# Parameter redundancy in mark-recovery models

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We provide a definitive guide to parameter redundancy in mark-recovery models, indicating, for a wide range of models, in which all the parameters are estimable, and in which models they are not. For these parameter-redundant models we identify the parameter combinations that can be estimated. Simple, general results are obtain, which hold irrespective of the duration of the studies. We also examine the effect real data have on whether or not models are parameter redundant, and show that results can be robust even with very sparse data. Covariates, as well as time-varying or age-varying trends, can be added to models to overcome redundancy problems. We show how to determine, without further calculation, whether or not models with covariates or trends are still parameter redundant.

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## 1 Introduction

### 1.1 Parameter redundancy

Models are said to be parameter redundant when they contain too many parameters to be estimated, however much data are collected. The terminology was introduced by Catchpole and Morgan (1997), though the idea has a long history, described in Cole et al (2010), who also provide the latest developments for identifying parameter redundancy and dealing with its consequences. Parameter redundancy can be considered to be an extreme form of over-parameterisation. It arises in many different areas of stochastic modelling, and can be a consequence of complex mechanistic models being devised without regard to what may or may not be estimated when the models are fitted to data.

In this paper we assume that the method of model-fitting that will be used is maximum-likelihood. It is shown in Catchpole and Morgan (1997) that parameter-redundant models possess a flat likelihood. Unfortunately, even in cases of simple parameter-redundant models, sophisticated methods of non-linear function optimisation can stop and return optima corresponding to flat regions of the function being considered, without warning. It is therefore important that tools are developed to check for parameter redundancy. Such tools are now available, making use of methods of computerised symbolic algebra, and they are described in Cole et al (2010). An alternative to using symbolic algebra is to use numerical methods, but these can result in incorrect conclusions, as demonstrated by Cole and Morgan (2010a). Choquet and Cole (2010) have developed a hybrid method which is more reliable than standard numerical methods, and is easier to use than pure symbolic methods.

Quite often stochastic models are devised for data structures of particular dimensions, for a particular experimental study. A natural question is then whether the conclusions regarding parameter redundancy

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hold for data of different dimensions, but for which the model is the same. Once again, tools are available which allow this question to be answered. Ideally one would like models of a particular structure to have a simple description of their parameter redundancy, the best situation being when there is no change in conclusions, and dimensionality can be disregarded.

Using the fully symbolic tools that are now available is not entirely straightforward: they are not automatic, as they may involve finding a reparameterisation that is particular to the problem being considered; in some cases symbolic algebra packages might run out of memory, for especially complex models, and some of the procedures and checks require care in how they are applied. Furthermore, parameter redundancy may change in the presence of real data. Ideally, therefore, statisticians working in particular areas of modelling require tables of parameter redundancy results, for the families of models considered, augmented with explanations of how those results may be modified if data are missing. However there is no guarantee that simple forms of such tables can be constructed.

The parameter redundancy of any exponential-family model can be examined by considering a derivative matrix formed by differentiating the means with respect to the parameters. The rank of the derivative matrix is the number of estimable parameters in the model. A model is termed parameter redundant, with deficiency $d$, and will be non-identifiable, if the rank of the derivative matrix is $d$ less than the number of parameters in the model, where $d > 0$. If $d = 0$ the model is termed full rank, and in theory every parameter within the model can be estimated (Catchpole and Morgan, 1997). For a parameter-redundant model the estimable parameter combinations can be found by solving a set of partial differential equations (Catchpole et al, 1998). The derivative matrix can be evaluated by a computer algebra package such as `Maple` (see for example Catchpole et al, 2002), and the same is true in principle of its rank. More recently this approach has been generalised and extended by Cole et al (2010). They relax the exponential family assumption and develop a reparameterisation approach, which allows the derivative matrix to be simplified. The reparameterisation approach allows the evaluation of the rank of the derivative matrix in `Maple` even for complex models (see for example Cole and Morgan, 2010a; Cole, 2010).

### 1.2 Mark-recovery data and models

Models for mark-recovery provide a striking illustration of the issues raised above. Such data arise when wild animals are given unique identifiers, so that when they are recovered dead it is possible to use the recovery data to estimate mortality, and how it may vary with factors such as age, time and cohort. Models for mark-recovery data include survival probabilities and the probabilities of dead marked animals being found and reported dead. These parameters could depend on time or the age of the animal. It is obviously not possible to estimate all the parameters if both survival and recovery parameters are dependent on both age and time, as there would be more parameters than there are multinomial cell values. However if the survival and recovery parameters are constant then these two parameters can be estimated. For models between these two extremes it is often not clear what can and cannot be estimated.

Data sets of different dimension are a consequence of studies of differing lengths, and probability models for survival can be complex, depending on how the models incorporate features such as time- and age-dependence in the survival and recovery probabilities. We therefore use the mark-recovery paradigm to show that, for a very wide class of models, it is possible to construct relatively simple tables of parameter redundancy. We also show how results are modified for particular types of missing data. For these models, our results are all that is required to answer questions relating to parameter redundancy.

An example of mark-recovery data arises from ring-recovery experiments, where animals are ringed and some are recovered dead later (see for example Freeman and Morgan, 1990, 1992). Three examples of ring-recovery data are given in Table 1. The first (a) is data collected on Lapwing, *Vanellus vanellus*, when birds are ringed in their first year of life. The second and third data sets are collected on male mallards, *Anas platyrhynchos*, ringed in their first year of life (b) and as adults (c). The results of this paper apply to all mark-recovery data, not just ring-recovery experiments.

 

Frequently animals are marked in their first year of life and data are accumulated on a yearly timescale. The first assumption can be relaxed if animals are of known age at marking, or if there is no age structure to any of the parameters – for example for the adult mallard data in Table 1c. The second assumption can be changed to any time unit. We let $N_i, j$ denote the number of animals marked in year $i$, $i = 1,\ldots,n_1$ and recovered in year $j$, $j = 1,\ldots,n_2$, where $n_2 \geq n_1$, and let $F_i$ denote the number of animals marked in year $i$. The probability of an animal being ringed in year $i$ and recovered in year $j$ is given by

$$P_{i,j} = \left( \prod_{k=i}^{j-1} \phi_{k-i+1,k} \right) (1 - \phi_{j-i+1,j}) \lambda_{j-i+1,j}, \tag{1}$$

where $\phi_{i,j}$ is the probability of an animal aged $i$ surviving the $j$th year of the study and where $\lambda_{i,j}$ is the probability of recovering a dead animal aged $i$ in the $j$th year of the study. These probabilities can be summarized by an upper triangular matrix, $\mathbf{P}$, consisting of all the $P_{i,j}$, which we call the p-array. The likelihood is given by the product multinomial distribution below

$$L \propto \prod_{i=1}^{n_1} \left\{ \prod_{j=1}^{n_2} P_{i,j}^{N_{i,j}} \left( 1 - \sum_{j=i}^{n_2} P_{i,j} \right)^{F_i - \sum_{j=i}^{n_2} N_{i,j}} \right\}.$$

For product-multinomial models Catchpole and Morgan (1997) showed that it is sufficient to form a derivative matrix by differentiating the terms of the p-array (or their logarithm) with respect to the parameters, as long as there is perfect data. We define perfect data as data with $N_{i,j} \neq 0$ for all $i$ and $j$. Using the p-array terms rather than the means is structurally simpler, because the probabilities of being ringed and never being seen again are excluded.

