# Parameter Redundancy in Capture-Recapture-Recovery Models

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**Abstract**

In principle it is possible to use recently-derived procedures to determine whether or not all the parameters of particular complex ecological models can be estimated using classical methods of statistical inference. If it is not possible to estimate all the parameters a model is parameter redundant. Furthermore, one can investigate whether derived results hold for such models for all lengths of study, and also how the results might change for specific data sets. In this paper we show how to apply these approaches to entire families of capture-recapture and capture-recapture-recovery models. This results in comprehensive tables, providing the definitive parameter redundancy status for such models. Parameter redundancy can also be caused by the data rather than the model, and how to investigate this is demonstrated through two applications, one to recapture data on dippers, and one to recapture-recovery data on great cormorants.

*Keywords:* Capture-recapture models, Cormorants, Derivative matrix, Dippers, Exhaustive summary, Identifiability

## 1. Introduction

The general topic of this paper is the estimation of parameters in stochastic models in ecology, using maximum likelihood. The models in question are mechanistic and are populated by key demographic rates and probabilities. The increasing sophistication of data collection technology, and the availability of long historical data sets both allow complex models to be devised for the data.

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However in some cases, it is not possible to estimate all the model parameters, as some are confounded, and we say that the model is parameter redundant. The area of parameter redundancy has a long history, which is described in [20]. Using procedures of computerised symbolic algebra it is now, in principle, possible to determine whether or not any model is parameter redundant, and if it is to determine which parameters and parameter combinations may be estimated. It is also possible to examine the moderating effect of data on the conclusions. As we shall demonstrate, this approach involves finding a suitable exhaustive summary, which is a sufficient set of parameter combinations that determines the model. That summary is then differentiated with respect to the set of parameters to form a derivative matrix, the properties of which provide the parameter redundancy information that is needed. Models are naturally fitted to data sets resulting from studies of particular lengths, and extension theorems exist that allow the conclusions from any particular study to be generalised to studies of any length for any model structure. Furthermore, this approach can be carried out for entire families of models. This procedure has only recently been developed, and so far only two examples are published, for ring-recovery data, in [19], and for mixture models for recovery data, in [40]. In this paper we apply the approach to very wide families of models for capture-recapture and capture-recapture-recovery studies resulting in capture-history and capture/recovery-history data.

Capture-recapture and capture-recapture-recovery models are of central importance in ecology for estimating the survival probabilities of wild animals. Data collection involves marking animals, if they are not already uniquely distinguishable from one and other, and then subsequently recapturing live animals and in some cases also recovering dead animals. The parameter set contains survival probabilities, as well as probabilities of recapture of live animals and possibly also the recovery of dead animals. These survival, recapture, and recovery probabilities can be constant, dependent on time, or age, or both time and age. Cohort-dependence may also be included, but we do not consider that possibility in this paper. If all the parameters are constant then in theory it is possible to estimate all the parameters. However in the capture-recapture model if the survival and recapture probabilities are both dependent on time, the well-known Cormack-Jolly-Seber (CJS) model, the last time-point survival and recapture probabilities only ever appear as a product. It is only possible to estimate the product of these two parameters; see for example [20]. Such a model is known as parameter redundant, and it is also non-identifiable.

## 2. Capture-recapture and capture-recapture-recovery models

### *2.1. No recovery of dead animals*

The CJS model, with fully time-dependent parameters and no age dependence, was presented by Cormack [21], Jolly [31] and Seber [45] and has been widely applied to a variety of contexts; see for example [33].

In capture-recapture studies animals, are marked at $n_1$ occasions and recaptured at $n_2$ subsequent occassions; typically there will be $T$ capture and recapture occasions with $n_1 = n_2 = T - 1$. These occasions are usually annual, but many other possibilities also arise. Each individual will have a capture history consisting of 1 to represent an occasion when an animal was captured and a 0 to represent an occasion where the animal was not recaptured. For example

$$h_1 = 0010010$$

is a history for an individual first caught at occasion 3, then not recaptured at occasions 4 and 5, then recaptured at occasion 6 and not recaptured at occasion 7. At this last time point the animal could either have died or have not been recaptured, whereas at occasions 4 and 5 we know that animal was alive but not recaptured. Capture histories on European dippers, *Cinclus cinclus*, are illustrated in Table 1, and we reconsider this data set later in the paper. The data set was first published in [36] and then examined in many publications since, see for example [4, 33, 44].

Let $\phi_{i,j}$ denote the probability that an animal of age $i-1$ at time $j$ survives until $j+1$ and $p_{i,j}$ denote the probability that an animal of age $i-1$ is recaptured at occasion $j$. Suppose an animal was first recaptured at time $a$ and was last

Table 1: Dipper capture-recapture histories, taken from [36]

| Capture-History | Number of males | Number of females | Total number of animals |
|---|---|---|---|
| 1111110 | 1 | 0 | 1 |
| 1111100 | 0 | 1 | 1 |
| 1111000 | 1 | 1 | 2 |
| 1101110 | 0 | 1 | 1 |
| 1100000 | 4 | 2 | 6 |
| 1010000 | 1 | 1 | 2 |
| 1000000 | 5 | 4 | 9 |
| 0111111 | 0 | 2 | 2 |
| 0111110 | 0 | 1 | 1 |
| 0111100 | 1 | 2 | 3 |
| 0111000 | 1 | 1 | 2 |
| 0110110 | 0 | 1 | 1 |
| 0110000 | 7 | 4 | 11 |
| 0100000 | 11 | 18 | 29 |
| 0011111 | 0 | 2 | 2 |
| 0011110 | 1 | 1 | 2 |
| 0011100 | 4 | 2 | 6 |
| 0011000 | 8 | 4 | 12 |
| 0010110 | 1 | 0 | 1 |
| 0010000 | 11 | 18 | 29 |
| 0001111 | 6 | 2 | 8 |
| 0001110 | 3 | 4 | 7 |
| 0001100 | 6 | 5 | 11 |
| 0001011 | 0 | 1 | 1 |
| 0001001 | 1 | 1 | 2 |
| 0001000 | 6 | 10 | 16 |
| 0000111 | 10 | 6 | 16 |
| 0000110 | 3 | 6 | 9 |
| 0000100 | 9 | 7 | 16 |
| 0000011 | 12 | 11 | 23 |
| 0000010 | 11 | 12 | 23 |

