the introduction of maximum likelihood techniques.

Depending on their basic assumptions, there are generally speaking three main types of models used in estimating the survival rates.

These types contain:

1. a constant survival rate. In these models survival is considered to be independent of age and calendar year.
2. a calendar-year dependent survival rate. In these models survival is considered to be independent of age, but may vary with calendar year.
3. an age-dependent survival rate. In these models survival is thought to be independent of calendar year but may vary with age.

These types are often used in combination. For instance, in models of age-dependent survival rates, survival is mostly considered to be constant from a certain age onward. BROWNIE (1973, cited in ANDERSON 1975) and JOHNSON (1974) have brought age dependency in a calendar-year dependent model using birds ringed at different ages.

The estimation of constant survival rates has been solved satisfactorily. LACK'S (1943) estimate, originating from a deterministic life table, has been shown to be a maximum likelihood estimate if all birds are dead at the end of the observations (HALDANE 1955). HALDANE extended this estimate to incomplete data with the help of maximum likelihood techniques, which result was generalized by SEBER (1972, 1973).

The problem of the estimation of calendar-year dependent survival rates has been solved by SEBER (1970, 1973). For this estimate the numbers ringed in each year are needed; this is in contrast with the estimation of the rate of constant survival.

The estimation of age-dependent survival rates remains a problem. Since it is likely that survival of birds varies not only with calendar year but also with age, it is of paramount importance that satisfactory methods become available for its estimation. This paper is intended to give a contribution to this problem.

A second pending problem is the estimation of mortality rates due to different causes of death. The approach of CHIANG (1961), intended for human populations, can not be used for the recoveries of dead birds. The different (uneven) reporting probabilities of birds dying by different causes makes this problem far more difficult to solve. A number of authors, working on game birds, estimated the rate of hunting mortality separately by making use of independently obtained estimates of the hunting reporting probabilities (ANDERSON 1975, GEIS & ATWOOD 1961, HENNY & BURNHAM 1976, MARTINSON 1966, MARTINSON & McGANN 1966, TOMLINSON 1968). Such estimates are not available for most birds and are difficult to obtain. Hence, this method has no general application. In the present paper it will be shown that the solution of this problem, apart from its own importance for the understanding of the population dynamics of birds, is essential for the estimation of age-dependent survival rates.

2. Age-dependent survival rates without a distinction between causes of death

The general model for the expected number of recoveries in a certain year after ringing used to obtain survival estimates is given in appendix 1:(1).

The existence of age-dependent survival is a more complicated assumption than a constant survival since more parameters are involved. For that reason, if estimates of age-dependent survival rates do not give a significant better fit to the observed recoveries than a constant one, the latter assumption has to be preferred. Therefore, in models of age-dependent survival rates, the rate of survival is generally assumed to be constant from a certain age onward. This age can be estimated with a χ^2 -test.

Age-dependent survival rates can be estimated with the method of CORMACK (1970). For this method the numbers ringed yearly are needed. Since these numbers are not easily obtainable from the files of the European ringing administration centres, there is need for a method to estimate age-dependent survival rates without making use of them. If the reporting probability (this is the probability that a dead bird will be found and reported to the administration centre) is assumed to be constant the equations (4) and (5) of appendix 1 can be used. These equations have been applied to estimate age-dependent survival rates of the Coot (*Fulica atra*) ringed as pullus in The Netherlands (Table 1). For reasons of comparison the recoveries are divided into two groups, »shot« and »found dead«. The table shows that for the »shot« recoveries the survival rate is dependent on age, while this is not the case for the group found dead. This can be seen both from the result of the χ^2 -test and from the overlap of the uncertainties of the estimates of the first year and subsequent years. The most remarkable feature of the table is the large difference between the estimates of the first year survival rate of the two groups. This difference can not be explained by the uncertainties of the estimates, as given by their standard deviations. Since both are estimates of the survival rate in the population as a whole, these estimates are clearly biased. Such differences between estimates of survival rates from »shot« birds and birds »found dead« are a common feature of many birds if we calculate both estimates.