### 1.3 Notation

Mark-recovery models contain both survival and recovery parameters, which could be constant (C), dependent on time (T), dependent on the age of the animal (A) or dependent on both age and time (A,T). We follow the notation of Catchpole and Morgan (1996a) and Catchpole et al (1996b) to represent different models. Each model is denoted as y/z, with y denoting survival and z denoting reporting probability. For example the model T/A has survival probabilities that are dependent on time and recovery probabilities that are dependent on age. Frequently first year birds experience higher mortality than older animals, and therefore it is sensible to consider models which separate first-year survival from that of subsequent years. The notation x/y/z is used for this situation, with x denoting first year survival, y denoting adult survival and z denoting reporting probability. The options are again constant (C) or dependent on age (A), time (T) or age and time (A,T), but x can only be C or T. There are additional options for the reporting probability; it could depend on whether the animal is in its first year of life or is older, indicated by $\mathrm{A}_{1:2}$. The reporting probability can have these two age classes and also be dependent on time, which we denote by $\mathrm{A}_{1:2}, T$.

### 1.4 Aims and structure of the paper

The purpose of this paper is to provide a set of general results on the parameter redundancy of various mark-recovery models, and in the case of parameter-redundant models, find exactly how many parameters can be estimated and what combinations of the original parameters can be estimated. An important feature of the results provided is that they are perfectly general, and explicitly take account of the dimensionality of the data. For completeness we include some cases already considered by Catchpole and Morgan (1997), Catchpole et al (1998) and Catchpole et al (2002). The three methods used are explained in Section 2. The first method comes from Catchpole and Morgan (1997) and is also included here for completeness. The second method demonstrates a new application of for the reparameterisation method of Cole et al (2010). Here it is used to obtain general results in parameter-redundant models and for examining all models in the presence of imperfect data, where some $N_{i,j} = 0$. The third method has not be presented before. The results are given in Section 3.

The general results assume perfect data. Real data, such as the data in Table 1, often have some $N_{i,j}$ which are zero. How this affects the parameter-redundancy of a model is discussed in Section 4. Many of the models examined are parameter redundant, in which case adding time- or age-varying trends, or adding time-varying covariates may result in a full rank model. This is discussed in Section 5, where it is shown that, given knowledge of the number of estimable parameters in the model without covariates, the number of estimable parameters in the model with covariates can be obtained without further calculation. For completeness, in Section 6 we briefly consider parameter redundancy in conditional models, which apply when cohort sizes are not available. `Maple` code for the examples is provided in the supplementary material.

## 2 Methods

An exhaustive summary is a vector of parameters that uniquely define the model. The exponential family means and the p-array and its logarithm are examples of exhaustive summaries for mark-recovery models. The basic method involves forming a derivative matrix by differentiating the exhaustive summary with respect to the parameters. The rank of the resulting derivative matrix is calculated and this is equal to the number of estimable parameters (Cole et al, 2010). Generalising this result for all years of ringing ($n_1$ ) and recovery ($n_2 \geq n_1$ ), makes the use of one of the following methods.

### 2.1 Method 1: the extension theorem for full-rank models

Firstly the lowest values of $n_1$ and $n_2$ for which the model is full rank is found. The extension theorem of Catchpole and Morgan (1997) is then applied. It states that if a full-rank model is extended by adding extra p-array terms $\kappa_2$ and extra parameters $\theta_2$ and the derivative matrix $\mathbf{D}_2 = [\partial \kappa_2 / \partial \theta_2]$ is also full rank, then the extended model is full rank. The result can then be generalised further by induction (Theorem 6, Catchpole and Morgan, 1997), hence providing general results for any number of years of ringing and recovery. If the extension involves no extra parameters or one extra parameter then the extension theorem applies trivially (remark 5, Catchpole and Morgan, 1997). Note that this method only makes used of the methods of Catchpole and Morgan (1997) and does not require the use of any more recently developed methods.

*Example 1.* Consider a model for animals that have constant first-year survival, $\phi_1$, time-dependent adult survival, $\phi_{a,t}$ and time-dependent recovery, $\lambda_t$ (model C/T/T). We consider an $3 \times 3$ p-array, resulting from $n_1 = 3$ years of ringing and $n_2 = 3$ years of recovery. An exhaustive summary is
$\kappa_1 = [\bar{\phi}_1 \lambda_1, \phi_1 \bar{\phi}_{a,2} \lambda_2, \phi_1 \phi_{a,2} \bar{\phi}_{a,3} \lambda_3, \bar{\phi}_1 \lambda_2, \phi_1 \bar{\phi}_{a,3} \lambda_3, \bar{\phi}_1 \lambda_3]^T$, where $\bar{\nu} = 1 - \nu$, and the parameters are
$\theta_1 = [\phi_1, \phi_{a,2}, \phi_{a,3}, \lambda_1, \lambda_2, \lambda_3]$. The derivative matrix $\mathbf{D}_1 = [\partial \kappa_1 / \partial \theta_1]$ has rank 6, and there are 6 parameters in the model, therefore this model is full rank. Adding an extra year of recovery adds the extra p-array terms $\kappa_2 = [\phi_1 \phi_{a,2} \phi_{a,3} \bar{\phi}_{a,4} \lambda_4,\ \phi_1 \phi_{a,3} \bar{\phi}_{a,4} \lambda_4, \phi_1 \bar{\phi}_{a,4} \lambda_4]^T$ and extra parameters $\theta_2 = [\phi_{a,4}, \lambda_4]$. The derivative matrix $\mathbf{D}_2 = [\partial \kappa_2 / \partial \theta_2]$ only has rank 1, so is not full rank. In fact the extended model can be shown to be parameter redundant with deficiency 1. As an alternative consider adding an extra year of recovery and an extra year of ringing simultaneously. The extra exhaustive summary terms are now $\kappa_2 = \left[\phi_1 \phi_{a,2} \phi_{a,3} \bar{\phi}_{a,4} \lambda_4, \phi_1 \phi_{a,3} \bar{\phi}_{a,4} \lambda_4, \phi_1 \bar{\phi}_{a,4} \lambda_4, \bar{\phi}_1 \lambda_4\right]^T$ with the extra parameters remaining the same as for the previous extension. The derivative matrix $\mathbf{D}_2 = [\partial \kappa_2 / \partial \theta_2]$ has rank 2, and is therefore full rank. The generalisation from an $n \times n$ array to $(n+1) \times (n+1)$ follows in a similar manner. Therefore by the extension theorem this model has full rank $2n_2$ for the case $n_1 = n_2$. This is unusual as most full-rank mark-recovery models do not require $n_1 = n_2$; see Tables 2 and 3. □

 

### 2.2 Method 2: reparameterisation method

The reparameterisation method is used for parameter-redundant models to generalise results to any $n_1$ and $n_2$; it is also used for full-rank models to find general results in the presence of imperfect data, described in Section 4. First the model is reparameterised. The new parameterisation is chosen so that it is full rank and extends if $n_1$ and $n_2$ are increased. The extension theorem is then applied to the full-rank reparameterised model. By the reparameterisation theorem of Cole et al (2010) the number of parameters in the full-rank reparameterised model will be the number of estimable parameters in the original model.