recaptured at time $b$, with individual capture history entry $\delta_k$ at time $k$, then the probability associated with a particular history, $h$, is

$$Pr(h) = \left\{ \prod_{k=a+1}^{b} \phi_{k-a,k-1} \left( \delta_k p_{k-a+1,k} + \bar{\delta}_k \bar{p}_{k-a+1,k} \right) \right\} \chi_{b-a+1,b}, \qquad (1)$$

where $\bar{x} = 1 - x$ and $\chi_{i,j} = \bar{\phi}_{i,j} + \phi_{i,j}\bar{p}_{i+1,j+1}\chi_{i+1,j+1}$ is the probability that an animal of age $i$ at time $t_j$ is not recaptured during the study again, with

$\chi_{i,n_2} = 1$ for all $i$. For example in history $h_1$ above, $a = 3$ and $b = 6$, which gives a probability of $Pr(h_1) = \phi_{1,3}\bar{p}_{2,4}\phi_{2,4}\bar{p}_{3,5}\phi_{3,5}p_{4,6}(\bar{\phi}_{4,6} + \phi_{4,6}\bar{p}_{5,7})$. A likelihood can be formed as $L = \prod_{m=1}^{N} Pr(h_m)$ for the $N$ individual observed capture-histories. This model assumes that animals are in their first year of life when first captured and marked. Frequently animals are of unknown age when first captured, and then the dependence on age is typically excluded from the model; see [40] for an alternative. The capture-history data can then be summarised by a triangular table known as an m-array, the rows of which correspond to successive cohorts of released animals, including animals previously captured, and the columns give the first times of capture/recapture following the latest release. The m-array for the dipper data is given in [33].

### *2.2. Recovery as well as recapture*

The parameter redundancy of mark-recovery models alone has been examined in [19], which provides complete parameter redundancy information for most common models for recovery data. It is sometimes the case that capture-history information can include records of death, as well as of recaptures, and the capture-recapture-recovery model has been examined in [1, 2, 6, 8, 32, 34, 37]. The individual capture/recovery-histories are extended to include a 2 to represent the recovery of a dead animal, which will always be followed by zeros for the rest of the study. For example

$$h_2 = 0101200$$

is a history for an individual first caught at occasion 2, then not recaptured at occasion 3, recaptured at occasion 4 and then recovered dead at occasion 5.

Let $\lambda_{i,j}$ denote the probability that an animal of age $i-1$ at time $j$ died in the period $j$ to $j+1$. Suppose an animal was first recaptured at time $a$ and was last recaptured alive or recovered dead at time $b$, then the probability associated with a particular capture/recovery-history is

$$Pr(h) = \begin{cases} \displaystyle\prod_{k=a+1}^{b} \phi_{k-a,k-1}\left(\delta_k p_{k-a+1,k} + \bar{\delta}_k \bar{p}_{k-a+1,k}\right)\chi_{b-a+1,b} & \text{if } \delta_b = 1 \\ \displaystyle\prod_{k=a+1}^{b-1} \phi_{k-a,k-1}\left(\delta_k p_{k-a+1,k} + \bar{\delta}_k \bar{p}_{k-a+1,k}\right)\bar{\phi}_{b-a,b-1}\lambda_{b-a,b-1} & \text{if } \delta_b = 2, \end{cases} \tag{2}$$

where $\chi_{i,j} = \bar{\phi}_{i,j}\bar{\lambda}_{i,j} + \phi_{i,j}\bar{p}_{i+1,j+1}\chi_{i+1,j+1}$ is the probability that an animal of age $i$ at time $t_j$ is not recaptured during the study again, with $\chi_{i,n_2} = 1$ for all $i$. For example in history $h_2$ above, $a = 1$, $b = 4$ and $\delta_4 = 2$, giving a probability of $Pr(h_2) = \phi_{1,2}\bar{p}_{2,3}\phi_{2,3}p_{3,4}\bar{\phi}_{3,4}\lambda_{3,4}$. Again the likelihood can be formed as $L = \prod_{m=1}^{N} Pr(h_m)$ for the $N$ individual observed capture/recovery-histories. Alternative forms for the likelihood are given in [8, 11, 32, 37].

We follow the $y/z$ notation of [7] to denote capture-recapture models, where $y$ refers to the survival probability and $z$ refers to the recapture probability. In this paper we consider $y$ and $z$ having four options for every year in the study: C for the probability being a constant regardless of age and time, T for the probability being only time-dependent, A for the probability being only age-dependent, and A,T for the probability being age- and time-dependent. We extend this model to the capture-recapture-recovery model by using the form $y/(z_1; z_2)$, where $y$ refers to the survival probability, $z_1$ refers to the recapture probability, and $z_2$ refers to the recovery probability, with the same four options as above being the possibilities.

## 3. Parameter Redundancy

Parameter redundancy can be investigated using computerised symbolic algebra, which involves forming a particular derivative matrix and calculating its rank. This method was first used for ecological models by [9], and has a long history in both ecology and other areas, see for example [3, 9, 10, 12–20, 22, 24, 26, 27, 41, 42, 46, 47].

