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Determining Parameter Redundancy of Multi-state Mark-recapture Models for Sea Birds

Diana J. Cole

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Abstract At Euring 2007 Hunter and Caswell presented a paper 'Rank and redundancy of multi-state mark-recapture models for seabird populations with unobservable states', where they were interested in whether their multi-state mark-recapture models were parameter redundant. The models were said to be too complex to use symbolic methods developed by Catchpole and Morgan (1997) to detect parameter redundancy, so instead Hunter and Caswell developed a numerical method (automatic differentiation) to determine whether their multi-state mark-recapture models were parameter redundant or not.

Since Euring 2007 we have extended and developed the symbolic methods of Catchpole and Morgan (1997), so that it is now possible to determine the parameter redundancy of more complex models, such as multi-state mark-recapture models (Cole and Morgan, 2009a). The new method uses exhaustive summaries, which are parameter combinations that uniquely define the model. A derivative matrix can be formed from the exhaustive summary with respect to the parameters, and the rank of this derivative matrix contains information on the number of estimable parameters. Complex models, where the symbolic rank is difficult to calculate, may be simplified structurally using reparameterisation and by finding an alternative exhaustive summary.

The advantage of this approach is that you can determine exactly how many parameters can be estimated in a model for any number of years of marking and recovery, as well as which combinations of parameters can be estimated. Here we illustrate how the new methodology works for the multi-state models of Hunter and Caswell. We further develop rules for determining the parameter redundancy status of a whole family of multi-state mark-recapture models.

Keywords derivative matrix · ecology · exhaustive summaries · identifiability · Maple

D. Cole
School of Mathematics, Statistics and Actuarial Science University of Kent, Canterbury, Kent, CT2 7NF, UK.
Tel: +44-(0)1227-823664
E-mail: D.J.Cole@kent.ac.uk

1 Introduction

An important question to answer before trying to actually fit a model is whether all the model parameters can be estimated. If parameters cannot be estimated, regardless of the data used, a model is known as parameter redundant. A parameter redundant model will be non-identifiable, and can be written in terms of a smaller set of parameters. For example in the Cormack Jolly Seber (CJS) model for single state mark-recapture data (Cormack, 1964, Jolly, 1965 and Seber, 1965), where both the probability of recapture and the survival probability are dependent on time, the last recapture and survival probabilities are confounded. These two parameters only ever appear as a product, therefore the model is parameter redundant (a more in depth analysis of the parameter redundancy of the time varying CJS is given in Cole and Morgan, 2009a).

Parameter redundancy is not as obvious as in the time varying CJS model. Catchpole and Morgan (1997) developed a symbolic method for detecting parameter redundancy, which involves finding a derivative matrix and calculating its rank. The symbolic rank can be calculated using a symbolic algebra package such as Maple. The rank identifies the number of estimable parameters in the model, so that a parameter redundant model will have a rank less than the number of parameters in the model. A parameter redundant model will have a smaller set of estimable parameters; these can be found by solving a set of partial differential equations that are formed by making use of further information contained within the derivative matrix (Catchpole *et al*, 1998). Parameter redundancy in multi-state models has been examined in Gimenez *et al* (2003).

However as models become more complex, so does the structure of the appropriate derivative matrix. Calculating the rank of the derivative matrix using Maple may then become impossible, because the resulting matrix is structurally too complex. Instead, numerical methods are used; for example Jiang *et la* (2007) and Hunter and Caswell (2009). Cole and Morgan (2009a) extend this symbolic derivative matrix approach to determine symbolically whether a complex model is parameter redundant or is fully estimable.

Ecological models in particular are becoming more complex. As mentioned above a particular an example of this is shown in Hunter and Caswell (2009), who examine multi-state mark-recapture models for sea-bird populations with the added complexity of unobservable states. Their multi-state capture-recapture model allows for S different states, which are not all necessarily observable, and N different sampling occasions, i.e. marking in years 1 to $(N-1)$ and recapture in years 2 to N. The basis of the model is a transition matrix, $\boldsymbol{\Phi}_t$, and a recapture matrix $\mathbf{P}_t$. $\boldsymbol{\Phi}_t$ is an $S \times S$ matrix with elements $\phi_{i,j}(t)$, the probability of transition from state j at time t to state i at time $t+1$. $\mathbf{P}_t$ is a diagonal matrix of size S, with diagonal elements $p_{i,i}$, the probability of recapturing an animal in state i at time t. The probability of a particular release-recapture combination is then a combination of the appropriate transition and recapture matrices, represented by a p-array matrix $\boldsymbol{\Psi}^{(r,c)}$, for release occasion r and recapture occasion c, with $\Psi_{i,j}(r,c)$ denoting the probability that an individual released in stage i at time r is next recaptured in stage j at time c. In an unobservable state i, $\Psi_{i,j}^{(r,c)} = 0$ for all j. The p-array can be found from the transition and recapture matrices via

$$\boldsymbol{\Psi}^{(r,c)} = \begin{cases} (\mathbf{P}_{r+1}\boldsymbol{\Phi}_r)^T & c = r+1 \\ \{\mathbf{P}_c\boldsymbol{\Phi}_{c-1}(\mathbf{I}-\mathbf{P}_{c-1})\boldsymbol{\Phi}_{c-2}\dots & \\ (\mathbf{I}-\mathbf{P}_{r+1})\boldsymbol{\Phi}_r\}^T & c > r+1 \end{cases}$$

(Hunter and Caswell, 2009). This matrix notation allows for ease of calculation, but the structure of the model is still complex.

An alternative to the numerical methods used in Hunter and Caswell (2009) is to use the extended symbolic methods of Cole and Morgan (2009a). The basis of the Cole and Morgan method is to consider forming a simpler derivative matrix, by considering the inherent structure of the model. Cole and Morgan (2009a) show that a derivative matrix can be formed by differentiating an exhaustive summary of a model with respect to the model's parameters. An exhaustive summary is a vector of parameter combinations that uniquely define the model. For example, in capture-recapture models, the exhaustive summary could be formed from the expected number of animals for a particular release-recapture combination, which includes the expected number of animals that are never seen again. Alternatively the exhaustive summary could be formed from the simpler probabilities of a particular release-recapture combination, which excluded the more complicated probabilities that animals are never seen again. In Hunter and Caswell (2009)'s multi-state capture-recapture models, an exhaustive summary consists of the non-zero terms of the p-array, $\boldsymbol{\Psi}^{(r,c)}$. The rank of the derivative matrix is the same regardless of which exhaustive summary is used. This rank still gives the estimable number of parameters and in a parameter redundant model a set of partial differential equations can be solved to find the estimable parameter combinations (Cole and Morgan, 2009a).

The key to using this method is finding a simple exhaustive summary for the model in question. However in complex models, such as Hunter and Caswell (2009)'s multi-state capture-recapture models, the p-array exhaustive summary is still not structurally simple enough for Maple to be able to calculate the symbolic rank. If this is the case, reparameterisation can be used to find a structurally simpler exhaustive summary. This involves choosing a reparameterisation that simplifies the model structure. A derivative matrix, $\mathbf{D}_s$ can then be formed from by differentiating the original exhaustive summary, rewritten in terms of the reparameterisation, with respect to the new parameters of the reparameterisation. If the reparameterisation is unique (that is, the derivative matrix of the reparameterisation with respect to the original parameters has a rank equal to the number elements in the reparameterisation), then the rank of $\mathbf{D}_s$ is equal to the number of estimable parameters. A new exhaustive summary can also be found, regardless of whether the reparameterisation is unique or not, from the reparameterisation. If the rank of $\mathbf{D}_s$ is equal to the number of terms in the reparameterisation then the reparameterisation itself is an exhaustive summary. Otherwise, in the same way that a set of partial differential equations can be solved to find the estimable parameter combination, a set of partial differential equations, formed using extra information available in $\mathbf{D}_s$, can be used to find a new exhaustive summary (Cole and Morgan, 2009a). This symbolic algebra can be executed in a symbolic algebra computer package such as Maple. Maple proceddures and Maple code for this paper is available at www.kent.ac.uk/ims/personal/djc24/multistate.htm .