*Example 2.* Consider the model where survival is fully age dependent and recovery is dependent on time (model A/T). In the case with $n_1 = 2$ and $n_2 = 3$ the exhaustive summary, which consists of all of the non-zero terms of the p-array, is $\kappa_1 = [\bar{\phi}_1\lambda_1, \phi_1\bar{\phi}_2\lambda_2, \phi_1\phi_2\bar{\phi}_3\lambda_3, \bar{\phi}_1\lambda_2, \phi_1\bar{\phi}_2\lambda_3]^T$. This is differentiated with respect to the 6 parameters, $\theta = [\phi_1, \phi_2, \phi_3, \lambda_1, \lambda_2, \lambda_3]$ to form a derivative matrix that has rank 5. Therefore this model is parameter redundant with deficiency 1. To apply the extension theorem using reparameterisation we first choose the reparameterisation $\mathbf{s} = [s_1, s_2, s_3, s_4, s_5] = [\bar{\phi}_1\lambda_1, \phi_1\bar{\phi}_2/\bar{\phi}_1, \lambda_2/\lambda_1, \phi_1\phi_2\bar{\phi}_3/\bar{\phi}_1, \lambda_3/\lambda_1]$. We rewrite $\kappa_1$ in terms of the elements $\mathbf{s}$, giving $\kappa_1(\mathbf{s}) = [s_1, s_1s_2s_3, s_1s_4s_5, s_1s_3, s_1s_2s_5]^T$. The exhaustive summary rewritten in terms of the reparameterisation, $\kappa_1(\mathbf{s})$, is then differentiated with respect to $\mathbf{s}$, to form a derivative matrix with full rank 5. We then apply the extension theorem to the full-rank reparameterised model. Adding an extra year of ringing adds the extra exhaustive summary term $\kappa_2(\mathbf{s}) = [s_1s_5]$, but adds no extra $s_i$, and therefore is trivially full rank by the extension theorem. Alternatively, adding an extra year of recovery gives the extra exhaustive summary term $\kappa_2(\mathbf{s}) = [s_1s_6s_7, s_1s_4s_7, s_1s_2s_7]^T$, where the extra $s_i$ are $s_6 = \phi_1\phi_2\phi_3\bar{\phi}_4/\bar{\phi}_1$ and $s_7 = \lambda_4/\lambda_1$ with $\mathbf{s}_e = [s_6, s_7]$. The derivative matrix $\mathbf{D}_2 = [\partial\kappa_2(\mathbf{s})/\partial\mathbf{s}_e]$ has full rank 2. The general induction step follows in a similar manner. By the extension theorem, the reparameterised model will always have full rank $2n_2 - 1$. By the reparameterisation theorem the original model will also have rank $2n_2 - 1$. As the original model has $2n_2$ parameters it is always parameter redundant with deficiency 1 for $n_1 \geq 2$ and $n_2 \geq 3$. □

### 2.3 Method 3: limited by the number of unique exhaustive summary terms

It is obvious that the model with age- and time-dependence in both survival and recovery parameters is parameter redundant because there are many more parameters than there are multinomial cell values. Rather than the multinomial cell values themselves, it is the number of individual exhaustive summary terms, (which in this case are the p-array terms), that is limiting the number of estimable parameters. As there are $E = n_1n_2 - \frac{1}{2}n_1^2 + \frac{1}{2}n_1$ non-zero terms in the p-array, the maximum possible rank is $E$. There are several models where it is obvious that the rank is equal to $E$, because each $P_{i,j}$ contains a unique parameter not occurring in any other $P_{i,j}$.

It is also possible to use this method if any of the $P_{i,j}$ are identical with each distinct $P_{i,j}$ containing a parameter not in any other distinct $P_{i,j}$. Then the rank is equal to the number of distinct $P_{i,j}$.

*Example 3.* The model with age-dependent survival, $\phi_i$, and age-dependent recovery, $\lambda_i$, (model A/A), with $n_1 = 3$ and $n_2 = 3$ has p-array

$$\mathbf{P} = \begin{bmatrix} \bar{\phi}_1\lambda_1 & \phi_1\bar{\phi}_2\lambda_2 & \phi_1\phi_2\bar{\phi}_3\lambda_3 \\ & \bar{\phi}_1\lambda_1 & \phi_1\bar{\phi}_2\lambda_2 \\ & & \bar{\phi}_1\lambda_1 \end{bmatrix}$$

The distinct terms of $\mathbf{P}$ are $\{\bar{\phi}_1\lambda_1, \phi_1\bar{\phi}_2\lambda_2, \phi_1\phi_2\bar{\phi}_3\lambda_3\}$. Each of these terms contains a different parameter, $\lambda_i$. As there are three distinct terms the rank of this model is 3. If there are $n_1$ years of ring and $n_2$ years of recovery, there will now be $n_2$ unique terms. The rank of this model is therefore $n_2$, but there are $2n_2$ parameters therefore the model is always parameter redundant with deficiency $n_2$ for $n_1 \geq 2$ and $n_2 \geq 2$. □

### 2.4 How the method is chosen

Above we presented three different methods for determining the rank of a model. We choose the method as follows:

Step 1 Firstly a model is checked to see if it is limited by the number of exhaustive summary terms, in which case the rank is deduced using method 3. This normally occurs if one or more of the parameters are dependent on both age and time.

Step 2 Secondly the rank of a small case (for example $n_1 = 4$, $n_2 = 4$) is checked.

Step 3 If the model is full-rank method 1 is applied, otherwise method 2 is applied.

### 2.5 Estimable parameter combinations

The derivative matrix contains more information than just the number of estimable parameters. In parameter-redundant models it is possible to find the estimable parameter combinations by solving a set of partial differential equations. This involves solving $\alpha^T \mathbf{D} = 0$, where $\mathbf{D}$ is a derivative matrix with rank less than the number of parameters. There will be $d = p - r$ solutions to $\alpha^T \mathbf{D} = 0$, labelled $\alpha_j$ for $j = 1 \ldots d$, with individual entries $\alpha_{ij}$. Any $\alpha_{ij}$ which are zero for all $d$ solutions correspond to a parameter, $\theta_i$, which is estimable. The solutions of the system of linear first-order partial differential equations,

$$\sum_{i=1}^{p} \alpha_{ij} \frac{\partial f}{\partial \theta_i} = 0, \; j = 1 \ldots r,$$

form the set of estimable parameters. This method was developed by Catchpole et al (1998) for exponential family models including compartment models and separately developed for continuous state-space models, such as compartment models, by Chappell and Gunn (1998) and Evans and Chappell (2000).

This partial differential equation approach can be applied to a model with a particular number of years of ringing and recovery. To generalise the result to any number of years of ringing and recovery we use the reparameterisation method (Cole et al, 2010). This involves using the particular reparameterisation used to apply the extension theorem.