If we let $M(\boldsymbol{\theta})$ be a function that defines a model with unknown parameters $\boldsymbol{\theta} \in \Omega$, then that model is parameter redundant if $M(\boldsymbol{\theta})$ can be written as a function of just the parameters $\boldsymbol{\beta}$, where $\boldsymbol{\beta} = f(\boldsymbol{\theta}) \in \Omega_{\boldsymbol{\beta}}$, in which $\Omega_{\boldsymbol{\beta}}$ has dimension $\dim(\boldsymbol{\beta}) < \dim(\boldsymbol{\theta})$ [9]. An exhaustive summary, $\boldsymbol{\kappa}$, is a vector of parameters and parameter combinations that uniquely define a model [20]. The parameter redundancy status of a model can be determined by evaluating the symbolic rank of the derivative matrix $\mathbf{D} = [\partial \boldsymbol{\kappa}/\partial \boldsymbol{\theta}]$. In capture-recapture and capture-recapture-recovery models, the probabilities of each possible capture-recapture(-recovery) history form an obvious exhaustive summary, and there are many other options for exhaustive summaries. For example the probabilities associated with independent sufficient statistics given in [32, 37] can be used to form exhaustive summaries, or in models without age-dependence, the probabilities associated with m-array terms form an exhaustive summary. In this paper we start with the exhaustive summary consisting of the probabilities of histories as this is an easy exhaustive summary to use when considering the effect of parameter redundancy on the data, but the results of Section 4 can also be derived by starting with other exhaustive summaries.

The rank, $r$, of the derivative matrix denotes how many parameters in a model can estimated. If there are $q$ parameters in a model, then that model is parameter redundant if $r < q$, and the model deficiency is then $d = q - r$. If $r = q$, a model is termed full rank and it is theoretically possible to estimate all parameters in this case. If a model is parameter redundant, it can be determined whether any of the original parameters are estimable by solving the equation $\boldsymbol{\alpha}(\boldsymbol{\theta})^T \mathbf{D}(\boldsymbol{\theta}) = 0$. This is equivalent to finding the null-space of $\mathbf{D}^T$. There will be $d$ non-zero solutions, $\boldsymbol{\alpha}_j(\boldsymbol{\theta})$, with individual entries $\alpha_{ij}(\boldsymbol{\theta})$. Any parameter $\theta_i$ can still be estimated if $\alpha_{ij}(\boldsymbol{\theta}) = 0$ for all $j = 1, \ldots, d$. The combinations of other parameters that can be estimated, which contribute to $\boldsymbol{\beta}$, can then be found by solving the system of linear first-order partial, Lagrange differential equations, $\sum_{i=1}^{p} \alpha_{ij} \partial \psi / \partial \theta_i = 0$ where $\psi$ is an arbitrary function of the parameters [12, 14, 22].

In capture-recapture and capture-recapture-recovery models, the numbers of years of marking and recapture/recovery vary from study to study. It is possible to generalise results to any number of years of marking and recapture/recovery via an extension theorem. This states that if a full-rank model is extended by adding extra terms $\boldsymbol{\kappa}_2$ and extra parameters $\boldsymbol{\theta}_2$ and the derivative matrix $\mathbf{D}_2 = [\partial\boldsymbol{\kappa}_2/\partial\boldsymbol{\theta}_2]$ is also full rank, then the extended model is full rank. The result can then be generalised further by induction [9, 20].

However, this symbolic algebra approach may not be computationally feasible for more complex problems [23, 29, 30, 43]. This difficulty is overcome in [20], which extended the use of the symbolic approach by means of reparameterisation to simplify the structure of more complex models [15–18, 20]. In this method a new parameterisation, $\mathbf{s}$, is chosen so that $\partial\boldsymbol{\kappa}(\mathbf{s})/\partial\mathbf{s}$ is full rank. By the reparameterisation theorem of [20] the number of parameters in the full-rank reparameterised model will be the number of estimable parameters in the original model. This method is used in Section 4 to find relatively simple exhaustive summaries. The reparameterisation theorem in complex models can also be used to form general results in parameter-redundant models [19], by first reparameterising and then applying the extension theorem to the full-rank reparameterised model.

A model can be parameter redundant due to either the structure of the model or the form of a particular set of data. The former case is known as intrinsic parameter redundancy, while the later is known as extrinsic parameter redundancy. We present a simple exhaustive summary that can be used to study intrinsic parameter redundancy in Section 4, with results given in Section 5. We examine extrinsic parameter redundancy, and how data affect parameter redundancy, in Section 6.

The symbolic algebra of the paper can be executed in a computer symbolic algebra package, such as Maple. Maple procedures for this paper can be found in the supplementary material for the paper and at `http://www.kent.ac.uk/smsas/personal/djc24/parameterredundancy.htm`.

## 4. New parameter redundancy results

An exhaustive summary to study intrinsic parameter redundancy for the capture-recapture or capture-recapture-recovery models consists of the probabilities of all possible histories. However there are $2^{n_2+1} - 2^{n_2-n_1+1}$ possible histories for the capture-recapture model, and $3(2^{n_2} - 2^{n_2-n_1})$ possible histories for the capture-recapture-recovery model. In general, Maple will be unable to calculate the rank of the derivative matrix if the exhaustive summary consisting of all possible histories is used. To solve this problem a simpler exhaustive summary can be found with fewer terms, but which still captures the inherent structure of the model. The simpler exhaustive summary is given by Theorem 1 below.

**Theorem 1.** ***a.*** *A simpler exhaustive summary for the capture-recapture model consists of the terms:*

- $s_{i,j} = \phi_{i,j} p_{i+1,j+1}$ *for all* $i = 1, \ldots, n_2$ *and* $j = i, \ldots, \min(n_1 + i - 1, n_2)$,
- $t_{i,j} = \phi_{i,j}(1 - p_{i+1,j+1})$ *for all* $i = 1, \ldots, n_2 - 1$ *and* $j = i, \ldots, \min(n_1 + i - 1, n_2 - 1)$.

***b.*** *A simpler exhaustive summary for the capture-recapture-recovery model consists of the terms:*

- $s_{i,j} = \phi_{i,j} p_{i+1,j+1}$ *for all* $i = 1, \ldots, n_2$ *and* $j = i, \ldots, \min(n_1 + i - 1, n_2)$,
- $t_{i,j} = \phi_{i,j}(1 - p_{i+1,j+1})$ *for all* $i = 1, \ldots, n_2 - 1$ *and* $j = i, \ldots, \min(n_1 + i - 1, n_2 - 1)$,
- $r_{i,j} = (1 - \phi_{i,j})\lambda_{i,j}$ *for all* $i = 1, \ldots, n_2$ *and* $j = i, \ldots, \min(n_1 + i - 1, n_2)$.