The conclusion from these findings is that age-dependent survival rates estimated in this way are biased.

The reasons can be found in the basic assumptions of the model. Birds die of many causes, and each cause brings about a different risk to die. One or more of these risks might be age dependent. It is unlikely that they are age dependent all in exactly the same way. This simply means that one cause of death is more important in youth than another. For instance, it is likely that in many birds the young individuals are more susceptible for shooting than older ones.

This has the consequence that when we consider only one cause of death, its share in the total mortality is likely to decrease or increase with age. For that reason a selection of only »shot« birds as we made in our example of the Coot is not likely to be representative for the sequence of the number of death for the population as a whole, since its share varies with age. The same argument holds for the birds found dead. The conclusion from these considerations is that it is incorrect to estimate age-dependent survival from a selection of recoveries and that such a selection leads to a biased estimate.

However, what happens if we do not make such a selection? The probability to be reported depends on the cause of death. For instance, it is far more likely that a shot bird will be reported than a bird hit by an aeroplane. Even if we assume that for each cause of death the probability to be reported is independent of age, the total probability to be reported for a mixed lot of dead birds is dependent on age, since the composition of the causes of death depends on age. The conclusion from these considerations is that if age-dependent survival

Table 1. Survival of the Coot (*Fulica atra*)

Ringed as pullus in the Netherlands 1934-1973, recovered up to 1973-74. The year starts at the mean ringing date (day 173). The recoveries before the starting date in the first year of birds ringed earlier are included. For the selection of »shot« and »found dead« see PERDECK in this issue. For calculations see appendix 1, equations (4) and (5).

| | age groups | survival | P value χ^2 constant survival |
|--------------------------|----------------------|---------------------|--|
| shot N = 93 | all ages together | 0.30 S.D. = 0.04 | <0.001 |
| | 1 st year | 0.21 S.D. = 0.07 | |
| | later years | 0.75 S.D. = 0.13 | 0.23 |
| found dead N = 138 | all ages together | 0.69 S.D. = 0.04 | 0.26 |
| | 1 st year | 0.68 S.D. = 0.06 | |
| | later years | 0.78 S.D. = 0.07 | 0.76 |

is estimated from a mixed lot of recoveries the assumption of a constant reporting probability is incorrect and the estimate is biased. So, a model with a constant reporting probability and without a distinction between causes of death leads to biased estimates of age-dependent survival.

3. Age-dependent survival rates with a distinction between causes of death

The main difficulty in the last section appeared to lie in the fact that there is more than one cause of death, each with its own reporting probability. Let us suppose for the sake of simplicity that we have only two causes of death (A and B). For instance shooting as one cause and as a second cause the circumstances that produce the recoveries labelled as »found dead«. This simply means that a part of the birds that die in a certain year after ringing did so from cause A and that the remaining dead birds died from cause B. We assume for each cause a different reporting probability, each independent of age. This assumption might be invalidated if young individuals stay at other places than old ones and the reporting probabilities vary between places. If the manner of recovery represents a mixed lot of causes of death, it seems also unlikely that their reporting probability is independent of age. Despite this, the assumption of a constant reporting probability seems nearer to the truth for a selection than for all recoveries together.