*Example 4.* Consider a model with time-dependent survival and recovery (model T/T). It can be shown using method 2 that this model has rank $n_1 + n_2 - 1$ and deficiency $n_2 - n_1 + 1$. For this case we used the reparameterisation

$$\begin{aligned} s_{w,i} &= (1-\phi_i)\lambda_i, \text{ for } i = 1, \ldots, n_1 \\ s_{y,j} &= (1-\phi_j)\lambda_j \prod_{k=1}^{j-1} \phi_k, \text{ for } j = 2, \ldots, n_2. \end{aligned}$$

Then $s_{y,2}/s_{w,2} = \phi_1$ so $\phi_1$ is estimable and $s_{y,3}/s_{w,3} = \phi_1\phi_2$ which means $\phi_2$ is estimable. This continues until $s_{y,n_1}/s_{y,n_1} = \prod_{k=1}^{n_1} \phi_k$, resulting in $\phi_{n-1}$ being estimable. From the $s_{w,i}$ for $i = 1, \ldots, n_1 - 1$ it then follows immediately that $\lambda_1, \ldots, \lambda_{n_1-1}$ are also estimable. However $\phi_i$ and $\lambda_i$ are confounded for $i \geq n_1$. For example if $n_2 = n_1$ the last estimable parameters is $s_{w,n_1} = (1-\phi_{n_1})\lambda_i$. □

Note that if a model is limited by the number of exhaustive summary terms, $E = n_1 n_2 - \frac{1}{2} n_1^2 + \frac{1}{2} n_1$, it is not possible to find a simpler set of estimable parameter combinations other than the terms of the exhaustive summary. In such cases the set of estimable parameters is $\{P_{i,j}\}_{\substack{j=i,\ldots,n_2 \\ i=1,\ldots,n_1}}$, where $P_{i,j}$ is given by equation 1.

*Example 3 revisited.* The estimable parameter combinations in example 3 are the distinct $P_{i,j}$ terms, namely $\{P_{1,j}\}_{i=1,\ldots,3} = \{\bar{\phi}_1\lambda_1, \phi_1\bar{\phi}_2\lambda_2, \phi_1\phi_2\bar{\phi}_3\lambda_3\}$. □

 

## 3 General results

For $n_1$ years of marking and $n_2$ years of recovery with $n_1 \leq n_2$, the rank, $r$, and the deficiency, $d$ for all y/z and x/y/z models are given in Tables 2 and 3. It is assumed that animals are ringed in their first year of life, however any model that does not include any age dependence could also be used for animals ringed at any age. The model A/C was presented by Seber (1971), and explicit maximum-likelihood parameter estimates are given by Catchpole and Morgan (1991). General results for age-dependent ring-recovery models are presented in Catchpole et al (1996b). Models C/T, T/C and T/A were considered in Freeman and Morgan (1992). Model T/A/C was considered by Morgan and Freeman (1989), while models T/A/T, C/A/T and C/C/T were considered by Freeman and Morgan (1990, 1992). Note the model combinations C/A/z and T/(A,T)/z are excluded from Table 3 as they are identical to models A/z and (A,T)/z respectively in Table 2.

Table 3 presents x/y/z models for animals that have a separately modelled first-year survival probability. This format can be extended further to consider any animal that has a separate survival probability for the first $J > 1$ years of their life; parameter redundancy results for this extension are given in Web Appendix A.

It is commonly believed that to estimate age-dependent survival two data sets are required, one for animals marked as young and one for animals marked as adults (see for example Robinson, 2010). This is not true. Although it is not possible to estimate all parameters in a model with a survival probability that is fully age dependent (models A/* are parameter redundant), it is possible if first year survival is separated from adult survival, as long as the recovery probability is not dependent on age, (models C/C/C, C/C/T and C/T/C are all full rank). Or, if first-year survival is time dependent, adult survival can be age dependent as long as recovery is not age dependent (models T/A/C and T/A/T are full rank). This ties in with results of Catchpole et al (1996b). It is also possible to have up to $J+1$ age classes and still have full rank models (see Web Appendix A).

The mallard data in Tables 1b and 1c are an example of a pair of data-sets. It is possible to combine these two data sets in one analysis and such combined analysis can result in an increased rank compared to models for the two component models considered separately. In this model framework for the adult data set it is only possible to fit models in Table 2 which do not involve age-dependence, therefore a fully age dependent model is still not possible for the combined data set. The following x/y/z models are no longer parameter redundant when combined with appropriate x/y models:

- C/C/$A_{1:J+1}$ combined with C/C;
- C/C/($A_{1:J+1}$,T) combined with C/T;
- C/T/$A_{1:J+1}$ combined with T/C.

The full results are given in Web Appendix B.

Other reparameterisations of the ring-recovery models are also possible. For example the recovery probability $\lambda_j$ at time $j$ can be reparameterised as $f_j = (1-\phi_j)\lambda_j$. (This is a reparameterisation used in models commonly known as tag-return models or Brownie models, see for example Hoenig et al, 2005). By the reparameterisation theorem of Cole et al (2010) the number of estimable parameters will be the same regardless of the parameterisation used.

## 4 The effect of missing cells in real data

Parameter redundancy can occur because of the model structure or it can also arise as a consequence of a particular set of data. The former case is known as intrinsic parameter redundancy, while the later is known as extrinsic parameter redundancy. So far we have only considered intrinsic parameter redundancy, so that the parameter redundancy results of Section 3 apply when there are perfect data, such that $N_{i,j} \neq 0$

 

for all $i \le j \le n_2$ and $1 \le i \le n_1$. Real data sets usually have some instances of $N_{i,j} = 0$. In this Section we explore the effect this has on parameter redundancy.

The appropriate exhaustive summary to use when considering extrinsic parameter redundancy is the elements of the log-likelihood (Cole *et al*, 2010). This is an exhaustive summary that includes the data, whereas the exhaustive summary used in Sections 2 and 3 only considers the probabilities corresponding to the fundamental model structure. For the mark-recovery model this log-likelihood exhaustive summary consists of the terms $N_{i,j}\log(P_{i,j})$, for $i \le j \le n_2$ and $1 \le i \le n_1$ as well as the terms

$$\left(F_i - \sum_{j=i}^{n_2} N_{i,j}\right)\log\left(1 - \sum_{j=i}^{n_2} P_{i,j}\right), \quad \text{for } 1 \le i \le n_1.$$

Note that if $N_{i,j} = 0$, one of the exhaustive summary terms will disappear. We can simplify the exhaustive summary used to contain the terms $P_{i,j}$ if $N_{i,j} \neq 0$ and the terms $\left(1 - \sum_{j=i}^{n_2} P_{i,j}\right)$, which come from the probabilities of being ringed and never seen again. This is because multiplying by a constant and taking exponentials are one-to-one transformations; see Cole et al (2010).

In the mallard data set of Table 1b there is one zero entry ($N_{2,9} = 0$). Similarly in the mallard data set of Table 1c ($N_{1,9} = 0$). Here the parameter redundancy results for this data set will be the same as if the data set was perfect. This is because $P_{2,9}$ or $P_{1,9}$ also appear in the probability of being ringed and never seen again, so we can still use the exhaustive summary that consists of all the $P_{i,j}$. This result is generalised in Theorem 4.1 below.

**Theorem 4.1** *If at most one $N_{i,j} = 0$ for each row i then the model rank is identical to the model with perfect data.*

The proof of Theorem 4.1 stems from the fact that if $N_{i,j} = 0$ the missing $P_{i,j}$ terms also occur in $\left(1 - \sum_{j=i}^{n_2} P_{i,j}\right)$.