The number of estimable parameters in the model of Jiang *et la* (2007) is found symbolically in Cole and Morgan (2009b) using reparameterisation to find a simpler exhaustive summary. In Cole and Morgan (2009a), the Hunter and Caswell (2009) time-invariant four state breeding success model is used as a illustration of the reparameterisation method. Below Hunter and Caswell (2009)'s time-invariant 3 state model illustrates how reparameterisation can be used to find a simpler exhaustive summary.

Hunter and Caswell (2009)'s time-invariant 3 state model has two observable states to represent two different breeding locations and a third unobservable state representing non-breeding or an unobservable location. The model's transition matrix is

$$\boldsymbol{\Phi} = \begin{bmatrix} \sigma_1\beta_1\gamma_1 & \sigma_2\beta_2\gamma_2 & \sigma_3\beta_3\gamma_3 \\ \sigma_1\beta_1\bar{\gamma}_1 & \sigma_2\beta_2\bar{\gamma}_2 & \sigma_3\beta_3\bar{\gamma}_3 \\ \sigma_1\bar{\beta}_1 & \sigma_2\bar{\beta}_2 & \sigma_3\bar{\beta}_3 \end{bmatrix},$$

where $\bar{\gamma}_1 = 1 - \gamma_1$ etc... and which depends on the parameters σ_i, survival at location i, β_i, breeding at an observable site given survival at location i, and γ_i, probability of breeding at site 1, given survival at site i and breeding. Its recapture matrix is

$$\mathbf{P} = \begin{bmatrix} p_1 & 0 & 0 \\ 0 & p_2 & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

where p_i is the probability of being recaptured at site i. The starting exhaustive summary consists of the non-zero elements of the p-array:

$$\boldsymbol{\kappa} = \left[p_1\sigma_1\beta_1\gamma_1,\, p_2\sigma_1\beta_1(1-\gamma_1),\, p_1\sigma_2\beta_2\gamma_2,\, \ldots\right]^T,$$

(with later terms being structurally more complicated).

Unlike the other models from Hunter and Caswell (2009), in this case Maple can find the rank of derivative matrix. In the Maple code it is shown that the rank of the derivative matrix is 10. This means there are 10 out of a possible 11 estimable parameters. The deficiency of a model is the number of parameters that cannot be estimated. For this example the deficiency is 1. Whilst in this example the standard derivative method works, this 3-state model is used to illustrate how the reparameterisation method works.

First a reparameterisation is chosen. As the parameters come into the model through the transition and recapture matrices, the non-zero elements of these matrices form a sensible choice for a reparameterisation. This gives the reparameterisation

$$\begin{aligned} \mathbf{s} &= [\ s_1,\ s_2,\ \ldots,\ s_9,\ s_{10},\, s_{11}\ ]^T \\ &= [\ \sigma_1\beta_1\gamma_1,\, \sigma_2\beta_2\gamma_2,\, \ldots,\, \sigma_3(1-\beta_3),\ p_1,\ p_2,\ ]^T. \end{aligned}$$

Next the starting exhaustive summary is rewritten in terms of this reparameterisation giving

$$\boldsymbol{\kappa}(\mathbf{s}) = \left[s_1s_{10},\, s_4s_{11},\, s_2s_{10},\, \ldots\right]^T. \tag{1}$$

A derivative matrix, $\mathbf{D}_s$ is formed by differentiating (1) with respect to the s_i. This derivative matrix has rank 10 (and the reparameterisation is shown to be unique in the Maple worksheet by forming a derivative matrix of the reparameterisation with respect to the original parameters, and showing this has rank 11). Therefore we have shown again that there are 10 estimable parameters within this model. By solving an appropriate set of partial differential equations (see the Maple worksheet for details) we can show that a simpler exhaustive summary is

$$\mathbf{s}^e = \begin{bmatrix} \sigma_1\beta_1\gamma_1 \\ \sigma_2\beta_2\gamma_2 \\ \sigma_1\beta_1(1-\gamma_1) \\ \sigma_2\beta_2(1-\gamma_2) \\ \dfrac{1-\gamma_3}{\gamma_3} \\ \sigma_3\beta_3\sigma_1(1-\beta_1) \\ \sigma_3\beta_3\sigma_2(1-\beta_2) \\ \sigma_3(1-\beta_3) \\ p_1 \\ p_2 \end{bmatrix}^T.$$

Further it is shown that this is an exhaustive summary for all $N \geq 4$ and for most of the constraint models considered in Hunter and Caswell (2009), except when $\{\sigma_1 = \sigma_3, \beta_1 = \beta_3, \gamma_1 = \gamma_3\}$ and/or $\{\sigma_2 = \sigma_3, \beta_2 = \beta_3, \gamma_2 = \gamma_3\}$. It is then relatively easy to go through each of the constraint models in Table 2 of Hunter and Caswell (2009) and determine the deficiency of that model. More detail is given in the Maple worksheet.

However the 3-state breeding model illustrated above and the four state breeding success model illustrated in Cole and Morgan (2009a) are both time-invariant. If there is any time dependence within the model, finding the appropriate reparameterisation is much more complex, so instead in Section 2 a general simpler exhaustive summary is presented. The seabird examples of Hunter and Caswell (2009) are examined in detail in Section 3.

2 An Exhaustive Summary for Multi-State Capture-Recapture Models

Consider a multi-state model with S states, of which are U unobservable. Re-number the states so that the last U states are unobservable (states $(S-U+1),...,S$). Let the transition matrix be of the form

$$\boldsymbol{\Phi}_t = \begin{bmatrix} a_{1,1}(t) & a_{1,2}(t) & \ldots & a_{1,S}(t) \\ a_{2,1}(t) & a_{2,2}(t) & \ldots & a_{2,S}(t) \\ \vdots & & & \vdots \\ a_{S,1}(t) & a_{S,2}(t) & \ldots & a_{S,S}(t) \end{bmatrix}$$

and the recapture matrix be of the form

$$\mathbf{P}_t = \begin{bmatrix} p_1(t) & 0 & \ldots & 0 \\ 0 & p_2(t) & \ldots & 0 \\ \vdots & & & \vdots \\ 0 & 0 & \ldots & p_S(t) \end{bmatrix},$$

with $p_{S-U+1},...,p_S$ equal to zero, as the states are unobservable (and no p_i are equal to zero if all states are observable). If there are more than one observable state, $(S-U > 1)$ and N is large enough for there to have been enough release-recapture occasions to get to the maximum possible number of estimable parameters, that is N needs to satisfy:

$$(S^2+S-2U)(N-1)-S-2U(S-1) < \frac{1}{2}(N^2-N)(S-U)^2,$$

then a simpler exhaustive summary consists of the terms given in Table 1. The proof involves using reparameterisation and is given in Appendix A.

There are a total of $(S^2 + S - 2U)(N - 1) - S - 2U(S - 1)$ exhaustive summary terms as long as there are no zero $a_{i,j}$. This number of $(S^2+S-2U)(N-1)-S-2U(S-1)$ gives an upper bound for the number of estimable parameters. So if you have more than $(S^2 + S - 2U)(N - 1) - S - 2U(S - 1)$ parameters the model will be parameter redundant. (Having less than $(S^2 + S - 2U)(N - 1) - S - 2U(S - 1)$ parameters does not guarantee the model will be fully estimable, as there could be confounding of parameters). If there are any zero $a_{i,j}$ some exhaustive summary terms will be zero, so there will be correspondingly less actual exhaustive summary terms and the maximum number of estimable parameters will be correspondingly less. If any of the $a_{j,1}$ $(j = S - U + 1,..,S)$ are zero then $a_{j,1}$ can be replaced by $a_{j,2}$ in the last three types of exhaustive summary terms and the range changed appropriately (any terms equalling 1 can be excluded). If $a_{j,2}$ should be zero then use $a_{j,3}$ and so on. This is the case for the 4-state breeding success model of Hunter and Caswell (2009) examined in Section 3.2.