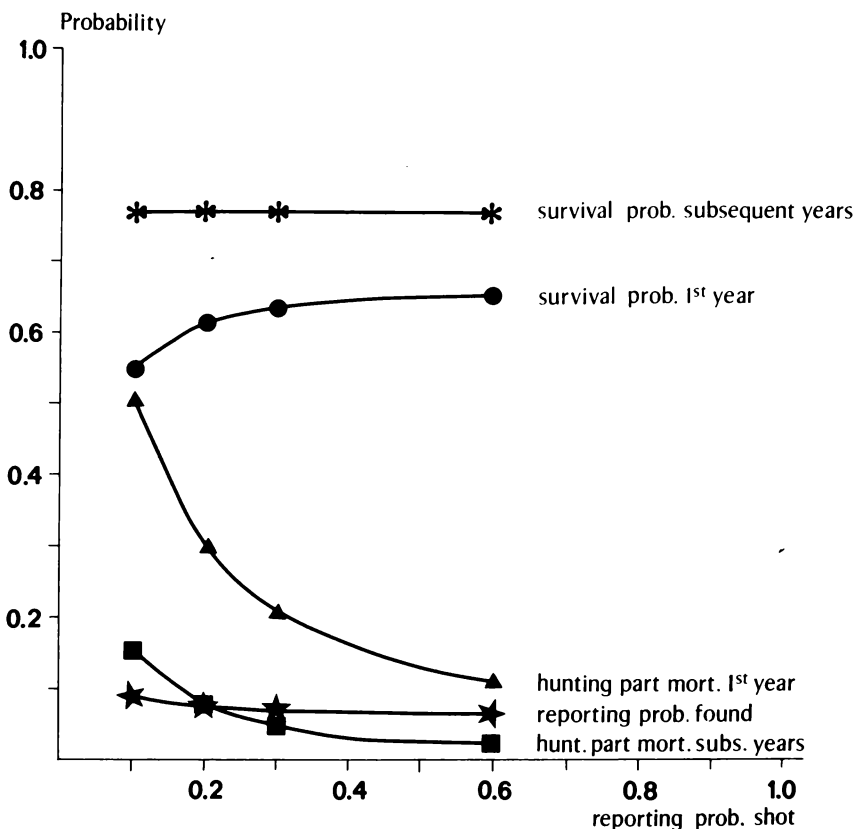


Fig. 1. Estimates of the parameters of age-dependent survival with two causes of death («shot» and «found dead» of the Coot (*Fulica atra*). Assumed values of the hunting reporting probability along the abscis. Ringing and recovery data are used of pulli ringed 1958-73 and recovered up to 1973-74. Survival probability is assumed constant from the second year onward. For calculations see appendix 2.

A model of age-dependent survival with two causes of death based on these assumptions is given in appendix 2. In this model the survival is thought to be independent of age from a certain age onward. Only this constant survival can be estimated separately. This is, however, not possible for the other parameters, except when one of them is known from other sources, e.g. the hunting reporting probability as estimated from questionnaires and reward systems.

To get some idea about the interdependence of the estimates for the Coot we have given values to the hunting-reporting probability and estimated the other parameters subsequently. For this purpose we have used the recoveries of birds ringed from 1958 onward, because for the earlier ringed recoveries the numbers ringed were not available. The results are given in Fig. 1. This figure shows that the estimate of the survival rate in subsequent years assumed to be independent of age is independent of the other parameters. The estimate of the first year survival rate is also rather independent of the assumed value of the hunting-reporting probability (reporting prob. shot) if the latter is higher than about 0.25. This means that if we have reasons to believe that this is the case, we have rather good estimates of the survival rates of this species. However, in the case of the Coot we have no reasons for such a supposition.

The estimate of the hunting part of mortality in the first year is highly dependent on the assumed value of the hunting-reporting probability. In subsequent years this value is less important for the solution. This means that we need a rather precise estimate of the hunting-reporting probability to estimate the contribution of hunting to mortality.

The conclusion from these findings is that the inclusion of two different causes of death with two different reporting probabilities in an age-dependent model gives no solution to the problem of age-dependent survival, unless we have estimates of at least one of the remaining parameters from an independent source.

4. Calendar-year dependent survival rates with a distinction between causes of death

Up till now we have considered age-dependent survival rates irrespective of the variation in survival from one calendar year to the other.

Let us now assume that survival rates are independent of age but depend on calendar year. We meet this situation when adult birds of unknown age are ringed. SEBER (1970, 1973) showed that in that case the survival rates can be estimated for each calendar year separately. If we suppose that there is one cause of death operating in the population the reporting probability for each separate year can also be estimated.

Let us assume that there are two causes of death operating in the population and that the reporting probabilities connected with these two causes of death are constant. Then it seems possible to estimate for each separate year the survival probability for the population as a whole, the parts of the mortality rate due to each cause of death and the two reporting probabilities. This is shown in appendix 3: (9). This method has still to be tested out.