However the lapwing data set, in Table 1a, has more than one zero entry in some rows. Therefore potentially the parameter-redundancy results of Tables 2 and 3 are no longer valid. This can be studied individually for any data set with specific zero $N_{i,j}$'s. Here we consider the effect of particular patterns of zero $N_{i,j}$'s.

It is not feasible to consider every combination of zero $N_{i,j}$'s. Instead because the probability of a zero $N_{i,j}$ increases as $j$ increases, we consider the effect of having only $m \ge 1$ diagonals so that $N_{i,j} = 0$ if $j - i + 1 > m$ and $N_{i,j} > 0$ if $j - i + 1 \le m$. The maximum value of $m$ we consider is $m = n_2 - 2$. If $m = n_2 - 1$, Theorem 4.1 applies. The effect on the parameter redundancy status of the models in Tables 2 and 3 is summarized in Table 4. We present the results in terms of when the rank differs from the ideal situation of perfect data.

*Example 5.* Consider the model where the recovery probability, $\lambda$, is constant and the survival probability for first year animals, $\phi_1$ is also constant, but the survival probability for older adult animals, $\phi_{a,i}$, is time dependent (model C/T/C). The model with perfect data is full rank, with rank $n_2 + 1$. This can be shown using method 1 (see Maple code). Consider a model with imperfect data. Suppose there is only $m = 1$ diagonal of data. In the case with $n_1 = 3$ and $n_2 = 3$ the exhaustive summary is

$$\begin{aligned}\kappa_1 &= [\kappa_{1,1}, \kappa_{1,2}, \kappa_{1,3}, \kappa_{1,4}, \kappa_{1,5}, \kappa_{1,6}] \\ &= [\bar{\phi}_1\lambda, 1 - \bar{\phi}_1\lambda - \phi_1\bar{\phi}_{a,2}\lambda - \phi_1\phi_{a,2}\bar{\phi}_{a,3}\lambda, \bar{\phi}_1\lambda, 1 - \bar{\phi}_1\lambda - \phi_1\bar{\phi}_{a,3}\lambda, \bar{\phi}_1\lambda, 1 - \bar{\phi}_1\lambda]\end{aligned}$$

This is differentiated with respect to the 4 parameters, $\theta = [\phi_1, \phi_{a,2}, \phi_{a,3}, \lambda]$ to form a derivative matrix that has rank 3. Therefore with only $m = 1$ diagonal of data this model is no longer full rank and has deficiency 1. We can show that for any $n_1 \ge 3$ and $n_2 \ge 3$ with $m = 1$ this model always has deficiency 1 using the reparameterisation

$$\mathbf{s} = [s_1, s_2, s_3] = [\kappa_{1,1}, -\kappa_{1,2} + 1 - \kappa_{1,1}, -\kappa_{1,4} + 1 - \kappa_{1,1}] = [\bar{\phi}_1\lambda, \phi_1\bar{\phi}_{a,2}\lambda + \phi_1\phi_{a,2}\bar{\phi}_{a,3}\lambda, \phi_1\bar{\phi}_{a,3}].$$

Rewriting $\kappa_1$ in terms of the elements $\mathbf{s}$ gives

$$\kappa_1(\mathbf{s}) = [s_1, 1-s_1-s_2, s_1, 1-s_1-s_3, s_1, 1-s_1].$$

The derivative matrix $\partial\kappa_1(\mathbf{s})/\partial\mathbf{s}$ is of full rank 3. Adding an extra year of recovery changes the exhaustive summary to

$$\begin{aligned}\kappa_2 &= [\kappa_{2,1}, \kappa_{2,2}, \kappa_{2,3}, \kappa_{2,4}, \kappa_{2,5}, \kappa_{2,6}] \\ &= [\bar{\phi}_1\lambda, 1-\bar{\phi}_1\lambda-\phi_1\bar{\phi}_{a,2}\lambda-\phi_1\phi_{a,2}\bar{\phi}_{a,3}\lambda-\phi_1\phi_{a,2}\phi_{a,3}\bar{\phi}_{a,4}\lambda, \bar{\phi}_1\lambda, \\ &\quad 1-\bar{\phi}_1\lambda-\phi_1\bar{\phi}_{a,3}\lambda-\phi_1\phi_{a,3}\bar{\phi}_{a,4}\lambda, \bar{\phi}_1\lambda, 1-\bar{\phi}_1\lambda-\phi_1\bar{\phi}_{a,4}].\end{aligned}$$

We change the reparameterisation to

$$\begin{aligned}\mathbf{s} &= [s_1, s_2, s_3, s_4] = [\kappa_{2,1}, -\kappa_{2,2}+1-\kappa_{2,1}, -\kappa_{2,4}+1-\kappa_{2,1}, -\kappa_{2,6}-\kappa_{2,1}] \\ &= [\bar{\phi}_1\lambda, \phi_1\bar{\phi}_{a,2}\lambda+\phi_1\phi_{a,2}\bar{\phi}_{a,3}\lambda+\phi_1\phi_{a,2}\phi_{a,3}\bar{\phi}_{a,4}\lambda, \phi_1\bar{\phi}_{a,3}+\phi_1\phi_{a,3}\bar{\phi}_{a,4}\lambda, \phi_1\bar{\phi}_{a,4}\lambda].\end{aligned}$$

Rewriting $\kappa_2$ in terms of the elements $\mathbf{s}$ gives

$$\kappa_2(\mathbf{s}) = [s_1, 1-s_1-s_2, s_1, 1-s_1-s_3, s_1, 1-s_1-s_4].$$

Using the two-part extension theorem of Cole and Morgan (2010a), which is an extension of the standard extension theorem (Catchpole and Morgan, 1997), and following a similar argument for adding an extra year of ringing we conclude that this reparameterised model is always full rank with rank $n_2$. By the reparameterisation theorem the rank of the original parameterisation is also $n_2$, but there are $n_2+1$ parameters so the model with $m=1$ diagonals of data always has deficiency 1. When $m=2$ the model returns to being full rank, which can again be shown using method 1. It follows that when $m>2$ as there are more exhaustive summary terms that the model will also be full rank. □

The general conclusion is that many $N_{i,j}$ can be zero and the rank of the model does not change from when there is perfect data. The ideal situation is that the rank never changes. In this case if the data have only the leading diagonal ($m=1$) the rank is still the same as having perfect data. Obviously in this case if $n>1$ the rank is also unchanged. Twelve of the models listed in Table 4 have this ideal situation. There are sixteen models for which the rank changes if $m=1$. This means that if $m=1$ then the rank is smaller than the rank for perfect data. There are several models which are full rank in the presence of perfect data (given in bold in Table 4), and which become parameter redundant if $m=1$, but remain full rank if there are at least the first two diagonals of data ($m\geq 2$). There are also six models whose rank changes if $m\leq 2$.