A Maple procedure, `simexsum`, has been written to find this simpler exhaustive summary. Given values the transition matrix, recapture matrix and N the procedure loops through appropriate code, given in Appendix D, to return the exhaustive summary of Table 1. (Note that if either of the constraints $S - U > 1$ and $(S^2+S-2U)(N-1)-S-2U(S-1) < \frac{1}{2}(N^2-N)(S-U)^2$ are violated then the procedure returns 0). There are also procedures for finding the derivative matrix and the estimable set of parameters, should the model be parameter redundant.

To illustrate the use of this simpler exhaustive summary we revisit the 3-state time-invariant model discussed in the introduction. Although it is not necessary to use this simpler exhaustive summary, it is relatively simple to reproduce the result that there are 10 out of a possible 11 estimable parameters using the Maple code below (with $\mathbf{\Phi}$ replaced by `A` and γ replaced by `g` and where the maple procedure `Dmat` finds the derivative matrix). The estimable parameters are to found be $\sigma_3(\beta_3-1)$, $\frac{\sigma_3(\beta_3-\beta_1)}{\beta_1}$, $\sigma_1\beta_1$, $\frac{\sigma_3(\beta_3-\beta_2)}{\beta_2}$, $\sigma_2\beta_2, \gamma_1, \gamma_2, \gamma_3, p_1, p_2$ using the Maple procedure `Estpars`, given below:

```
> A:=Matrix(1..3,1..3):
  A[1,1]:=sigma[1]*beta[1]*g[1]:
  A[1,2]:=sigma[2]*beta[2]*g[2]:
  A[1,3]:=sigma[3]*beta[3]*g[3]:
  A[2,1]:=sigma[1]*beta[1]*(1-g[1]):
  A[2,2]:=sigma[2]*beta[2]*(1-g[2]):
  A[2,3]:=sigma[3]*beta[3]*(1-g[3]):
  A[3,1]:=sigma[1]*(1-beta[1]):
  A[3,2]:=sigma[2]*(1-beta[2]):
  A[3,3]:=sigma[3]*(1-beta[3]):
> P := <<p[1]|0|0)>,<0|p[2]|0>,<0|0|0>>:
> pars:=<sigma[1],sigma[2],sigma[3],beta[1],
  beta[2],beta[3],g[1],g[2],g[3],p[1],p[2]>:
> kappa:=simexsum(A,P,4):
> DD:=Dmat(kappa,pars):
> r:=Rank(DD); d := Dimension(pars)-r;
  pp := Dimension(pars);
      r:=10
      d:=1
      p:=11
> simplify(Estpars(DD,pars));
      f(sigma[1],sigma[2],sigma[3],beta[1],
      beta[2],beta[3],g[1],g[2],g[3],p[1],p[2])
      = _F1( sigma[3]beta[3]-sigma[3] ,
      sigma[3](beta[1]-beta[3])/beta[1],
      sigma[1]beta[1],
      sigma[3](-beta[2]+beta[3])/beta[2],
      sigma[2] beta[2],
      [1],g[2],g[3],p[1],p[2])
```

Note that the exhaustive summary of Table 1 requires that $S-U > 1$ and that $(S^2+S-2U)(N-1)-S-2U(S-1) > \frac{1}{2}(N^2-N)(S-U)^2$. These rules tend to be violated when there is little information available, such as if there is only one observable state (rule $S-U > 1$ does not apply). If there are a small number

Exhaustive Summary Terms	Range	No. of Terms
$p_i(t+1)a_{i,j}(t)$	$t = 1, ..., N-1$ $i = 1, .., S-U$ $j = 1, .., S-U$	$(N-1)(S-U)^2$
$p_i(t)$	$t = 2, ..., N-1$ $i = 1, .., S-U$	$(N-2)(S-U)$
$p_i(t+1)a_{i,j}(t)a_{j,1}(t)$	$t = 2, ..., N-1$ $i = 1, .., S-U$ $j = S-U+1, .., S$	$U(N-2)(S-U)$
$\frac{a_{j,i}(t-1)}{a_{j,1}(t-1)}$	$t = 2, ..., N-1$ $i = 2, .., S-U$ $j = S-U+1, .., S$	$U(N-2)(S-U-1)$
$\frac{a_{j,i}(t-1)a_{i,1}(t-2)}{a_{j,1}(t-1)}$	$t = 3, ..., N-1$ $i = S-U+1, .., S$ $j = S-U+1, .., S$	$U^2(N-3)$

Table 1 Table of a simpler exhaustive summary for a multi-state mark-recapture model with $N-1$ years of marking and $N-1$ years of recapture, with S states, U of which are unobservable. This is only an exhaustive summary if $S-U > 1$ and $(S^2+S-2U)(N-1)-S-2U(S-1) < \frac{1}{2}(N^2-N)(S-U)^2$ (see the text and Appendix A for details).

of observable states compared with the number of unobservable states the later condition requires a very large N. If these conditions are not satisfied another simpler exhaustive summary would need to be found. An example is given below in Section 3.3 below, which is a 9-state example with only two observable states. Whilst the condition $S-U > 1$ is satisfied, the condition $(S^2+S-2U)(N-1)-S-2U(S-1) > \frac{1}{2}(N^2-N)(S-U)^2$ requires $N \geq 40$. Other work includes the development of a simple exhaustive summary for the case $S = 2$ and $U = 1$, in particular to examine a two-state model for breeding and non-breeding of Great Crested Newts (McCrea and Cole, work in progress).

3 Seabird Examples

In this Section the simpler exhaustive summary, given in Table 1, is used to examine the parameter redundancy of 2 out of the 3 examples presented in Hunter and Caswell (2009). Section 3.1 examines a 3-state multiple site breeding model. Section 3.2 considers a 4-state breeding success and failure model. In the case of the third example of Hunter and Caswell (2009) a different simpler exhaustive summary is found for recruitment models in Section 3.3.

3.1 3-state Multiple Site Breeding Model

The 3-state time-invariant model discussed in the introduction can be extended to include time variation. In this case the transition matrix becomes

$$\boldsymbol{\Phi}_t = \begin{bmatrix} \sigma_{1,t}\beta_{1,t}\gamma_{1,t} & \sigma_{2,t}\beta_{2,t}\gamma_{2,t} & \sigma_{3,t}\beta_{3,t}\gamma_{3,t} \\ \sigma_{1,t}\beta_{1,t}\bar{\gamma}_{1,t} & \sigma_{2,t}\beta_{2,t}\bar{\gamma}_{2,t} & \sigma_{3,t}\beta_{3,t}\bar{\gamma}_{3,t} \\ \sigma_{1,t}\bar{\beta}_{1,t} & \sigma_{2,t}\bar{\beta}_{2,t} & \sigma_{3,t}\bar{\beta}_{3,t} \end{bmatrix},$$

which depends on the parameters $\sigma_{i,t}$, survival at location i at time t, $\beta_{i,,t}$, breeding at an observable site given survival at location i at time t, and $\gamma_{i,t}$, probability of breeding at site 1, given survival at site i and breeding at time t. Its recapture matrix becomes

$$\mathbf{P}_t = \begin{bmatrix} p_{1,t} & 0 & 0 \\ 0 & p_{2,t} & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

where $p_{i,t}$ is the probability of being recaptured at site i at time t.