5. Concluding remarks

Maximum likelihood techniques as used in the present paper provide opportunities to analyse survival patterns in birds in much more detail than the still often used deterministic life-table techniques. Moreover, variances and covariances can be estimated, providing measures of accuracy not always available for conventioned life table estimates. A further advantage of maximum likelihood methods is that they make better use of the available data.

A maximum likelihood method for the estimation of age-dependent survival is presented in appendix 1: (4), (5). As usual, the reporting probability has been assumed to be constant. However, it is shown in the present paper that this assumption is incorrect. The overall reporting probability (no distinction between mortality categories) is dependent on age. Each mortality category has its own age dependency and reporting probability. This makes the overall reporting probability dependent on age. The greater the differences between the separate reporting probabilities are, the greater is the age dependency of the overall reporting probability. The difference between the separate reporting probabilities is especially large in the case of shooting as compared with other causes of death. Therefore, it can be expected that hunted species give biased estimates of age-dependent survival if the overall reporting probability is assumed to be constant. This conclusion is far-reaching since it invalidates many hitherto made analyses. However, if shooting pressure is low, recoveries of birds died by causes other than shooting can still give reasonable estimates of the survival.

The problem arising from this age dependency of the overall reporting probability is not easy to overcome. The methods introduced by BROWNIE (1973, cited in ANDERSON 1975) and JOHNSON (1974) solve the problem to some extent for those species of which individuals are ringed at different ages. However, many species are ringed at an unknown age, and/or at only one age class (pullus), thus defying this method. A possible solution for birds ringed as pullus is suggested in this paper (appendix 2). It has no general application,

since an independently obtained estimate of one of the parameters is needed. Unfortunately, such an estimate is generally lacking.

It would be of great interest to find a method for estimating survival from different causes of death. This seems possible if survival is considered to be independent of age, but dependent on calendar year, as shown in appendix 3: (9). However, in this case many parameters have to be estimated iteratively which takes much computer time. Another drawback is that the number of recoveries has to be large to obtain estimates of reasonable accuracy.

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7. Zusammenfassung

Fehlermöglichkeiten bei der Berechnung altersabhängiger Überlebensraten bei Vögeln aufgrund der Wiederfunde beringter Vögel.

1. Zwei voneinander abhängige Probleme werden behandelt: a) die Berechnung altersabhängiger Überlebensraten, b) die Berechnung der von verschiedenen Todesursachen abhängigen Mortalität.
2. Für die Berechnung der altersabhängigen Überlebensraten wurde eine Methode erarbeitet, die von den jährlichen Beringungszahlen unabhängig ist (Appendix 1: (4), (5)).
3. Es wird gezeigt, daß die meisten der gegenwärtig verwendeten Berechnungsmethoden einschließlich der oben erwähnten ungenaue Ergebnisse liefern, da für eine exakte Berechnung die Unterschiede in der Meldewahrscheinlichkeit zwischen verschiedenen Todesursachen in Rechnung gestellt werden müssen.
4. Wenn die Meldewahrscheinlichkeit einer Todesursache bekannt ist oder geschätzt werden kann und wenn angenommen wird, daß nur zwei verschiedene Todesursachen in einer Population wirksam sind, kann die in Appendix 2: (7) dargestellte Berechnungsmethode verwendet werden.
5. Für den Fall einer vom Kalenderjahr abhängigen Überlebensrate mit zwei verschiedenen Todesursachen ist eine vielleicht brauchbare Berechnungsmethode für die jährliche Überlebensrate und den Anteil, den die beiden Todesursachen daran haben, in Appendix 3: (9) dargestellt. Dabei wird davon ausgegangen, daß die Meldewahrscheinlichkeit bei beiden Todesursachen konstant bleibt.

8. Literature

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R_i = number ringed at the start of year i

λ_j = reporting probability in year j after ringing (the reporting probability is the probability that a bird died in year j after ringing will be found and reported as such to the ringing administration centre).

ϕ_j = probability that a bird survives year j after ringing, given that it is alive at the start of year j .