The ranks of the remaining models change whenever $m\leq n_2-2$. However these are all parameter redundant models which have rank $E=n_1n_2-\frac{1}{2}n_1^2+\frac{1}{2}n_1$ when there is perfect data, so that the model rank is limited by the number of unique exhaustive summary terms, and therefore it follows the new model rank will be limited by the now smaller number of exhaustive summary terms when there are some zero $N_{i,j}$ values. The maximum number of unique exhaustive summary terms is denoted by $E_m$ with

$$E_m = \begin{cases} E-\frac{1}{2}(n_2-m)(n_2-m+1) & n_2-n_1 < m-1 \\ mn_1 & n_2-n_1 \geq m-1 \end{cases}.$$

As we can see from the lapwing data set (Table 1a) real data typically will not have $m$ diagonals of non-zero data. It may be possible to calculate the number of estimable parameters for such models from Table 4, by considering the highest value of diagonal $m$ for which there are perfect data. The lapwing data set (Table 1a) has non-zero entries the first three diagonals of data, therefore all the full-rank models considered in Table 4 remain full rank. The rank also does not change for the parameter-redundant models whose rank is not limited by the number of exhaustive summary terms. (This is not the case for all models where animals have a separate survival probability for $J>1$ years, see Web Appendix C for more details).

 

## 5 Covariates and time/age varying trends

Adding time- or age-dependent covariates or time- or age-varying trends to parameter redundant models can result in models which are no longer parameter redundant. For example in the models T/*, a time-varying covariate for the survival parameter could be $\phi_i = 1/[1+\exp\{-(a_\phi + b_\phi x_i)\}]$, where $x_i$ is a time dependent covariate, such as a measure of the weather. An example of a time-varying trend in the models */T for the recovery parameter is $\lambda_i = 1/[1+\exp\{-(a_\lambda + b_\lambda i)\}]$. Cole and Morgan (2010b) show that if the covariate model has $p_c$ parameters and the same model without covariates has rank $q$, the model with covariates has rank equal to $\min(p_c, q)$. This result means that in order to determine the rank of a ring-recovery model with covariates, we first look up the rank of the same model without covariates, $q$, in Tables 2 or 3 (or Web Appendix Table 1), then determine the number of parameters in the model with covariates, $p_c$. Finally, we evaluate $\min(p_c, q)$ to determine the rank.

*Example 2 revisited.* Consider again the model A/T. The model without covariates has rank $q = 2n_2 - 1$ and deficiency 1 for $n_1, n_2 \geq 2$. Suppose that the recovery parameter is thought to vary on a logit scale with the time-varying covariate $x_i$, giving $\lambda_i = 1/[1+\exp\{-(a_\lambda + b_\lambda x_i)\}]$. The model now has $p_c = n_2 + 2$ parameters. The rank of the model with covariates is $\min(p_c, q) = \min(n_2+2, 2n_2-1) = n_2+2$ if $n_2 \geq 3$. The rank is equal to the number of parameters, so this covariate model is full rank when there are 3 or more years of recovery data. □

*Example 3 revisited.* Consider the model with age-dependent survival and recovery (model A/A). The model without covariates has rank $n_2$ and deficiency $n_2$. Now consider adding an age-varying trend to the survival parameter, $\phi_i = 1/[1+\exp\{-(a_\phi + b_\phi i)\}]$. The covariate model has $p_c = n_2 + 2$ parameters. The rank of the model with covariates is $\min(p_c, q) = \min(n_2+2, n_2) = n_2$. The rank of the model is less than the number of parameters so the model is still parameter redundant but with a smaller deficiency of 2. □

## 6 Ringing data without cohort numbers

In historical ring-recovery data the total number of birds ringed in each year may be unknown or unreliable. Before 2000 the British Trust for Ornithology recorded ring-recovery data on paper forms, where full details of the total numbers of birds ringed are not known (Robinson, 2010). In such a case a model can be fitted by conditioning on the number of birds recovered from each cohort. The parameter redundancy of such models is examined in detail in Web Appendix D. The only conditional models that are full rank assume constant reporting probability, $\lambda$. The constant reporting probability is not estimable as it disappears from the model, but survival parameters are estimable. However there is evidence that the reporting probability of wild birds in Britain in recent years has been decreasing over time (Baillie & Green, 1987). In such cases it is possible to fit conditional covariate models or time varying trends (Cole and Morgan, 2010b).

Robinson (2010) shows that if the full age information is known for recoveries, but only the numbers of birds ringed are known each year rather than the proportion of birds marked in each age class, then survival rates for birds can still be estimated. Robinson (2010) used an adhoc method to estimate the proportion; it is possible to estimate the proportion as an additional parameter (Cole and Freeman work in progress). Alternatively if there is no age structure available at all, a mixture model can be used. This model including a detailed analysis of the parameter redundancy is given in McCrea et al (2011).

## 7 Discussion

This paper has examined the parameter redundancy of a large number of ring-recovery models. We have shown how general results for the rank deficiency of ring-recovery results can be derived. For some full-rank models, this has simply involved applying the theorems of Catchpole and Morgan (1997). However for other full-rank models and parameter-redundant models this has involved applying the reparameterisation theorem of Cole et al (2010). A priori, there was no reason to suppose that results of Table 2 and 3 would be as simple as they are.

We have also shown the effect of empty cells on the results. It is interesting to note that full rank models often remain full rank even if most of the cells are empty. Unless a ring-recovery data set is incredibly sparse, parameter redundancy is most likely to be caused by the inherent structure of the model rather than the data itself.

When fitting a model, it is of particular interest to determine whether or not a model is parameter redundant. In parameter-redundant models it is not possible to estimate model parameters using classical inference and a weakly-identifiable model may result if Bayesian analysis is used (Gimenez et al, 2009). The exact rank or deficiency of a parameter-redundant model is of less interest. However knowing the exact rank of a parameter-redundant model is then useful if covariates are added to the model, as no further derivative calculations are required to find the rank of the model with covariates.

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**Table 1** Example Ring-Recovery Data on: (a) Lapwings ringed as nestlings (Catchpole et al, 1999), (b) male mallards ringed as nestlings, and (c) male mallards ringed as adults (Brownie et al, 1985).

(a)

| Year of Ringing | Number Ringed | Year of recovery (-1962) 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1963 | 1147 | 13 | 4 | 1 | 2 | 1 | 0 | 0 | 1 | 0 |
| 1964 | 1285 | | 16 | 4 | 3 | 0 | 1 | 1 | 0 | 0 |
| 1965 | 1106 | | | 11 | 1 | 1 | 1 | 0 | 2 | 1 |
| 1966 | 1615 | | | | 10 | 4 | 2 | 1 | 1 | 1 |
| 1967 | 1618 | | | | | 11 | 1 | 5 | 0 | 0 |
| 1968 | 2120 | | | | | | 9 | 5 | 4 | 0 |
| 1969 | 2003 | | | | | | | 11 | 9 | 4 |
| 1970 | 1963 | | | | | | | | 8 | 4 |
| 1971 | 2463 | | | | | | | | | 4 |

(b)

| Year of Ringing | Number Ringed | Year of recovery (-1962) 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1963 | 962 | 82 | 35 | 18 | 16 | 6 | 8 | 5 | 3 | 1 |
| 1964 | 702 | | 103 | 21 | 13 | 11 | 8 | 6 | 6 | 0 |
| 1965 | 1132 | | | 82 | 36 | 26 | 24 | 15 | 18 | 4 |
| 1966 | 1201 | | | | 153 | 39 | 22 | 21 | 16 | 8 |
| 1967 | 1199 | | | | | 109 | 38 | 31 | 15 | 1 |
| 1968 | 1155 | | | | | | 113 | 64 | 29 | 22 |
| 1969 | 1131 | | | | | | | 124 | 45 | 22 |
| 1970 | 906 | | | | | | | | 95 | 25 |
| 1971 | 353 | | | | | | | | | 28 |