The parameter redundancy status of this 3-state model is examined (see Maple code) and the results are displayed in Table 2. The first models examined are general models with all parameters and no constraints. In the CJS model the last survival and capture probabilities are confounded and cannot be estimated. In Hunter and Caswell (2009) they also point out that for unobservable states the parameters can not be identified at $t = 1$. For this example, parameters $\sigma_{3,1}$, $\beta_{3,1}$ and $\gamma_{3,1}$, from the unobservable state 3, never appear in the model, and are therefore are called completely redundant. They therefore suggest that all freely time-varying parameters should be set equal at $t = 1$ and $t = 2$, and at $t = N-2$ and $t = N-1$ ($t = 2$ and $t = 3$, and $t = N-1$ and $t = N$ for recapture probability) to ensure identifiability. This is of course sensible if there is biological evidence to suggest this is true. However this is not necessary for all parameters. The next models examined allow for the constraints of Hunter and Caswell (2009). It can be noted that whilst the deficiency is reduced it is not completely eliminated, and unlike the general model, this constraint is not making use of the maximum possible number of estimable parameters. In this 3-state model there are a maximum

	General Model			Hunter and Caswell Constraints			Alternative Constraints		
N	r	d	p	r	d	p	r	d	p
4	23	7	30	10	1	11	23	0	23
5	33	8	41	21	1	22	33	0	33
6	43	9	52	31	2	33	43	0	43
7	53	10	63	41	3	44	53	0	53
N	$10N-17$	$N+3$	$11N-14$	$10N-29$	$N-4$	$11N-33$	$10N-17$	0	$10N-17$

Table 2 Parameter redundancy of the 3-state model. N denotes the number of years of marking and recapture. r denotes the rank of the model, p denotes the number of parameters in the model and $d = p - r$ denotes the deficiency of the model. Note completely redundant parameters, $\sigma_{3,1}$, $\beta_{3,1}$ and $\gamma_{3,1}$ are ignored and not counted in parameter numbers as they never appear in the model. The general model consists of all possible parameters. The Hunter and Caswell (2009) constraints model applies the constraints $\sigma_{j,1} = \sigma_{j,2}, \sigma_{j,N-1} = \sigma_{j,N-2}, \beta_{j,1} = \beta_{j,2}, \beta_{j,N-1} = \beta_{j,N-2}, \gamma_{j,1} = \gamma_{j,2}, \gamma_{j,N-1} = \gamma_{j,N-2}, p_{i,2} = p_{i,3}, p_{i,N} = p_{i,N-1}$. The alternative constraints model applies the constraints $\sigma_{2,t} = \sigma_{1,t}, \sigma_{j,N-1} = \sigma_{j,N-2}, p_{i,N} = p_{i,N-1}$.

of $10N - 17$ estimable parameters; this is determined by the length of the exhaustive summary in the case $S = 3, U = 1$. The general model without constraints has rank $10N-17$ and hence has $10N-17$ estimable parameters. However Hunter and Caswell (2009) only has $10N-29$ because some of the constraints result in identical terms in the simple exhaustive summary. Both the general model and the Hunter and Caswell constraint model have deficiency that increases with N.

Instead, as we can never estimate the completely redundant parameters, $\sigma_{3,1}$, $\beta_{3,1}$ and $\gamma_{3,1}$, we exclude them from the parameter set. By considering estimable parameter combinations of the general model we suggest an alternative model that is not parameter redundant. This model has the constraints $\sigma_{2,t} = \sigma_{1,t}, \sigma_{j,N-1} = \sigma_{j,N-2}, p_{i,N} = p_{i,N-1}$ for $t = 1, ..., N-1$ and $i = 1, ..., 3$ for σ and $i = 1, ..., 2$ for p. This model has the advantage that it has the maximum number of estimable parameters, and therefore makes use of all possible available information. Other such models that are fully estimable can be built in a similar way, and could be based on biological theory. It is also possible to iterate through any sets of other constraints of interest, such as those presented in Hunter and Caswell (2009) Table 3, but rather than produce results for a specific value of N (Hunter and Caswell, 2009 use $N = 6$), general results about parameter redundancy can be produced for any N.

3.2 4-state Breeding Success and Failure Model

The 4-state model has the following states:

- State 1 for successful breeding. This is an observable state.
- State 2 for unsuccessful breeding. This is an observable state.
- State 3 for the year post-successful breeding. This is an unobservable state.
- State 4 for the year post-unsuccessful breeding. This is an unobservable state.

The transition matrix for this model is

$$\boldsymbol{\Phi}_t = \begin{bmatrix} \sigma_{1,t}\beta_{1,t}\gamma_{1,t} & \sigma_{2,t}\beta_{2,t}\gamma_{2,t} & \sigma_{3,t}\beta_{3,t}\gamma_{3,t} & \sigma_{4,t}\beta_{4,t}\gamma_{4,t} \\ \sigma_{1,t}\beta_{1,t}\bar{\gamma}_{1,t} & \sigma_{2,t}\beta_{2,t}\bar{\gamma}_{2,t} & \sigma_{3,t}\beta_{3,t}\bar{\gamma}_{3,t} & \sigma_{4,t}\beta_{4,t}\bar{\gamma}_{4,t} \\ \sigma_{1,t}\bar{\beta}_{1,t} & 0 & \sigma_{3,t}\bar{\beta}_{3,t} & 0 \\ 0 & \sigma_{2,t}\bar{\beta}_{2,t} & 0 & \sigma_{4,t}\bar{\beta}_{4,t} \end{bmatrix},$$

where $\bar{\gamma}_{1,t} = 1 - \gamma_{1,t}$ etc... and which depends on the parameters $\sigma_{i,t}$, the probability of survival at location i at time t, $\beta_{i,,t}$, the probability of breeding given survival at location i at time t, and $\gamma_{i,t}$, the probability of successful breeding given breeding and survival at location i at time t. Its recapture matrix is

$$\mathbf{P} = \begin{bmatrix} p_{1,t} & 0 & 0 & 0 \\ 0 & p_{2,t} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

where $p_{i,t}$ is the probability of being recaptured at state i at time t.

In a similar way to the 3-state model the parameter redundancy of this 4-state model is examined (see Maple code); the results are given in Table 3 for the general model and using Hunter and Caswell (2009)'s constraints. These results illustrate similar findings as for the 3-state model. The constraints imposed by Hunter and Caswell (2009) result in fewer estimable parameters than the maximum number of estimable parameters, $12N - 36$ compared with $12N - 22$. One possible alternative set of constraints is also shown in Table 3. This also illustrates that the symbolic method allows general rules on deficiency to be found for any N.

3.3 Recruitment Model

The pre-breeding survival and recruitment model of Hunter and Caswell (2009) models delayed maturity.

	General Model			Hunter and Caswell Constraints			Alternative Constraints		
N	r	d	p	r	d	p	r	d	p
7	62	16	78	48	8	56	62	0	62
8	74	18	92	60	10	70	74	0	74
9	86	20	106	72	12	84	86	0	86
N	$12N-22$	$2N+2$	$14N-20$	$12N-36$	$2N-6$	$14N-42$	$12N-22$	0	$12N-22$

Table 3 Parameter redundancy of the 4-state model. N denotes the number of years of marking and recapture. r denotes the rank of the model, p denotes the number of parameters in the model and $d = p - r$ denotes the deficiency of the model. Note completely redundant parameters, $\sigma_{3,1}$, $\beta_{3,1}$, $\gamma_{3,1}$, $\sigma_{4,1}$, $\beta_{4,1}$ and $\gamma_{4,1}$ are ignored and not counted in parameter numbers as they never appear in the model. The general model consists of all possible parameters. The Hunter and Caswell constraints model applies the constraints $\sigma_{j,1} = \sigma_{j,2}, \sigma_{j,N-1} = \sigma_{j,N-2}, \beta_{j,1} = \beta_{j,2}, \beta_{j,N-1} = \beta_{j,N-2}, \gamma_{j,1} = \gamma_{j,2}, \gamma_{j,N-1} = \gamma_{j,N-2}, p_{i,2} = p_{i,3}, p_{i,N} = p_{i,N-1}$. The alternative constraints model applies the constraints $\beta_{4,N-1} = \beta 4, N-2, \sigma_{2,t} = \sigma_{1,t}, \sigma_{4,t} = \sigma_{3,t} \sigma_{j,N-1} = \sigma_{j,N-2}, p_{i,N} = p_{i,N-1}$.

The first state represents first year animals, the last state represents breeding animals and the states in between represent non-breeders of different ages. Recruitment is possible from the kth year onwards, with probability $\alpha_{i,t}$ for animals aged i at time t. There are up to y possible recruitment years. The probability of survival, dependent on age i and time t, is denoted by $\sigma_{i,t}$, with $\sigma_{y+k,t}$ denoting survival in the last breeding state. The animal is observed in the first year and when it is breeding in the last state. The transition matrix for this recruitment model is

$$\boldsymbol{\Phi}_t = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \sigma_{1,t} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \ddots & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_{k-1,t} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_{k,t}\bar{\alpha}_{k,t} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & \sigma_{k,t}\alpha_{k,t} & \dots & \sigma_{b-1,t}\alpha_{b-1,t} & \sigma_{b,t} \end{bmatrix},$$

where $\bar{\alpha}_{i,t} = 1 - \alpha_{i,t}$. The recapture matrix is

$$\mathbf{P}_t = \begin{bmatrix} 1\, 0 \dots 0\; 0 \\ 0\, 0 \quad\; 0\; 0 \\ \vdots \quad \ddots \quad \vdots \\ 0\, 0 \quad\; 0\; 0 \\ 0\, 0 \dots 0\; p_t \end{bmatrix}$$

where p_t is the probability of being recaptured in the breeding state at time t. (The first year recapture probability is set to 1 for convenience, but would never actually appear in the model.)