The proof of Theorem 1 is given in Appendix A of the supplementary material. A modified PLUR decomposition, or Turing factorisation, of the derivative matrix can reveal whether or not full rank results are valid for the whole parameter space [20]. In this case PLUR decompositions show that Theorem 1 is valid everywhere in the parameter space except at boundary values.

Theorem 1 gives a much simpler exhaustive summary than the exhaustive summary consisting of all possible histories. For example when $n_1 = n_2 = 12$ there are 12285 possible histories whereas there are only 222 exhaustive summary terms in the simpler exhaustive summary of Theorem 1.

**Example 1:**

Consider the capture-recapture model T/C with $n_1 = n_2 = 3$ years of marking and recapture. This is the CJS model with constant recapture probability. In this case Theorem 1a. results in the exhaustive summary $\boldsymbol{\kappa} =$

$[\phi_1 p, \phi_2 p, \phi_3 p, \phi_1(1-p), \phi_2(1-p)]$, with repeated terms excluded. The parameters in this model are $\boldsymbol{\theta} = [\phi_1, \phi_2, \phi_3, p]$. The derivative matrix,

$$\mathbf{D} = \left[\frac{\partial \boldsymbol{\kappa}}{\partial \boldsymbol{\theta}}\right] = \begin{bmatrix} p & 0 & 0 & 1-p & 0 \\ 0 & p & 0 & 0 & 1-p \\ 0 & 0 & p & 0 & 0 \\ \phi_1 & \phi_2 & \phi_3 & -\phi_1 & -\phi_2 \end{bmatrix},$$

has rank 4. Therefore the model is full rank and all 4 parameters can be estimated. The model can be extended using the extension theorem of [9, 20] for larger values of $n_1$ and $n_2$ to show that the T/C model is actually full rank for all values of $n_1 \geq 2$ and $n_2 \geq 2$ (as the same result can also be shown to be valid for $n_1 = n_2 = 2$). □

**Example 2:**

Consider the capture-recapture-recovery model A,T/(A;A,T) with $n_1 = n_2 = 3$ years of marking and recapture/recovery. In this case Theorem 1b. results in the exhaustive summary $\boldsymbol{\kappa} = [\phi_{1,1}p_2,\ \phi_{1,2}p_2,\ \phi_{1,3}p_2,\ \phi_{2,2}p_3,\ \phi_{2,3}p_3,\ \phi_{3,3}p_4,\ \phi_{1,1}(1-p_2),\ \phi_{1,2}(1-p_2),\ \phi_{2,2}(1-p_3),\ (1-\phi_{1,1})\lambda_{1,1},\ (1-\phi_{1,2})\lambda_{1,2},\ (1-\phi_{1,3})\lambda_{1,3},\ (1-\phi_{2,2})\lambda_{2,2},\ (1-\phi_{2,3})\lambda_{2,3},\ (1-\phi_{3,3})\lambda_{3,3}]$. The parameters in this model are $\boldsymbol{\theta} = [\phi_{1,1},\ \phi_{1,2},\ \phi_{1,3},\ \phi_{2,2},\ \phi_{2,3},\ \phi_{3,3},\ p_2,\ p_3,\ p_4,\ \lambda_{1,1},\ \lambda_{1,2},\ \lambda_{1,3},\ \lambda_{2,2},\ \lambda_{2,3},\ \lambda_{3,3}]$. The derivative matrix $\mathbf{D} = \partial\boldsymbol{\kappa}/\partial\boldsymbol{\theta}$ has rank 14. As there are 15 parameters the model is parameter redundant with deficiency 1. To find if any of the original parameters can be estimated we solve $\boldsymbol{\alpha}^T\mathbf{D} = 0$ to give

$$\boldsymbol{\alpha}^T = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & \frac{(1-\phi_{3,3})}{\phi_{3,3}\lambda_{3,3}} & 0 & 0 & \frac{(1-\phi_{3,3})}{\lambda_{3,3}} & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}.$$

The position of the zeros shows we can estimate the 12 parameters $\phi_{1,1}$, $\phi_{1,2}$, $\phi_{1,3}$, $\phi_{2,2}$, $\phi_{2,3}$, $p_2$, $p_3$, $\lambda_{1,1}$, $\lambda_{1,2}$, $\lambda_{1,3}$, $\lambda_{2,2}$ and $\lambda_{2,3}$. The remaining estimable terms can be found by solving the partial equation

$$\frac{\partial\psi}{\partial\phi_{3,3}}\frac{(1-\phi_{3,3})}{\phi_{3,3}\lambda_{3,3}} + \frac{\partial\psi}{\partial p_4}\frac{(1-\phi_{3,3})}{\lambda_{3,3}} + \frac{\partial\psi}{\partial\lambda_{3,3}} = 0.$$

The solutions to this equation are $\phi_{3,3}p_4$ and $(1-\phi_{3,3})\lambda_{3,3}$, and these 2 parameter combinations complete the set of 14 parameters that can be estimated. The reparameterisation and extension theorems of [20] can then be used to show that this capture-recapture-recovery model has a parameter deficiency of 1 for any $n_1, n_2 \geq 2$. □