(c)

| Year of Ringing | Number Ringed | Year of recovery (-1962) 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1963 | 231 | 10 | 13 | 6 | 1 | 1 | 3 | 1 | 2 | 0 |
| 1964 | 649 | | 58 | 21 | 16 | 15 | 13 | 6 | 1 | 1 |
| 1965 | 885 | | | 54 | 39 | 23 | 18 | 11 | 10 | 6 |
| 1966 | 590 | | | | 44 | 21 | 22 | 9 | 9 | 3 |
| 1967 | 943 | | | | | 55 | 39 | 23 | 11 | 12 |
| 1968 | 1077 | | | | | | 66 | 46 | 29 | 18 |
| 1969 | 1250 | | | | | | | 101 | 59 | 30 |
| 1970 | 938 | | | | | | | | 97 | 22 |
| 1971 | 312 | | | | | | | | | 21 |

**Table 2** Table of parameter redundancy results for y/z models for mark-recovery studies with $n_1$ years of marking and $n_2$ years of recoveries. The number of nonzero terms in the p-array is $E = n_1 n_2 - \frac{1}{2}n_1^2 + \frac{1}{2}n_1$. $r$ and $d$ denote the rank and deficiency of a model. M denotes the method used. The results are valid for $n_1, n_2 \geq 2$ except for *, which is valid for $n_1, n_2 \geq 3$ (otherwise $d = 1$). The last column is empty if $d = 0$ as all parameters are estimable.

| Model | $r$ | $d$ | M | Estimable Parameter Combinations |
|---|---|---|---|---|
| C/C | 2 | 0 | 1 | |
| C/T | $n_2+1$ | 0 | 1 | |
| C/A | $n_2$ | 1 | 3 | $\left\{P_{1,j}\right\}_{j=1,\ldots,n_2}$ |
| C/(A,T) | $E$ | 1 | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |
| T/C | $n_2+1$ | 0 | 1 | |
| T/T | $n_1+n_2-1$ | $n_2-n_1+1$ | 2 | see footnote † |
| T/A* | $2n_2$ | 0 | 1 | |
| T/(A,T) | $E$ | $n_2$ | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |
| A/C | $n_2$ | 1 | 2 | $\left\{P_{1,j}\right\}_{j=1,\ldots,n_2}$ |
| A/T | $2n_2-1$ | 1 | 2 | $\left\{P_{1,j}\right\}_{i=1,\ldots,n_2}$, $\left\{\frac{\lambda_i}{\lambda_{i-i}}\right\}_{i=2,\ldots,n_2}$ |
| A/A | $n_2$ | $n_2$ | 3 | $\left\{P_{1,j}\right\}_{i=1,\ldots,n_2}$ |
| A/(A,T) | $E$ | $n_2$ | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |
| (A,T)/C | $E$ | 1 | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |
| (A,T)/T | $E$ | $n_2$ | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |
| (A,T)/A | $E$ | $n_2$ | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |
| (A,T)/(A,T) | $E$ | $E$ | 3 | $\left\{P_{i,j}\right\}_{\substack{j=i,\ldots,n_2\\ i=1,\ldots,n_1}}$ |

† For the T/T model the estimable parameter combinations are:

$$\begin{cases} \lambda_1,\ldots,\lambda_{n_1-1},\phi_1,\ldots,\phi_{n_1-1},\phi_{n_1}(1-\phi_{n_1})\lambda_{n_1} & \text{if } n_2 = n_1 \\ \lambda_1,\ldots,\lambda_{n_1-1},\phi_1,\ldots,\phi_{n_1-1},\phi_{n_1}(1-\phi_{n_1})\lambda_{n_1},\left\{\bar{\phi}_{i+1}\lambda_{i+1}\prod_{k=n_1}^{i-1}\phi_k\right\}_{i=n_1+1,\ldots,n_2} & \text{if } n_2 > n_1 \end{cases}$$