As there are only two observable states, to use the simpler exhaustive summary given in Table 1 would require a large number years of ringing and recovery. For example in the 9-state illustrative example of Hunter and Caswell (2009), $N \geq 40$ would be required. Instead of using this simpler exhaustive summary, the reparameterisation method is used to find a simpler exhaustive summary that is specific for just this recruitment model with only two observable states. This exhaustive summary is given in Table 4 below and its proof is given in Appendix B.

To illustrate the general use of the exhaustive summary given in Table 4, the 9-state example used to illustrate the recruitment model in Hunter and Caswell (2009) is used in Appendix C. It is also possible to use the exhaustive summary's form to determine some general results. From the first two types of exhaustive summary terms in Table 4 it is obvious that the parameters $\sigma_{k+y,t}$ and p_{t+1} are estimable for $t = 1, ..., N-2$ and that $\sigma_{k+y,N-1}$ and p_N are confounded with only the product estimable. The third exhaustive summary term, $p_{t+1}\sigma_{k,t}\alpha_{k,t}\prod_{j=1}^{k-1}\sigma_{j,t+j-k}$, indicates the parameters $\sigma_{1,t}$ to $\sigma_{k,t}$ with $\alpha_{k,t}$ are always going to be confounded as they only ever appear in that product, and therefore not individually estimable. Similarly $\sigma_{i,t}$ is always going to be confounded with $\alpha_{i,t}$ and $\alpha_{i-1,t-1}$ for $k < i < k+y$. This exhaustive summary also shows that, even without time dependence, full age-dependence would not be estimable (as observed by Clobert *et al*, 1994). For $N \geq y+k-1$ there are $(2+Y)N - \frac{1}{2}(y^2-y) - yk - 3$ exhaustive summary terms, which will also be the maximum number of estimable parameters. A model with more than this number of parameters will be parameter redundant. To over come this confounding of parameter Hunter and Caswell (2009) examine the following constraints:

- a common survival for the non-recruiting years: $\sigma_{k-1} = ... = \sigma_2 = \sigma_1$
- when there is no time dependence in the model: $\text{logit}(\sigma_i) = a + bi$ for $i = k, .., k+y$
- when there is time dependence in the model: $\text{logit}(\sigma_{i,t}) = a_i + b_i t$ for $t = 1, .., N-1$
- when there is time dependence in the model and a time-dependent covariate: $\text{logit}(\sigma_{i,t}) = a_i + b_i x_t$ for $t = 1, .., N-1$.

Exhaustive Summary Terms	Range	No. Terms
$p_{t+1}\sigma_{k+y,t}$	$t = 1, \ldots, N-1$	$N-1$
p_t	$t = 2, \ldots, N-1$	$N-2$
$p_{t+1}\sigma_{k,t}\alpha_{k,t}\prod_{j=1}^{k-1}\sigma_{j,t+j-k}$	$t = k, \ldots, N-1$	$N-k$
$\frac{p_{t+1}\sigma_{i,t}\alpha_{i,t}(1-\alpha_{i-1,t-1})}{\alpha_{i-1,t-1}}$	$t = i, \ldots, N-1$ $i = k+1, \ldots, y+k-1$	$N(y-1) - \frac{1}{2}(y^2-y) - yk + k$

Table 4 Exhaustive summary for the recruitment model, when $k \geq 3$, $N \geq 3$ and $y \geq 2$.

Cole and Morgan (2007) show how to find the parameter redundancy of models with time varying covariates, such as the examples illustrated above. The number of estimable parameters is equal to the minimum of number of estimable parameters in the equivalent model without covariates and the number of parameters in the covariate model. As the number of terms in the exhaustive summary of Table 4 will also be equal to the rank of the derivative matrix (because the exhaustive summary is in reduced-form), and because we can deduce the number of estimable parameters in a covariate model from a model without covariates, it is possible to deduce general rules about various constraint models. These rules are presented in Table 5, and demonstrate how useful exhaustive summaries can be in producing general rules.

4 Discussion

Hunter and Caswell (2009) presented an improved numerical method for detecting parameter redundancy in multi-state mark-recapture models, because it was thought impossible to use symbolic methods. In this paper we have shown that it is now possible to use symbolic methods to detect parameter redundancy for these models. We have developed general exhaustive summaries for multi-site capture recapture models and shown how they can be applied. We have also demonstrated some of the general rules that it is possible to create using this symbolic method, whereas it is not possible to obtain such general rules using numerical methods.

Table 6 compares the numerical method with the symbolic methods. Based on these advantages and disadvantages, if interest lies in whether a particular model for a specific data set is parameter redundant then a numerical method would be sufficient. However if interest lies in the redundancy of a model in general or a particular class of models, general rules can be found using the symbolic method. Further if a model is fully estimable it is further possible to detect nested parameter redundant models and near redundancy (see Cole and Morgan, 2009a which extends work on decompositions of Gimenez *at al*, 2003).

The methodology discussed in this paper is perfectly general and could in theory be applied to any parametric model. The creation of simpler exhaustive summaries, such as those created here for multi-state models, could be developed for other families of ecological models. We have looked at parameter redundancy in Pledger *et al* (2009)'s stopover models (Matechou and Cole unpublished work). Future plans include developing these methods other ecological models such as Rouan *et al* (2009)'s memory models and MacKenzie *et al* (2009)'s multi-site occupancy models.

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time dep.	constraint	ex. sum. terms	no. ex. sum. terms	no. pars.	deficiency
no	$\sigma_{k-1} = ... = \sigma_2 = \sigma_1$	$p\sigma_{k+y}$ p $p\sigma_k \alpha_k \sigma_j^{k-1}$ $\frac{p\sigma_i \alpha_i (1-\alpha_{i-1})}{\alpha_{i-1}}$	$y+2$	$2y+3$	$y+1$
no	$\sigma_{k-1} = ... = \sigma_2 = \sigma_1$ $\text{logit}(\sigma_i) = a_\sigma + b_\sigma i$	as above	$y+2$	$y+4$	2
no	$\sigma_{k-1} = ... = \sigma_2 = \sigma_1$ $\text{logit}(\sigma_i) = a_\sigma + b_\sigma i$ $\text{logit}(\alpha_i) = a_\alpha + b_\alpha i$	as above	$y+2$	6	$\max(0, 4-y)$
yes	$p_N = p_{N-1}$ $\sigma_{k-1} = ... = \sigma_2 = \sigma_1$	as in table 4	$(2+y)N$ $-\frac{1}{2}(y^2-y)$ $-yk-3$	$2(1+y)N$ $-(y^2-y)$ $-2yk-2$	yN $-\frac{1}{2}(y^2-y)$ $-yk+1$
yes	$p_N = p_{N-1}$ $\sigma_{k-1} = ... = \sigma_2 = \sigma_1$ $\text{logit}(\sigma_{i,t}) = a_{i,\sigma} + b_{i,\sigma} t$ $\text{logit}(\alpha_{i,t}) = a_{i,\alpha} + b_{i,\alpha} t$ $k \geq i \geq y+k$	as in table 4	$(2+y)N$ $-\frac{1}{2}(y^2-y)$ $-yk-3$	$4y+2N$ -2	$\max(0,$ $3y-2Ny$ $+y^2+2yk)^\ddagger$
yes	$p_N = p_{N-1}$ $\sigma_{k-1} = ... = \sigma_2 = \sigma_1$ $\text{logit}(\sigma_{i,t}) = a_{i,\sigma} + b_{i,\sigma} x_t$ $\text{logit}(\alpha_{i,t}) = a_{i,\alpha} + b_{i,\alpha} x_t$ $k \geq i \geq y+k$	as in table 4	$(2+y)N$ $-\frac{1}{2}(y^2-y)$ $-yk-3$	$4y+2N$ -2	$\max(0,$ $3y-2Ny$ $+y^2+2yk)^\ddagger$

Table 5 Some general rules on deficiency of the recruitment model with constraints. Deficency is calculated as: no. pars − min(no. ex. sum. terms , no.pars)) ‡Will be zero in most cases.