**Example 3:**

Consider the capture-recapture-recovery model T/(C;A,T) also with $n_1 = n_2 = 3$ years of marking and recapture/recovery: the exhaustive summary consists of the terms in the vector $\boldsymbol{\kappa} = [\phi_1 p, \phi_2 p, \phi_3 p, \phi_1(1-p), \phi_2(1-p), (1-\phi_1)\lambda_{1,1}, (1-\phi_2)\lambda_{2,2}, (1-\phi_3)\lambda_{3,3}, (1-\phi_2)\lambda_{1,2}, (1-\phi_3)\lambda_{2,3}, (1-\phi_3)\lambda_{1,3}]$, with parameters $\boldsymbol{\theta} = [\phi_1, \phi_2, \phi_3, p, \lambda_{1,1}, \lambda_{1,2}, \lambda_{1,3}, \lambda_{2,2}, \lambda_{2,3}, \lambda_{3,3}]$. To determine the model rank it is possible to follow exactly the same procedure as above. However it is possible to deduce that the model T/(C;A,T) is full rank from knowledge of the capture-recapture T/C model of example 1. As the first part of the exhaustive summary is the same as that for the full rank T/C model, we can estimate $\phi_1$, $\phi_2$, $\phi_3$ and $p$. Then from the second part of the exhaustive summary, we see that every $\lambda_{i,j}$ term has a separate exhaustive summary term. As every exhaustive summary term in the T/C model is in the T/(C;A,T) model plus additional exhaustive summary terms containing $\lambda_{i,j}$, and each of these additional exhaustive summary terms contains only one distinct $\lambda_{i,j}$ parameter for each term, therefore we can estimate every $\lambda_{i,j}$. □

The intuitive observation of the last example is formalised for all full rank capture-recapture models via the Full Rank Theorem below.

**Theorem 2. (Full Rank Theorem)** *If the capture-recapture $y/z_1$ model is full rank, then the capture-recapture-recovery $y/(z_1; z_2)$ model with the same $y$ and $z_1$, but any $z_2$ is also full rank.*

Proof of Theorem 2 is given in Appendix A of the supplementary material. There is not a similar theorem for full-rank mark-recovery models.

## 5. Results

### *5.1. Models where we do not distinguish separate juvenile survival*

We now make use of the results of this paper in order to provide general tables of the parameter redundancy status of many common models for capture-recapture and capture-recapture-recovery.

Table 2: Table of parameter deficiencies for capture-recapture $y/z$ models

| Model | Rank | Deficiency | Confounded Parameters |
|---|---|---|---|
| C/C | $2$ | 0 | |
| C/T | $n_2+1$ | 0 | |
| C/A | $n_2+1$ | 0 | |
| C/A,T | $E+1$ | 0 | |
| T/C | $n_2+1$ | 0 | |
| T/T | $2n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1}$ |
| T/A | $2n_2$ | 0 | |
| T/A,T | $E+n_2-1$ | 1 | $\phi_{n_2}p^{\dagger}_{i+1,n_2+1}$ |
| A/C | $n_2+1$ | 0 | |
| A/T | $2n_2$ | 0 | |
| A/A | $2n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1}$ |
| A/A,T | $E+n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1,n_2+1}$ |
| A,T/C | $E+1$ | 0 | |
| A,T/T | $E+n_2-1$ | 1 | $\phi_{i,n_2}p^{\dagger}_{n_2+1}$ |
| A,T/A | $E+n_2-1$ | 1 | $\phi_{n_2,n_2}p_{n_2+1}$ |
| A,T/A,T | $2E-n_1$ | $n_1$ | $\phi_{i,n_2}p^{\dagger}_{i+1,n_2+1}$ |

Key: $E = n_1n_2 - \frac{1}{2}n_1^2 + \frac{1}{2}n_1$;
$^{\dagger}$ in the confounded parameters $i$ goes from $n_2 - n_1 + 1$ to $n_2$.

General results for $y/z$ capture-recapture models and $y/(z_1; z_2)$ capture-recapture-recovery models are given in Tables 2 and 3 respectively. The second column specifies the rank of the models, which is the number of estimable parameters. The third column provides the parameter deficiency, $d$. It is assumed that there are at least two years of marking and at least two years of recapture/recovery with $n_2 \geq n_1$.

The final columns of Tables 2 and 3 show which parameters are confounded in each case as appropriate; the parameters which are not listed are estimable. Observe that the parameter deficiency of the model is the number of original parameter minus the number of estimable parameter combinations there are in the model, and is not how many confounded parameter combinations there are in the model.

Table 3 excludes model combinations that are full rank due to the Full Rank Theorem. All the model listed below are full rank:

Table 3: Table of parameter deficiencies for capture-recapture-recovery $y/(z_1; z_2)$ models