**Table 3** Table of parameter redundancy results for x/y/z models. Notation is the same as Table 2.

| Model | $r$ | $d$ | Valid for $n_1 \geq$ | $n_2 \geq$ | M. | Estimable Parameter Combinations |
|---|---|---|---|---|---|---|
| C/C/C | 3 | 0 | 2 | 3 | 1 | |
| C/C/T | $n_2+2$ | 0 | 2 | 3 | 1 | |
| C/C/A | $n_2$ | 2 | 2 | 2 | 3 | $\{P_{1,j}\}_{j=1,\dots,n_2}$ |
| C/C/A$_{1:2}$ | 3 | 1 | 2 | 3 | 2 | $\phi_a, \phi_1\lambda_a, \bar{\phi}_1\lambda_1$ |
| C/C/(A$_{1:2}$,T) | $n_1+n_2$ | 1 | 2 | 3 | 2 | $\phi_a, \{P_{i,i}\}_{i=1,\dots,n_1}, \{\phi_1\lambda_{a,i}\}_{i=2,\dots,n_2}$ |
| C/C/(A,T) | $E$ | 2 | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| C/T/C | $n_2+1$ | 0 | 2 | 3 | 1 | |
| C/T/T | $n_2+n_1$ | $n_2-n_1$ | 2 | 3 | 2 | $n_2>n_1$: $\phi_1,\dots,\phi_{n_1},\lambda_1,\dots,\lambda_{n_1},\{P_{i,j}\}_{\substack{j=n_1+1,\dots,n_2\\ i=1,\dots,n_1}}$ |
| C/T/A | $2n_2-1$ | 1 | 3 | 4 | 2 | $\phi_2,\dots,\phi_{n_2},\{\phi_1\lambda_i\}_{i=2,\dots,n_2},\bar{\phi}_1\lambda_1$ |
| C/T/A$_{1:2}$ | $n_2+1$ | 1 | 2 | 3 | 2 | $\phi_2,\dots,\phi_{n_2},\phi_1\lambda_a,\bar{\phi}_1\lambda_1$ |
| C/T/(A$_{1:2}$,T) | $\min(n_1+2n_2-3,$ $2n_1+n_2-2)$ | $\max(2,$ $n_2-n_1+1)$ | 2 | 2 | 2 | $\{\phi_i\}_{i=2,\dots,\min(n_2-1,n_1)}, \left\{\frac{P_{1,j}}{\phi_1}\right\}_{j=\min(n_2,n_1+1),\dots,n_2}$, $\{\phi_1\lambda_{a,i}\}_{i=2,\dots,\min(n_2-1,n_1)}, \{P_{i,i}\}_{i=1,\dots,n_1}$ |
| C/T/(A,T) | $E$ | $n_2$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| C/(A,T)/C | $E-n_1+1$ | 1 | 2 | 2 | 3 | $P_{1,1}$ ,$\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=2,\dots,n_1}}$ |
| C/(A,T)/T | $E$ | $n_2-n_1+1$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| C/(A,T)/A | $E-n_1+1$ | $n_2$ | 2 | 2 | 3 | $P_{1,1}, \{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=2,\dots,n_1}}$ |
| C/(A,T)/A$_{1:2}$ | $E-n_1+1$ | 2 | 2 | 2 | 3 | $P_{1,1}, \{P_{i,j}\}_{\substack{j=2,\dots,n_2\\ i=1,\dots,n_1}}$ |
| C/(A,T)/(A$_{1:2}$,T) | $E$ | $n_2$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| C/(A,T)/(A,T) | $E$ | $E-n_1+1$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| T/C/C | $n_1+2$ | 0 | 2 | 3 | 1 | |
| T/C/T | $n_1+n_2+1$ | 0 | 3 | 4 | 1 | |
| T/C/A | $n_1+n_2$ | 1 | 2 | 3 | 2 | $\phi_{1,1},\dots,\phi_{1,n_1},\lambda_1,\left\{\phi_a^{j-2}(1-\phi_a)\lambda_j\right\}_{j=2,\dots,n_2}$ |
| T/C/A$_{1:2}$ | $n_1+3$ | 0 | 2 | 3 | 1 | |
| T/C/(A$_{1:2}$,T) | $\min(2n_1+n_2-2,$ $n_1+2n_2-3)$ | $\max(2,$ $n_1-n_2+3)$ | 2 | 2 | 2 | $\{P_{i,i}\}_{i=1,\dots,n_1}, \{P_{1,j}\}_{j=2,\dots,n_2} \left\{\frac{\phi_{1,j}}{\phi_{1,1}\phi_a^{j-1}}\right\}_{j=2,\dots,\min(n_2-1,n_1)}$ |
| T/C/(A,T) | $E$ | $n_1+1$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| T/T/C | $n_1+n_2$ | 0 | 2 | 2 | 1 | |
| T/T/T | $\min(n_1+2n_2-3,$ $n_2+2n_1-2)$ | $\max(2,$ $n_2-n_1+1)$ | 2 | 2 | 2 | $\{P_{i,j}\}_{\substack{j=i,\dots,\min(i+3,n_2)\\ i=1,\dots,n_1}}$ |
| T/T/A | $n_1+2n_2-1$ | 0 | 4 | 5 | 1 | |
| T/T/A$_{1:2}$ | $n_1+n_2+1$ | 0 | 3 | 4 | 1 | |
| T/T/(A$_{1:2}$,T) | $\min(2n_2+n_1-3,$ $n_2+2n_1-2)$ | $\max(n_1+1,$ $n_2)$ | 2 | 2 | 2 | $\{P_{i,i}\}_{i=1,\dots,n_1}, \{P_{1,j}\}_{j=2,\dots,n_2} \left\{\frac{\phi_{1,j+1}}{\phi_{1,1}\prod_{k=1}^{j}\phi_{k+1}}\right\}_{j=1,\dots,\min(n_2-2,n_1-1)}$ |
| T/T/(A,T) | $E$ | $n_1+n_2-1$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |
| T/A/C | $n_1+n_2$ | 0 | 2 | 2 | 1 | |
| T/A/T | $n_1+2n_2-1$ | 0 | 4 | 5 | 1 | |
| T/A/A | $n_1+n_2$ | $n_2-1$ | 2 | 3 | 2 | $\{\phi_{1,j}\}_{j=1,\dots,n_1},\lambda_1,\{(1-\phi_j)\lambda_j\prod_{k=2}^{j-1}\phi_k\}_{j=2,\dots,n_2}$ |
| T/A/A$_{1:2}$ | $n_1+n_2$ | 1 | 3 | 2 | 2 | $\{\phi_{1,j}\}_{j=1,\dots,n_1},\lambda_1,\{(1-\phi_j)\lambda_a\prod_{k=2}^{j-1}\phi_k\}_{j=2,\dots,n_2}$ |
| T/A/(A$_{1:2}$,T) | $\min(n_1+3n_2-6,$ $2n_1+2n_2-5)$ | $\max(n_1-n_2$ $+4,3)$ | 2 | 2 | 2 | $\left\{\frac{P_{i,i+1}}{P_{1,i}}\right\}_{i=2,\dots,n_2-1}, \left\{\frac{\lambda_{a,i}\lambda_{a,i+2}}{\lambda_{a,i+1}^2}\right\}_{i=2,\dots,\min(n_2-2,n_1-1)}$, $\{P_{i,i}\}_{i=1,\dots,n_1}, \{P_{1,j}\}_{j=2,\dots,n_2}$, |
| T/A/(A,T) | $E$ | $n_1+n_2-1$ | 2 | 2 | 3 | $\{P_{i,j}\}_{\substack{j=i,\dots,n_2\\ i=1,\dots,n_1}}$ |

**Table 4** The effect of missing values on parameter redundancy of y/z and x/y/z model with only $m$ diagonals of data, where $1 \leq m \leq n_2 - 2$. Here we record if the rank of the models changes when there are only $m$ diagonals of data, compared to having perfect data. Models in bold are full rank models if there is perfect data. The new rank is given for the situations when the rank changes, otherwise the rank remains the same as Tables 2 and 3. $E_m$ is the length of the exhaustive summary and the maximum possible rank when there are only $m$ diagonals of data (see text).

y/z models

| Rank Changes if | New Rank | Models |
|---|---|---|
| never | - | **C/C**; **C/T**; C/A; **T/C**; T/T; A/C; A/A |
| $m = 1$ | $E_m$ | **T/A**; A/T |
| $m \leq n_2 - 2$ | $E_m$ | C/(A,T); T/(A,T); A/(A,T); (A,T)/C; (A,T)/T; (A,T)/A; (A,T)/(A,T) |

x/y/z models

| Rank Changes if | New Rank | Models |
|---|---|---|
| never | - | **C/C/C**; **C/C/T**; C/C/A; C/C/$A_{1:2}$; **T/C/**$\mathbf{A}^{\star}_{1:2}$ |
| $m = 1$ | $n_2$ | **C/T/C** |
| $m = 1$ | $2n_2 - 1$ | C/T/T |
| $m = 1$ | $\min(2n_1, n_1 + n_2 - 1)$ | C/C/($A_{1:2}$,T) |
| $m = 1$ | $\min(n_2, n_1 + 1)$ | C/T/$A_{1:2}$; C/(A,T)/$A_{1:2}$ |
| $m = 1$ | $E_m$ | **T/C/C**; **T/C/T**; T/C/A; **T/T/C**; T/T/T; **T/T/**$\mathbf{A}_{1:2}$ T/A/$A_{1:2}$; T/T/($A_{1:2}$,T); **T/A/C** |
| $m \leq 2$ | $E_m$ | **T/A/T**; **T/T/A**; T/A/T; T/A/($A_{1:2}$,T) |
| $m \leq 2$ | $\begin{cases} n_2 & m = 1 \\ 2n_2 - 2 & m = 2 \end{cases}$ | C/T/A |
| $m \leq 2$ | $\min(n_1 + n_2 + m - 2, 2n_1 + 2m - 2)$ | C/C/$A_{1:2}$ |
| $m \leq n_2 - 2$ | $E_m$ | C/C/(A,T); C/T/(A,T); C/(A,T)/C; C/(A,T)/T; C/(A,T)/A; C/(A,T)/($A_{1:2}$,T); C/(A,T)/(A,T); T/C/(A,T); T/T/(A,T); T/A/(A,T) |

$^{\star}$ for $n_1 \geq 3$, $n_2 \geq 4$

 