Method:	Numerical	Symbolic
Ease of use	Fairly easy	Requires some algebra to find a simple exhaustive summary. Then relatively easy to use.
Computation	Can be added to any computer program	Needs a symbolic algebra package such as Maple
Estimable parameter combinations	Trial and error needed to find.	Can be found using a Maple procedure
Accuracy	Not always, although Hunter and Caswell's work improves this.	Finds the actual redundancy for all parameter values
Near Redundancy	Is not distinguishable from actual redundancy	Can be detected using PLUR decomposition
General rules	Not possible to deduce	Can be found using extension theorems

Table 6 Numerical versus Symbolic Methods for Detecting Parameter Redundancy

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A Proof of Simpler Exhaustive Summary

The Maple code form this proof can be found in Maple worksheet `simexsumproof.mw`. To show that Table 1 is an exhaustive summary, first consider the case of no unobservable states. Starting from $N = 3$, $S = 2$ we show that for transition and recapture matrices

$$\boldsymbol{\Phi}_t = \begin{bmatrix} a_{1,1}(t) & a_{1,2}(t) \\ a_{2,1}(t) & a_{2,2}(t) \end{bmatrix} \; \mathbf{P}_t = \begin{bmatrix} p_1(t) & 0 \\ 0 & p_2(t) \end{bmatrix}$$

a possible reparameterisation with 10 elements is

$$\mathbf{s} = [p_1(2)a_{1,1}(1), p_2(2)a_{2,1}(1), p_1(2)a_{1,2}(1), p_2(2)a_{2,2}(1), p_1(2), p_2(2), p_1(3)a_{1,1}(2), ..., p_2(3)a_{2,2}(2)]^T .$$

We rewrite the original exhaustive summary, consisting of the non-zero p-array terms, in terms of s_i. This is then differentiated with respect to the s_i to form the derivative matrix $\mathbf{D}_s$. The derivative matrix has full rank 10, so the reparameterisation $\mathbf{s}$ is an exhaustive summary. Now extend this to $N = 4$. The extra reparameterisation terms are

$$\mathbf{s}^{'} = [p_1(4)a_{1,1}(3), ..., p_2(4)a_{2,2}(2), p_1(3), p_2(3)]^T .$$

Extra original exhaustive summary terms are also added, which are differentiated with respect to $\mathbf{s}^{'}$ to form the derivative matrix $\mathbf{D}_{ex}$. The rank of $\mathbf{D}_{ex}$ is of full rank 6, therefore by the extension theorem and by induction (Cole and Morgan, 2009a)

$$\mathbf{s} = [p_1(2)a_{1,1}(1), ..., p_2(2)a_{2,2}(1), p_1(2), p_2(2), ..., p_1(N-1), p_2(N-1), p_1(N)a_{1,1}(N-1), ..., p_N(N)a_{2,2}(N-1),]^T$$

will always be an exhaustive summary for any $N \geq 3$.

Next consider extending to $S = 3$ again starting from $N = 3$. The transition and recapture matrices are

$$\boldsymbol{\Phi}_t = \begin{bmatrix} a_{1,1}(t) & a_{1,2}(t) & a_{1,3}(t) \\ a_{2,1}(t) & a_{2,2}(t) & a_{2,3}(t) \\ a_{3,1}(t) & a_{3,2}(t) & a_{3,3}(t) \end{bmatrix} \; \mathbf{P}_t = \begin{bmatrix} p_1(t) & 0 & 0 \\ 0 & p_2(t) & 0 \\ 0 & 0 & p_3(t) \end{bmatrix} . \quad (2)$$

The reparameterisation has the extra terms

- $p_3(t+1)a_{3,j}(t)$ for $j = 1, 2, 3$ and $t = 1, 2$,
- $p_i(t+1)a_{i,3}(t)$ for $i = 1, 2$ and $t = 1, 2$,
- $p_3(2)$,

and in a similar way we use the extension theorem and induction to deduce that when all states are observable an exhaustive summary consists of the terms:

- $p_i(t+1)a_{i,j}(t)$ for $t = 1, ..., N-1$, $i = 1, .., S$ and $j = 1, .., S$,
- $p_i(t)$ for $t = 2, ..., N-1$ and $i = 1, .., S$,

which are the only terms of the exhaustive summary given by Table 1 that apply when $U = 0$.

Then we move on to consider unobservable states. The first case we consider is $S = 3$, $N = 4$, with one unobservable state, so that $U = 1$. The transition and recapture matrices are the same as in equation 2, with $p_3(t) = 0$. A possible reparameterisation of length 23 has elements of the form given in Table 1. We rewrite the original exhaustive summary, consisting of the non-zero p-array terms, in terms of s_i. This is then differentiated with respect to the s_i to form the derivative matrix $\mathbf{D}_s$. The derivative matrix has full rank 23, so the reparameterisation given by Table 1 is an exhaustive summary, for $S = 3$, $N = 4$ and $U = 1$. This can then be extend to $N = 4$. There are 10 extra reparameterisation terms. The extra original exhaustive summary terms are analysed with respect to these 10 extra reparameterisation terms and the exhaustive summary is applied in three parts; the first two are shown to be full rank in the Maple worksheet. The third part contains no extra reparameterisation parameters. Therefore by the extension theorem and by induction Table 1 is an exhaustive summary, for $S = 3$, $N \geq 4$ and $U = 1$.

Next we consider extending the case $S = 3$, $N = 4$, $U = 1$ to the case $S = 4$, $N = 4$, $U = 1$. For convenience of the proof, we continue to label the 3rd state as unobservable and introduce a fourth new observable state. (This is contrast to the exhaustive summary presented in Table 1, where the fourth state would be labeled as unobservable.) The transition and recapture matrices are

$$\boldsymbol{\Phi}_t = \begin{bmatrix} a_{1,1}(t) & a_{1,2}(t) & a_{1,3}(t) & a_{1,4}(t) \\ a_{2,1}(t) & a_{2,2}(t) & a_{2,3}(t) & a_{2,4}(t) \\ a_{3,1}(t) & a_{3,2}(t) & a_{3,3}(t) & a_{3,4}(t) \\ a_{4,1}(t) & a_{4,2}(t) & a_{4,3}(t) & a_{4,4}(t) \end{bmatrix} \; \mathbf{P}_t = \begin{bmatrix} p_1(t) & 0 & 0 & 0 \\ 0 & p_2(t) & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & p_4(t) & 0 \end{bmatrix} .$$

By examining the extra original exhaustive summary terms with respect to the extra reparameterisation terms that are added:

- $p_4(t+1)a_{4,j}(t)$ for $j = 1, 2, 4$ and $t = 1, ..., 4$,
- $p_i(t+1)a_{i,4}(t)$ for $i = 1, 2$ and $t = 1, ..., 4$,
- $p_4(t)$ for $t = 2, ..., 4$,
- $p_4(t+1)a_{4,3}(t)a_{3,1}(t-1)$ for $t = 2, ..., 4$,
- $\dfrac{a_{3,4}(t-1)}{a_{3,1}(t-1)}$ for $t = 2, ..., 4$,

we show in the Maple worksheet using the extension theorem and by induction, that once the states are relabeled, that exhaustive summary presented in Table 1 is an exhaustive summary for $S \geq 3$, $N \geq 4$ and $U = 1$.