| Model | Rank | Deficiency | Confounded Parameters |
|---|---|---|---|
| T/(T;C) | $2n_2+1$ | 0 | |
| T/(T;T) | $3n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1}$, $(1-\phi_{n_2})\lambda_{n_2}$ |
| T/(T;A) | $3n_2$ | 0 | |
| T/(T;A,T) | $E+2n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1}$, $(1-\phi_{n_2})\lambda^{\dagger}_{i,n_2}$ |
| T/(A,T;C) | $E+n_2+1$ | 0 | |
| T/(A,T;T) | $E+2n_2-1$ | 1 | $\phi_{n_2}p^{\dagger}_{i+1,n_2+1}$, $(1-\phi_{n_2})\lambda_{n_2}$ |
| T/(A,T;A) | $E+2n_2$ | 0 | |
| T/(A,T;A,T) | $2E+n_2-1$ | 1 | $\phi_{n_2}p^{\dagger}_{i+1,n_2+1}$, $(1-\phi_{n_2})\lambda^{\dagger}_{i,n_2}$ |
| A/(A;C) | $2n_2+1$ | 0 | |
| A/(A;T) | $3n_2$ | 0 | |
| A/(A;A) | $3n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1}$, $(1-\phi_{n_2})\lambda_{n_2}$ |
| A/(A;A,T) | $E+2n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1}$, $(1-\phi_{n_2})\lambda_{n_2,n_2}$ |
| A/(A,T;C) | $E+n_2+1$ | 0 | |
| A/(A,T;T) | $E+2n_2$ | 0 | |
| A/(A,T;A) | $E+2n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1,n_2+1}$, $(1-\phi_{n_2})\lambda_{n_2}$ |
| A/(A,T;A,T) | $2E+n_2-1$ | 1 | $\phi_{n_2}p_{n_2+1,n_2+1}$, $(1-\phi_{n_2})\lambda_{n_2,n_2}$ |
| A,T/(T;C) | $E+n_2+1$ | 0 | |
| A,T/(T;T) | $E+2n_2$ | 0 | |
| A,T/(T;A) | $E+2n_2$ | 0 | |
| A,T/(T;A,T) | $2E+n_2-1$ | 1 | $\phi_{i,n_2}p^{\dagger}_{n_2+1}$, $(1-\phi_{i,n_2})\lambda^{\dagger}_{i,n_2}$ |
| A,T/(A;C) | $E+n_2+1$ | 0 | |
| A,T/(A;T) | $E+2n_2$ | 0 | |
| A,T/(A;A) | $E+2n_2-1$ | 1 | $\phi_{n_2,n_2}p_{n_2+1}$, $(1-\phi_{n_2,n_2})\lambda_{n_2}$ |
| A,T/(A;A,T) | $2E+n_2-1$ | 1 | $\phi_{n_2,n_2}p_{n_2+1,n_2+1}$, $(1-\phi_{n_2,n_2})\lambda_{n_2,n_2}$ |
| A,T/(A,T;C) | $2E+1$ | 0 | |
| A,T/(A,T;T) | $2E+n_2-1$ | 1 | $\phi_{i,n_2}p^{\dagger}_{i+1,n_2+1}$, $(1-\phi_{i,n_2})\lambda^{\dagger}_{n_2}$ |
| A,T/(A,T;A) | $2E+n_2-1$ | 1 | $\phi_{n_2,n_2}p_{n_2+1,n_2+1}$, $(1-\phi_{n_2,n_2})\lambda_{n_2}$ |
| A,T/(A,T;A,T) | $3E-n_1$ | $n_1$ | $\phi_{i,n_2}p^{\dagger}_{i+1,n_2+1}$, $(1-\phi_{i,n_2})\lambda^{\dagger}_{i,n_2}$ |

Key: $E = n_1n_2 - \frac{1}{2}n_1^2 + \frac{1}{2}n_1$;
$^{\dagger}$ in the confounded parameters $i$ goes from $n_2 - n_1 + 1$ to $n_2$.

- $C/(z_1, z_2)$,
- $T/(C, z_2)$,
- $T/(A, z_2)$,
- $A/(C, z_2)$,

- $A/(T, z_2)$,
- $A, T/(C, z_2)$,

where $z_1$ and $z_2$, can be any of $C$, $T$, $A$ or $A, T$. Their model ranks can be found by adding 1 if $z_2 = C$, by adding $n_2$ if $z_2 = T$ or $A$, or by adding $E = n_1 n_2 - \frac{1}{2}n_1^2 + \frac{1}{2}n_1$ if $z_2 = A, T$ to the model rank of the equivalent capture-recapture model. For example the model T/A,T has full rank $r = n_2 + E$; the model T/(A,T;C) therefore is also full rank with rank $r = n_2 + E + 1$. We further note that the T/T model is the CJS model.

*5.2. Modelling separate juvenile survival*

It is often the case that wild animals in their first/early years of life experience higher mortality than adult animals. The same may also be true of extremely old animals, who experience senescence. As an illustration of how to deal with this kind of age-dependent mortality, we present the parameter redundancy of models in which first year survival is different from that of older animals in Appendix B of the supplementary material.

## 6. Applications: the effect of data on parameter redundancy results

The results of Section 5 are concerned with intrinsic parameter redundancy. Specifically the results assume that every possible history is observed, and this is unlikely to be the case in practise. For example, if the recapture probability in a study is quite low or in a long study no animals may remain alive for the whole length of the study, then the probability of the history where an animal is recaptured at every recapture point in the study is extremely small. In this Section we consider extrinsic parameter redundancy.

It is possible to study the effect of a particular set of data on parameter redundancy, by using an exhaustive summary consisting of the probabilities of each history that is present. Maple code for analysing particular sets of animal histories is given in the supplementary material. If a model is parameter redundant it will remain parameter redundant, but the deficiency may increase due to there being less information in the exhaustive summary. If a model is full rank, there may be certain data sets for which the model will become parameter redundant. We consider two data sets. The first involves capture-recapture only, and is the European dipper data set of Table 1.

To create a general measure of sparseness, $c$, for data sets, consider the C/C model with $\phi = 0.5$ and $p = 0.5$. If 50 animals were marked in year 1 and followed for three further years the capture-histories with an expectation greater than 1 are 1110, 1100, 1010 and 1000. We would only expect to see an animal for $c = 3$ years. If 100 animals were marked in the first year, all 8 histories have an expectation great than 1. So we expect to see animals for all $c = 4$ years. These expectations vary with different models and with the values $\phi$ and $p$, but generally more sparse data should have a lower value of $c$. We take $c$ as the maximum number of years between marking and last recapture. We suppose we have all histories with $c$ or fewer years between first marking and last recapture and calculate the deficiency for each model. Real data will never have this exact pattern of histories, but we would expect a data set which is very sparse and/or has few recaptures per year to behave like a model with a low value of $c$.

### *6.1. Dipper data*

In this capture-recapture study the animals there are $n_1 = 6$ years of marking and $n_2 = 6$ years of recovery, with males and females combined and considered separately. This makes the data set quite sparse as less than a quarter of the possible capture-histories were observed in the study. There are 24 different male histories, 29 different female histories, and 31 different male and female combined (M & F) histories in total out of a maximum of 126 possible histories.