$j-1$

$$\prod_{p=0} \phi_p = \phi_0 \phi_1 \phi_2 \dots \phi_{j-1}$$

CORMACK (1970) used this expectation to estimate age-dependent survival with maximum-likelihood techniques assuming all λ_j to be equal ($\lambda_j = \lambda$). Then λ is not needed for the estimation of the survivals. In that case the conditional multinomial distribution can be used (see SEBER 1973).

The joint conditional multinomial distribution of the $\{n_{ij}\}$ is $f(\{n_{ij}\} | \{H_i\}) =$

$$\prod_{i=1}^t \left[\frac{H_i!}{\prod_{j=1}^{t-i+1} n_{ij}!} \left\{ \frac{1-\phi_1}{\theta_i} \right\}^{n_{i,1}} \left\{ \frac{(1-\phi_2)\phi_1}{\theta_i} \right\}^{n_{i,2}} \dots \left\{ \frac{(1-\phi_{t-i+1}) \prod_{p=0}^{t-i} \phi_p}{\theta_i} \right\}^{n_{i,t-i+1}} \right] \quad (2)$$

$$\theta_i = (1-\phi_1) + (1-\phi_2)\phi_1 + \dots + (1-\phi_{t-i+1}) \prod_{p=0}^{t-i} \phi_p = 1 - \prod_{p=0}^{t-i+1} \phi_p$$

$$\phi_0 = 1$$

The log L(likelihood) can be written as follows:

$$\log L = \sum_{j=1}^t V_j \log(1-\phi_j) + \sum_{p=1}^{t-1} \sum_{q=p+1}^t V_q \log \phi_p - \sum_{i=1}^t H_i \log \theta_i + \text{const.} \quad (3)$$

The parameters $\phi_1, \phi_2, \dots, \phi_{s-1}, \{\phi_k\}, k=1, 2, \dots, s-1$

are assumed to be dependent on age. From year s onward the survival rate is assumed to be constant. The latter parameter is called ϕ_c .

Differentiating (3) to ϕ_k and ϕ_c and equating the partial derivatives to zero to maximize log L gives for ϕ_k :

$$-\frac{V_k}{1-\hat{\phi}_k} + \sum_{l=k+1}^t \frac{V_l}{\hat{\phi}_k} + \sum_{i=1}^{t-k+1} \frac{H_i \prod_{p=0}^{t-i+1} \hat{\phi}_p}{(1 - \prod_{p=0}^{t-i+1} \hat{\phi}_p) \hat{\phi}_k} = 0 \quad (4)$$

and for ϕ_c (constant from years s after release):

$$-\sum_{j=s}^t \frac{V_j}{1-\hat{\phi}_c} + \sum_{j=s}^t \frac{(j-s)V_j}{\hat{\phi}_c} + \sum_{i=1}^{t-s+1} \frac{H_i (t-s-i+2) \prod_{p=0}^{t-i} \hat{\phi}_p}{1 - \prod_{q=1}^{t-i+1} \hat{\phi}_q} = 0 \quad (5)$$

The equations (4) and (5) can be solved iteratively. Using the Newton-Raphson method, the last iteration gives directly an estimate of the asymptotic variances.

The assumption that ϕ is constant from year s onward can be tested with a χ^2 -test on the column totals of years s and following years. We added the cells together in such a way that the expectation per cell becomes ≥ 5 .

Appendix 2. Age dependent survival rates, two causes of death.

Assumed is again that the birds are ringed as pullus at the start of year i , the number of years j after release is then equal to age.

Let n'_{ij} $i = 1, 2, \dots, t$ $j = 1, 2, \dots, (t-i+1)$ be the number of recoveries of category A (died by cause A) reported in year j after release at the start of year i .

Let n''_{ij} $i = 1, 2, \dots, t$ $j = 1, 2, \dots, (t-i+1)$ be the number of recoveries of category B (died by cause B) reported in year j after release at the start of year i . A and B are the only causes of death. The number of observation years (t) is assumed to be equal to the number of years of release (t). R_i birds are released at the start of year i .