Finally we consider extending the case $S = 3$, $N = 7$, $U = 1$ to the case $S = 4$, $N = 7$, $U = 2$. From the results above above we already know that Table 1 is an exhaustive summary for $S = 3$, $N = 7$, $U = 1$. We then use the extension theorem once more. Examining the extra original exhaustive summary terms with respect to the extra reparameterisation terms that are added:

- $p_4(t+1)a_{i,4}(t)a_{4,1}(t-1)$ for $t = 2, ..., 6$ and $i = 1, 2$,
- $\dfrac{a_{4,2}(t-1)}{a_{4,1}(t-1)}$ for $t = 2, ..., 6$,
- $\dfrac{a_{4,3}(t-1)a_{3,1}(t-2)}{a_{4,1}(t-1)}$ for $t = 3, ..., 6$,
- $\dfrac{a_{3,4}(t-1)a_{4,1}(t-2)}{a_{3,1}(t-1)}$ for $t = 3, ..., 6$,
- $\dfrac{a_{4,4}(t-1)a_{4,1}(t-2)}{a_{4,1}(t-1)}$ for $t = 3, ..., 6$,

we show in the Maple worksheet using the extension theorem and by induction, that the exhaustive summary presented in Table 1 is an exhaustive summary for $S \geq 4$, $N \geq 7$ and $U = 2$.

We have proved the case $S \geq 3$, $N \geq 4$ and $U = 1$. Then consider any other S and U such that $S - U > 1$. There will always be a $S' = S - 1$ $U' = U - 1$ so that a similar move as from $S = 3$, $U = 1$ to $S = 4$, $U = 2$ can be applied. All that is required is to start at an N large enough so that there will be more original exhaustive summary terms than reparameterisation terms. There are $(S^2+S-2U)(N-1)-S-2U(S-1)$ terms in the reparameterisation and $\frac{1}{2}(N^2-N)(S-U)^2$ terms in the original exhaustive summary. So this results in a restriction on N of $(S^2+S-2U)(N-1)-S-2U(S-1) < \frac{1}{2}(N^2-N)(S-U)^2$. Therefore by induction the exhaustive summary presented in Table 1 is an exhaustive summary for all cases as long as $U - S > 1$ and $(S^2 + S - 2U)(N - 1) - S - 2U(S - 1) < \frac{1}{2}(N^2 - N)(S - U)^2$.

B Proof of Recruitment Simpler Exhaustive Summary

This section provides the proof for the recruitment exhaustive summary given in Table 4. The Maple code for this proof can be found in Maple worksheet `recruitmentproof.mw`.

The proof starts by considering the case of $N = 3$ years of ringing and recovery, $k = 3$ years of recruitment and $y = 2$ recruiting classes. It is shown in the `recruitmentproof.mw` that

$$\mathbf{s} = \begin{bmatrix} s_1 \\ s_2 \\ s_3 \end{bmatrix} = \begin{bmatrix} p_2\sigma_{5,1} \\ p_2 \\ p_3\sigma_{5,2} \end{bmatrix},$$

is an exhaustive summary. This is shown by rewriting the original exhaustive summary, consisting of the entries of the p-array, in terms of $\mathbf{s}$ and then finding the derivative matrix of this with respect to the s_i. This derivative matrix has full rank 3, so $\mathbf{s}$ is an exhaustive summary. As well as $N = 3$ we then consider each of $N = 4$,$N = 5$ and $N = 6$ to show that

$$\mathbf{s} = \begin{bmatrix} s_1 \\ s_2 \\ s_3 \\ s_4 \\ s_5 \\ s_6 \\ s_7 \\ s_8 \\ s_9 \\ s_{10} \\ s_{11} \\ s_{12} \\ s_{13} \\ s_{14} \end{bmatrix} = \begin{bmatrix} \left.\begin{matrix} p_2\sigma_{5,1} \\ p_2 \\ p_3\sigma_{5,2} \end{matrix}\right\} N \geq 3 \\ \left.\begin{matrix} p_3 \\ p_4\sigma_{5,3} \\ p_4\sigma_{3,3}\alpha_{3,3}\sigma_{2,2}\sigma_{1,1} \end{matrix}\right\} N \geq 4 \\ \left.\begin{matrix} p_4 \\ p_5\sigma_{5,4} \\ p_5\sigma_{3,4}\alpha_{3,4}\sigma_{2,3}\sigma_{1,2} \\ p_5\sigma_{4,4}\alpha_{4,4}(1-\alpha_{3,3})/\alpha_{3,3} \end{matrix}\right\} N \geq 5 \\ \left.\begin{matrix} p_5 \\ p_6\sigma_{5,5} \\ p_6\sigma_{3,5}\alpha_{3,5}\sigma_{2,4}\sigma_{1,3} \\ p_6\sigma_{4,5}\alpha_{4,5}(1-\alpha_{3,4})/\alpha_{3,4} \end{matrix}\right\} N \geq 6 \end{bmatrix},$$

is an exhaustive summary by considering ranks of derivative matrices. The extension theorem (Catchpole and Morgan, 1997 and Cole and Morgan, 2009a) is also applied to show that each additional year of ringing and recovery would add the exhaustive summary terms:

$$\begin{bmatrix} p_{N-1} \\ p_N\sigma_{5,N-1} \\ p_N\sigma_{3,N-1}\alpha_{3,N-1}\sigma_{2,N-2}\sigma_{1,N-3} \\ p_N\sigma_{4,N-1}\alpha_{4,N-1}(1-\alpha_{3,N-2})/\alpha_{3,N-2} \end{bmatrix}.$$

Next consider increasing k by 1. It is shown in the Maple worksheet that apart from changing numbering, the only difference is that the exhaustive summary term

$p_N\sigma_{3,N-1}\alpha_{3,N-1}\sigma_{2,N-2}\sigma_{1,N-3}$

is replaced by

$p_N\sigma_{4,N-1}\alpha_{4,N-1}\sigma_{3,N-2}\sigma_{2,N-3}\sigma_{1,N-4}$

and it and the subsequent term each appear when N is one greater. This pattern continues as k is increased further.

Now consider again the case where $k = 3$ and instead increase y by 1 so $y = 3$. In each case of $N = 3, \ldots, 6$ the extension theorem can be used to show that adding an extra y adds an extra exhaustive summary term $s_{14} = p_N\sigma_{5,N-1}\alpha_{5,N-1}(1 - \alpha_{4,N-2})/\alpha_{4,N-2}$ when $N \geq 6$, but that $\mathbf{s}$ is still an exhaustive summary. Hence by induction we can prove that an exhaustive summary for the recruitment model is given by Table 4.

C 9-state recruitment example

The 9-state recruitment model of Hunter and Caswell (2009) has $k = 4$ and $y = 5$. The Maple procedure `recruitment` finds the exhaustive summary given in Table 4. Using Maple code of the form:

```
> N := 5:
> kappa := recruitment(N, 4, 5):
> pars := <seq(op(i,indets(kappa)),i=1..nops(indets(kappa)))>:
> DD := Dmat(kappa, pars):
> r := Rank(DD); d := Dimension(pars)-r; pp := Dimension(pars);
Estpars(DD, pars)
```

it is possible to find the rank and deficiency and estimable parameter combinations for each of $N \geq 3$. These results are displayed in Table 7. It is possible to find the general case for any $N \geq 8$, as the exhaustive summary is in reduced-form, and therefore the exhaustive summary is a vector of the minimum length. The minimum length of an exhaustive summary is equal to the rank of the derivative matrix, therefore the rank is $7N - 33$ for any $N \geq 8$. There are 15 new parameters each time (apart from first few) so the number of parameters is $15N - 74$. The deficiency is then calculated from $d = p - r$.