The dipper data set consists of adult birds of unknown age. So that we may illustrate when age-dependent models can be fitted to data similar to that of the dipper data, we suppose that all dippers were of the same known age when marked. The deficiencies for the dipper data are given in Table 4 in columns 2 to 4. Using the measure of spareness described the deficiency for any data

Table 4: Table of parameter deficiencies for capture-recapture $y/z$ models for the Dipper data set from [36]; M & F indicates male and female data sets are combined.

| Model | Male | Female | M & F | Statistic of Sparseness | Intrinsic |
|---|---|---|---|---|---|
| C/C | 0 | 0 | 0 | 0 | 0 |
| C/T | 0 | 0 | 0 | 0 | 0 |
| C/A | 0 | 0 | 0 | 0 | 0 |
| C/A,T | 2 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| T/C | 0 | 0 | 0 | 0 | 0 |
| T/T | 1 | 1 | 1 | 1 | 1 |
| T/A | 0 | 0 | 0 | 0 | 0 |
| T/A,T | 5 | 2 | 1 | $\frac{1}{2}(n_2-c)(n_2-c-1)+1$ | 1 |
| A/C | 0 | 0 | 0 | 0 | 0 |
| A/T | 0 | 0 | 0 | 0 | 0 |
| A/A | 2 | 1 | 1 | $n_2-c$ | 1 |
| A/A,T | 6 | 2 | 2 | $\frac{1}{2}(n_2-c+1)(n_2-c)+1$ | 1 |
| A,T/C | 2 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| A,T/T | 5 | 2 | 2 | $\frac{1}{2}(n_2-c)(n_2-c-1)+1$ | 1 |
| A,T/A | 6 | 2 | 2 | $\frac{1}{2}(n_2-c+1)(n_2-c)+1$ | 1 |
| A,T/A,T | 19 | 15 | 13 | $(n_2-c)^2+n_2$ | 6 |

set with $n_1 = n_2$ and $1 < c < 6$ is given in column 5. The final column of Table 4 shows the deficiency of the model with all 126 possible histories, i.e. the intrinsic deficiency with complete data.

Table 4 shows that the majority of the intrinsically full rank models remain full rank even with relatively sparse data sets; the exceptions are the models C/A,T and A,T/C. In these models, to be able to estimate $p_{i,j}$ or $\phi_{i,j}$ respectively, capture-histories are needed where the bird is marked in the first year and also seen in the seventh year.

### *6.2. Cormorant data*

The second data set involves dead recoveries as well as alive recaptures. This data set from [28] follows cormorants, *Phalacrocorax carbo*, for $n_1 = n_2 = 12$ years. The birds are observed over 6 different colonies, and the most appropriate models are multi-site models; see [5, 38, 39]. Here for illustration we examine colony 3 (Col. 3) and colony 1 (Col. 1) separately as well as all colonies together (All). When we consider all colonies together the multi-site information is ignored and common $\phi$ and $p$ parameters are assumed across all 6 colonies.

The colony 3 data set is the most sparse with 121 different histories; colony 1 only has 465 different histories, and all the colonies combined have 580 different histories. Tables 5 and 6 gives the parameter deficiency for colonies 1 and 3, and all colonies together, in columns 2 to 4. The final column of Tables 5 and 6 shows intrinsic deficiency for direct comparison.

These results are generalised by again considering having all capture/recovery-histories with a maximum of $c$ years between first capture and either recovery or last capture if there is no recovery. Column 5 in Tables 5 and 6 gives the deficiency for any $n_1 = n_2$ with $1 \leq c < n_2$.

There is obviously a lack of data in colony 3 alone, so that here more models are parameter redundant. However there are still some models that remain full rank. Ignoring colony 3 results, most models remain full rank even with relatively sparse data. The exceptions are again models where one parameter is age- and time-dependent.

## 7. Discussion

It is essential to know whether a model is parameter-redundant or not, as in a parameter redundant model it is not possible to estimate all the parameters using classical inference and a weakly-identifiable model may result if Bayesian analysis is used [25]. This paper uses a novel approach to derive a simple exhaustive summary for capture-recapture and capture-recapture-recovery models. This exhaustive summary has the advantage of being structurally simpler than other exhaustive summaries, which allows Maple to calculate the rank of the appropriate derivative matrix even for the most complex models. The exhaustive summary is also flexible so that it can accommodate both age- and time-dependency.

General results have been derived for a large number of capture-recapture and capture-recapture-recovery models. The models we consider are frequently used in ecology, and the tables of the paper and the supplementary material provide for the first time a comprehensive description of the parameter-redundancy

Table 5: Table of parameter deficiencies for capture-recapture-recovery $C/(z_1; z_2)$ and $T/(z_1; z_2)$ models for the Cormorant data set from [28]

| Model | Col.3 | Col.1 | All | Statistic of Sparseness | Intrinsic |
|---|---|---|---|---|---|
| C/(C;C) | 0 | 0 | 0 | 0 | 0 |
| C/(C;T) | 0 | 0 | 0 | 0 | 0 |
| C/(C;A) | 1 | 0 | 0 | 0 | 0 |
| C/(C;A,T) | 4 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| C/(T;C) | 0 | 0 | 0 | 0 | 0 |
| C/(T;T) | 1 | 0 | 0 | 0 | 0 |
| C/(T;A) | 1 | 0 | 0 | 0 | 0 |
| C/(T;A,T) | 5 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| C/(A;C) | 1 | 0 | 0 | 0 | 0 |
| C/(A;T) | 1 | 0 | 0 | 0 | 0 |
| C/(A;A) | 2 | 0 | 0 | $n_2-c$ | 0 |
| C/(A;A,T) | 7 | 0 | 0 | $\frac{1}{2}(n_2-c+1)(n_2-c)$ | 0 |
| C/(A,T;C) | 8 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| C/(A,T;T) | 9 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| C/(A,T;A) | 11 | 0 | 0 | $\frac{1}{2}(n_2-c+1)(n_2-c)$ | 0 |
| C/(A,T;A,T) | 36 | 1 | 1 | $(n_2-c)^2$ | 0 |
| T/(C;C) | 0 | 0 | 0 | 0 | 0 |
| T/(C;T) | 1 | 0 | 0 | 0 | 0 |
| T/(C;A) | 1 | 0 | 0 | 0 | 0 |
| T/(C;A,T) | 5 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| T/(T;C) | 1 | 0 | 0 | 0 | 0 |
| T/(T;T) | 5 | 1 | 1 | 1 | 1 |
| T/(T;A) | 1 | 0 | 0 | 0 | 0 |
| T/(T;A,T) | 8 | 1 | 1 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 1 |
| T/(A;C) | 1 | 0 | 0 | 0 | 0 |
| T/(A;T) | 1 | 0 | 0 | 0 | 0 |
| T/(A;A) | 2 | 0 | 0 | $n_2-c$ | 0 |
| T/(A;A,T) | 9 | 0 | 0 | $\frac{1}{2}(n_2-c+1)(n_2-c)$ | 0 |
| T/(A,T;C) | 9 | 0 | 0 | $\frac{1}{2}(n_2-c)(n_2-c-1)$ | 0 |
| T/(A,T;T) | 12 | 1 | 1 | $\frac{1}{2}(n_2-c)(n_2-c-1)+1$ | 1 |
| T/(A,T;A) | 12 | 0 | 0 | $\frac{1}{2}(n_2-c+1)(n_2-c)$ | 0 |
| T/(A,T;A,T) | 41 | 2 | 2 | $n_2^2-2n_2c+c^2+1$ | 1 |