The recovery data of category A can be represented by:

| Year of release | Number ringed | Number recovered in successive years after ringing | | | | | Total recovered |
|-----------------|---------------|--|------------|-------|--------------|------------|-----------------|
| | | 1 | 2 | | t-1 | t | |
| 1 | R_1 | $n'_{1,1}$ | $n'_{1,2}$ | | $n'_{1,t-1}$ | $n'_{1,t}$ | H'_1 |
| 2 | R_2 | $n'_{2,1}$ | $n'_{2,2}$ | | $n'_{2,t-1}$ | | H'_2 |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| t | R_t | $n'_{t,1}$ | | | | | H'_t |
| | Total | V'_1 | V'_2 | | V'_{t-1} | V'_t | |

The recovery data of category B can be represented by:

| Year of release | Number ringed | Number recovered in successive years after ringing | | | | | Total recovered |
|-----------------|---------------|--|-------------|-------|---------------|-------------|-----------------|
| | | 1 | 2 | | t-1 | t | |
| 1 | R_1 | $n''_{1,1}$ | $n''_{1,2}$ | | $n''_{1,t-1}$ | $n''_{1,t}$ | H''_1 |
| 2 | R_2 | $n''_{2,1}$ | $n''_{2,2}$ | | $n''_{2,t-1}$ | | H''_2 |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| ... | ... | ... | ... | | ... | ... | ... |
| t | R_t | $n''_{t,1}$ | | | | | H''_t |
| | Total | V''_1 | V''_2 | | V''_{t-1} | V''_t | |

The expected number of recoveries of the i^{th} release in year j after release can be given by:

$$E(n'_{ij}) = R_i \lambda^i m_j (1 - \phi_j)^{j-1} \prod_{p=0}^j \phi_p \tag{category A}$$

and

$$E(n''_{ij}) = R_i \lambda''^i (1 - m_j) (1 - \phi_j)^{j-1} \prod_{p=0}^j \phi_p \tag{category B}$$

- λ^i = reporting probability of a bird died by cause A. This parameter is treated as a constant.
- λ''^i = reporting probability of a bird died by cause B. This parameter is treated as a constant.
- m_j = the probability that a bird that died in year j after release, did so from cause A. $(1 - m_j)$ is the probability of a bird that died in year j after release, did so from cause B.
- ϕ_j = the probability for a bird to survive year j after release, given that it is alive at the start of that year ($\phi_0 = 1$).

The joint probability of the $n'_{ij} = n^i_{ij}$ and the $n''_{ij} = n''^i_{ij}$ ($i = 1, 2, \dots, t$ $j = 1, 2, \dots, t-i+1$) is proportional to:

| Year of release | Number ringed | Number recovered in successive calendar years | | | | | Total recovered |
|-----------------|----------------|---|--------------------|-------|----------------------|--------------------|------------------|
| | | 1 | 2 | | t-1 | t | |
| 1 | R ₁ | n' _{1,1} | n' _{1,2} | | n' _{1,t-1} | n' _{1,t} | H' ₁ |
| 2 | R ₂ | | n'' _{2,2} | | n'' _{2,t-1} | n'' _{2,t} | H'' ₂ |
| ... | ... | | | | | | |
| ... | ... | | | | | | |
| ... | ... | | | | | | |
| t | R _t | | | | | n' _{t,t} | H' _t |
| | Total | V' ₁ | V' ₂ | | V' _{t-1} | V' _t | |

The recovery data of category B can be represented by:

| Year of release | Number ringed | Number recovered in successive calendar years | | | | | Total recovered |
|-----------------|----------------|---|--------------------|-------|----------------------|--------------------|------------------|
| | | 1 | 2 | | t-1 | t | |
| 1 | R ₁ | n'' _{1,1} | n'' _{1,2} | | n'' _{1,t-1} | n'' _{1,t} | H'' ₁ |
| 2 | R ₂ | | n'' _{2,2} | | n'' _{2,t-1} | n'' _{2,t} | H'' ₂ |
| ... | ... | | | | | | |
| ... | ... | | | | | | |
| ... | ... | | | | | | |
| t | R _t | | | | | n'' _{t,t} | H'' _t |
| | Total | V'' ₁ | V'' ₂ | | V'' _{t-1} | V'' _t | |