D Maple Procedures

The procedure `Dmat` finds the derivative matrix given a vector of exhaustive summary term (`kappa`) and a vector of parameters (`pars`).

```
Dmat:=proc(kappa,pars)
local DD1, i, j;
description "Form the derivative matrix";
with(LinearAlgebra);
DD1:=Matrix(1..Dimension(pars),1..Dimension(kappa));
for i to Dimension(pars) do
    for j to Dimension(kappa) do
        DD1[i,j]:=diff(kappa[j],pars[i])
    end do
end do;
DD1
end proc
```

The procedure `Estpars` finds the estimable set of parameters given a derivative matrix (`DD1`) and a vector of parameters (`pars`).

```
Estpars:=proc(DD1,pars)
local r, d, alphapre, alpha, PDE, FF, i, ans;
description "Finds the estimable set of parameters";
with(LinearAlgebra);
r := Rank(DD1);
d := Dimension(pars)-r;
alphapre:=NullSpace(Transpose(DD1));
alpha:=Matrix(d, Dimension(pars));
PDE:=Vector(d);
FF:=f(seq(pars[i],i=1..Dimension(pars)));
for i to d do
    alpha[i,1..Dimension(pars)]:=alphapre[i];
    PDE[i]:=add((diff(FF,pars[j]))*alpha[i, j],
          j=1..Dimension(pars)):
end do;
ans := pdsolve({seq(PDE[i] = 0, i = 1 .. d)})
end proc
```

The procedure `simexsum` finds the simple exhaustive summary for a multi-state model. The inputs are a transition matrix `A`, a recapture matrix `P` and the number of years of ringing and recovery N. See the description for details and restrictions.

The procedure `recruitment` finds the simple exhaustive summary for the recruitment model. The inputs are N, the number of years of ringing and recovery, k, the age at recruitment, y the number of recruiting classes. Note that $k \geq 3$, and $y \geq 2$.

```
simexsum:=proc (A, P, N)
local S, U, i, j, kappa, kappaindex, tt, k, test;
description "Finds a simpler exhaustive summary. A is the transition matrix and must be square. If A is time dependent
the letter t must be used in a subscript to represent time. P is a diagonal recovery matrix and must be a square
matrix with entries only on the diagonal. Unobservable states must be numbered as the last states, and must have a
zero in the appropriate diagonal entry. N is the number of years of the study, with N-1 years of marking and N-1 years
of recovery. If kappa is returned as zero, this means the general exhaustive summary is not valid for that N, try a greater N";
with(LinearAlgebra);
S := Dimension(A)[1];
U := 0;
for i from S by -1 to 1 do
    if P[i, i] = 0 then U:=U+1: end if
end do;
if (S^2+S-2*U)*(N-1)-S-2*U*(S-1) < ((1/2)*N^2-(1/2)*N)*(S-U)^2 and 1 < S-U then
    kappa := Vector((S^2+S-2*U)*(N-1)-S-2*U*(S-1));
    kappaindex := 1;
    for tt to N-1 do
        for i to S-U do
            for j to S-U do
                kappa[kappaindex]:=(eval(P[i,i],t=tt+1))*(eval(A[i,j],t=tt));
                kappaindex:=kappaindex+1
            end do
        end do
    end do;
    for tt from 2 to N-1 do
        for i to S-U do
            kappa[kappaindex] := eval(P[i, i], t = tt);
            kappaindex := kappaindex+1
        end do
    end do;
    for tt from 2 to N-1 do
        for i to S do
                for j from S-U+1 to S do
                    if A[j, 1] <> 0 then
                        if i <= S-U then
                            kappa[kappaindex]:=(eval(P[i, i],t=tt+1))*(eval(A[i,j],t=tt))*(eval(A[j,1],t=tt-1));
                            kappaindex:=kappaindex+1
                        end if;
                        if 2 <= i and i <= S-U then
                            kappa[kappaindex]:=(eval(A[j,i],t=tt-1))/(eval(A[j,1],t=tt-1));
                            kappaindex:=kappaindex+1
                        end if;
                        if S-U < i and 2 < tt then
                            kappa[kappaindex]:=(eval(A[j i],t=tt-1))*
                            (eval(A[j,1],t=tt-2))/(eval(A[j, 1],t = tt-1));
                            kappaindex:=kappaindex+1
                        end if
                    else
                        test := 0;
                        for k from 2 to S while test = 0 do
                            if A[j, k] <> 0 then
                                if i <= S-U then
                                    kappa[kappaindex]:=(eval(P[i,i],t=tt+1))*(eval(A[i,j],t = tt))*(eval(A[j,k],t=tt-1));
                                    kappaindex := kappaindex+1
                                end if;
                                if 2 <= i and i <= S-U then
                                    kappa[kappaindex]:=(eval(A[j,i],t=tt-1))/(eval(A[j,k],t = tt-1));
                                    kappaindex:=kappaindex+1
                                end if;
                                if S-U < i and 2 < tt then
                                    kappa[kappaindex]:=(eval(A[j,i],t=tt-1))*(eval(A[j,k],t=tt-2))/(eval(A[j,k],t=tt-1));
                                    kappaindex:=kappaindex+1
                                end if;
                                test:=1
                            end if: end do: end if:
                end do:  end do: end do:
else
    kappa := 0
end if;
kappa
end proc
```

N	r	d	p	Estimable Parameters
3	3	1	4	$\sigma_{9,1}, p_2, p_3\sigma_{9,2}$
4	5	1	6	$\sigma_{9,1}, \sigma_{9,2}, p_2, p_3, p_4\sigma_{9,3}$
5	8	5	13	$\sigma_{9,1}, \ldots, \sigma_{9,3}, p_2 \ldots, p_4, p_5\sigma_{9,4}, p_5\sigma_{4,4}\alpha_{4,4}\prod_{j=1}^{3}\sigma_{j,j}$
6	12	10	22	$\sigma_{9,1}, \ldots, \sigma_{9,4}, p_2 \ldots, p_5, p_6\sigma_{9,5}, \sigma_{4,4}\alpha_{4,4}\prod_{j=1}^{3}\sigma_{j,j}, p_6\sigma_{4,5}\alpha_{4,5}\prod_{j=1}^{3}\sigma_{j,j+1}, \frac{p_6\alpha_{5,5}\sigma_{5,5}(1-\alpha_{4,4})}{\alpha_{4,4}}$
7	17	16	33	$\sigma_{9,1}, \ldots, \sigma_{9,5}, p_2 \ldots, p_6, p_7\sigma_{9,6}, \sigma_{4,4}\alpha_{4,4}\prod_{j=1}^{3}\sigma_{j,j}, \sigma_{4,5}\alpha_{4,5}\prod_{j=1}^{3}\sigma_{j,j+1}, \frac{\alpha_{5,5}\sigma_{5,5}(1-\alpha_{4,4})}{\alpha_{4,4}}, p_7\sigma_{4,6}\alpha_{4,6}\prod_{j=1}^{3}\sigma_{j,j+2}, \frac{p_7\alpha_{5,6}\sigma_{5,6}(1-\alpha_{4,5})}{\alpha_{4,5}}, \frac{p_7\alpha_{6,6}\sigma_{6,6}(1-\alpha_{5,5})}{\alpha_{5,5}}$
N	$7N-33$	$8N-41$	$15N-74$	$N \geq 8$

Table 7 Parameter Redundancy in the 9-state Recruitment Model.

```
recruitment := proc (N, k, y)
local i, t, sizekappa, kappa, indexkappa;
description "Gives an exhaustive summary for the recruitment model with N-1 years
of ringing N-1 years of recovery, recruitment age k, recruitment classes y";
with(LinearAlgebra);
sizekappa := 0;
for t to N-1 do
    sizekappa:=sizekappa+1;
    if 2 <= t then
        sizekappa:=sizekappa+1
    end if;
    if k <= t then
        sizekappa:=sizekappa+1
    end if
end do;
for i from k+1 to y+k-1 do
    for t from i to N-1 do
        sizekappa:=sizekappa+1
    end do
end do;
kappa := Vector(sizekappa);
indexkappa:=1;
for t to N-1 do
    kappa[indexkappa]:=p[k+y,t+1]*sigma[k+y,t];
    indexkappa := indexkappa+1;
    if 2 <= t then
        kappa[indexkappa]:=p[k+y, t];
        indexkappa:=indexkappa+1
    end if;
    if k <= t then
        kappa[indexkappa]:=p[k+y,t+1]*sigma[k,]*alpha[k,t]*(product(sigma[j,t+j-k],j=1..k-1));
        indexkappa:=indexkappa+1
    end if
end do;
for i from k+1 to y+k-1 do
    for t from i to N-1 do
        kappa[indexkappa]:=p[k+y,t+1]*sigma[i,t]*alpha[i,t]*(1-alpha[i-1,t-1])/alpha[i-1,t-1];
        indexkappa:=indexkappa+1
    end do
end do;
kappa
end proc
```