status of the models considered. Knowing the exact rank of a parameter-redundant model is useful if covariates or trends are added to the model, as no further derivative calculations are required to find the rank of the model with such covariates or trends [17, 19].

We have also shown that many models remain full rank, so that all param-

Table 6: Table of deficiency ($d$) for the capture-recapture-recovery $A/(z_1; z_2)$ and $A, T/(z_1; z_2)$ models for the cormorant data set of [28].

| Model | Col.3 | Col.1 | All | Statistic of Sparseness | Intrinsic |
|---|---|---|---|---|---|
| A/(C;C) | 1 | 0 | 0 | $0$ | 0 |
| A/(C;T) | 1 | 0 | 0 | $0$ | 0 |
| A/(C;A) | 2 | 0 | 0 | $n_2 - c$ | 0 |
| A/(C;A,T) | 8 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A/(T;C) | 1 | 0 | 0 | $0$ | 0 |
| A/(T;T) | 1 | 0 | 0 | $0$ | 0 |
| A/(T;A) | 2 | 0 | 0 | $n_2 - c$ | 0 |
| A/(T;A,T) | 9 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A/(A;C) | 2 | 0 | 0 | $n_2 - c$ | 0 |
| A/(A;T) | 2 | 0 | 0 | $n_2 - c$ | 0 |
| A/(A;A) | 6 | 2 | 2 | $2(n_2 - c)$ | 1 |
| A/(A;A,T) | 13 | 2 | 2 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c) + n_2 - c$ | 1 |
| A/(A,T;C) | 12 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A/(A,T;T) | 13 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A/(A,T;A) | 17 | 1 | 1 | $\frac{1}{2}(n_2 - c)(n_2 - c + 1) + n_2 - c + 1$ | 1 |
| A/(A,T;A,T) | 43 | 2 | 2 | $3(n_2 - c) + (n_2 - c - 1)^2$ | 1 |
| A,T/(C;C) | 3 | 0 | 0 | $\frac{1}{2}(n_2 - c)(n_2 - c - 1)$ | 0 |
| A,T/(C;T) | 5 | 0 | 0 | $\frac{1}{2}(n_2 - c)(n_2 - c - 1)$ | 0 |
| A,T/(C;A) | 7 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A,T/(C;A,T) | 42 | 10 | 6 | $(n_2 - c)^2$ | 0 |
| A,T/(T;C) | 6 | 0 | 0 | $\frac{1}{2}(n_2 - c)(n_2 - c - 1)$ | 0 |
| A,T/(T;T) | 9 | 0 | 0 | $\frac{1}{2}(n_2 - c)(n_2 - c - 1)$ | 0 |
| A,T/(T;A) | 10 | 1 | 1 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A,T/(T;A,T) | 48 | 12 | 8 | $n_2^2 - 2n_2c + c^2 + 1$ | 1 |
| A,T/(A;C) | 8 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A,T/(A;T) | 10 | 0 | 0 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c)$ | 0 |
| A,T/(A;A) | 12 | 1 | 1 | $\frac{1}{2}(n_2 - c + 1)(n_2 - c) + n_2 - c$ | 1 |
| A,T/(A;A,T) | 49 | 12 | 8 | $3(n_2 - c) + (n_2 - c - 1)^2$ | 1 |
| A,T/(A,T;C) | 41 | 7 | 6 | $(n_2 - c)^2$ | 0 |
| A,T/(A,T;T) | 46 | 8 | 7 | $n_2^2 - 2n_2c + c^2 + 1$ | 1 |
| A,T/(A,T;A) | 46 | 8 | 7 | $3(n_2 - c) + (n_2 - c - 1)^2$ | 1 |
| A,T/(A,T;A,T) | 96 | 32 | 28 | $\frac{3}{2}(n_2 - c + 1)(n_2 - c) + c$ | 12 |

eters can still be estimated, even when a data set is quite sparse. If parameters are constant, only depend on age or only depend on time, then parameter redundancy in practice is most likely to be caused by the inherent structure of the model rather than the data itself.

In parameter-redundant models, determining which parameters are confounded is possible by solving the appropriate set of partial differential equations, as demonstrated in example 2. This method works best when $n_1$ and $n_2$ are small, as when deriving intrinsic parameter redundancy results. The results can then be extended to a general $n_1$ and $n_2$ using the reparameterisation and extension theorems; see [20]. For a specific data set when $n_1$ and $n_2$ are large and extrinsic redundancy is considered, if the symbolic method does not work, the alternative hybrid-symbolic-numeric method of [15] can be used. This hybrid method will determine which of the original parameters can be estimated, but cannot be used to find any other estimable parameter combinations.

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