The expected number of recoveries of the ith release in calendar year i (j ≥ i) after the start of the observations can be given by:

$$E(n'_{ij}) = R_i \lambda^i m_j (1 - \phi_j)^{\prod_{p=0, i}^{j-1} \phi_p} \tag{category A}$$

and

$$E(n''_{ij}) = R_i \lambda'' (1 - m_j) (1 - \phi_j)^{\prod_{p=0, i}^{j-1} \phi_p} \tag{category B}$$

- λ' = reporting probability of a bird died by cause A. This parameter is treated as a constant.
- λ'' = reporting probability of a bird died by cause B. This parameter is treated as a constant.
- m_j = the probability that a bird died in calendar year j, did so from cause A. (1 - m_j) is the probability that a bird died in calendar year j, did so from cause B.
- φ_j = the probability for a bird to survive calendar year j, given that it is alive at the start of that year (φ₀ = 1).

The joint multinomial distribution of the {n'_{ij}} and the {n''_{ij}} is proportional to:

$$\prod_{i=1}^t \left[\{ \lambda^i m_i (1 - \phi_i) \}^{n'_{ii}} \{ \lambda'' (1 - m_i) (1 - \phi_i) \}^{n''_{ii}} \right. \\
\times \{ \lambda^i m_{i+1} (1 - \phi_{i+1}) \phi_i \}^{n'_{i,i+1}} \{ \lambda'' (1 - m_{i+1}) (1 - \phi_{i+1}) \phi_i \}^{n''_{i,i+1}} \\
\times \dots \\
\times \left. \{ \lambda^i m_t (1 - \phi_t)^{\prod_{p=0, i}^{t-1} \phi_p} \}^{n'_{it}} \{ \lambda'' (1 - m_t) (1 - \phi_t)^{\prod_{p=0, i}^{t-1} \phi_p} \}^{n''_{it}} \times K_i^{L_i} \right] \tag{8}$$

$$L_i = R_i - H_i' - H_i''$$

$$K_i = 1 - \lambda' \prod_{j=i}^t m_j (1 - \phi_j) \prod_{p=0, i}^{j-1} \phi_p - \lambda'' \prod_{j=i}^t (1 - m_j) (1 - \phi_j) \prod_{p=0, i}^{j-1} \phi_p$$

The log L(likelihood) can be written as follows:

$$\begin{aligned} \log L = & \sum_{j=1}^t V_j' \log \lambda' + \sum_{j=1}^t V_j'' \log \lambda'' \\ & + \sum_{j=1}^t V_j' \log m_j + \sum_{j=1}^t V_j'' \log (1 - m_j) \\ & + \sum_{j=1}^t (V_j' + V_j'') \log (1 - \phi_j) \\ & + \sum_{i=1}^{t-1} (T_i' + T_i'') \log \phi_i + \sum_{i=1}^t L_i \log K_i + \text{const.} \end{aligned} \quad (9)$$

$$T_i' = \sum_{p=1}^i \sum_{q=i+1}^t n_{pq}'$$

$$T_i'' = \sum_{p=1}^i \sum_{q=i+1}^t n_{pq}''$$

Preliminary attempts have indicated that ML estimates of the parameters λ' , λ'' , m_k and ϕ_k ($k=1, 2, \dots, t$) can be obtained by maximizing log L iteratively. However, variances and covariances are large and it was found that in one of the three cases to try out the model one of the two $\hat{\lambda}$'s reached the upper bound (one) of the range given to the estimate. This makes it doubtful whether the model has practical use.

Appendix 4. Variances and covariances.

The theory of maximum likelihood estimation (KENDALL & STUART 1967: 55) can be applied to determine the asymptotic distribution of the estimators. If the numbers ringed are large the joint estimators tend to a multivariate normal distribution with the true parameter values as means. The variance-covariance matrix is formed by inverting the matrix of the second partial derivatives of the log likelihood function, taking expectations and changing the sign of each element.

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