

CHAPTER SIX:
**USING COMPLEX ECOLOGICAL MODELLING SOFTWARE REQUIRES
CAREFUL THOUGHT, A THOROUGH UNDERSTANDING OF THE SOFTWARE
AND METICULOUS EXPERIMENTAL DESIGN**

Abstract

An incomplete understanding of sophisticated modelling software can camouflage inappropriate experimental design. Capture-mark-recapture (CMR) data is increasingly being used to address ecologically important questions. Various sophisticated software packages have made access to complex analytical procedures user-friendly, one such tool is the Program MARK. More than 1400 published studies have cited the use of MARK in less than 10 years and clearly the software has had a significant impact in ecology. We consider how well ecologists (that apply sophisticated analytical software, but are not necessarily expert biometrists/statisticians) understand what can- and cannot be accomplished in ecological studies with such complex software, using MARK as example. Using a long-term demographic study on southern elephant seals (*Mirounga leonina*) we illustrate how poor experimental design could be veiled due to the complexity of such software. We discuss one potentially hidden encumbrance in the MARK analytical process that can result in incorrect analyses. We suggest that users cultivate a thorough understanding of the software programmes they use, and that relevant experts are proposed as potential reviewers for their work, to increase the rigor with which published results report on the use of such analytical tools. This will help to ensure that flawed analyses are not published to the detriment of ecological theory advancement or wildlife management, and that students are not misled by published, but erroneous use of such powerful tools.

Introduction

Being able to reliably identify animals individually throughout their lives is the cornerstone of sound life-history and demographic work, given that individual identity forms the basis for long-term capture-mark-recapture studies (CMR). CMR experiments provide vital data for the advancement of animal population studies for a range of taxa and under various field scenarios. Such a variety of applications of the technique (including related adaptations such as mark-resight experiments) resulted in a great deal of research aimed at reducing bias and increasing the technique's scientific rigor. A progression of sophisticated software packages (e.g. POPAN, SURGE, DENSITY, CAPTURE) has become available to collate the significant analytical developments of the past decades into interfaces that have boosted the applicability of CMR. One particularly user-friendly application that has gained considerable popularity for specialists and non-specialists alike is Program MARK (White and Burnham 1999). To date more than 1400 published (1999 – 2009, Scopus®, Fig. 6.1) wildlife/biometric studies have cited the founding paper for this program, clearly with significant advances in our knowledge of animal populations throughout the world.

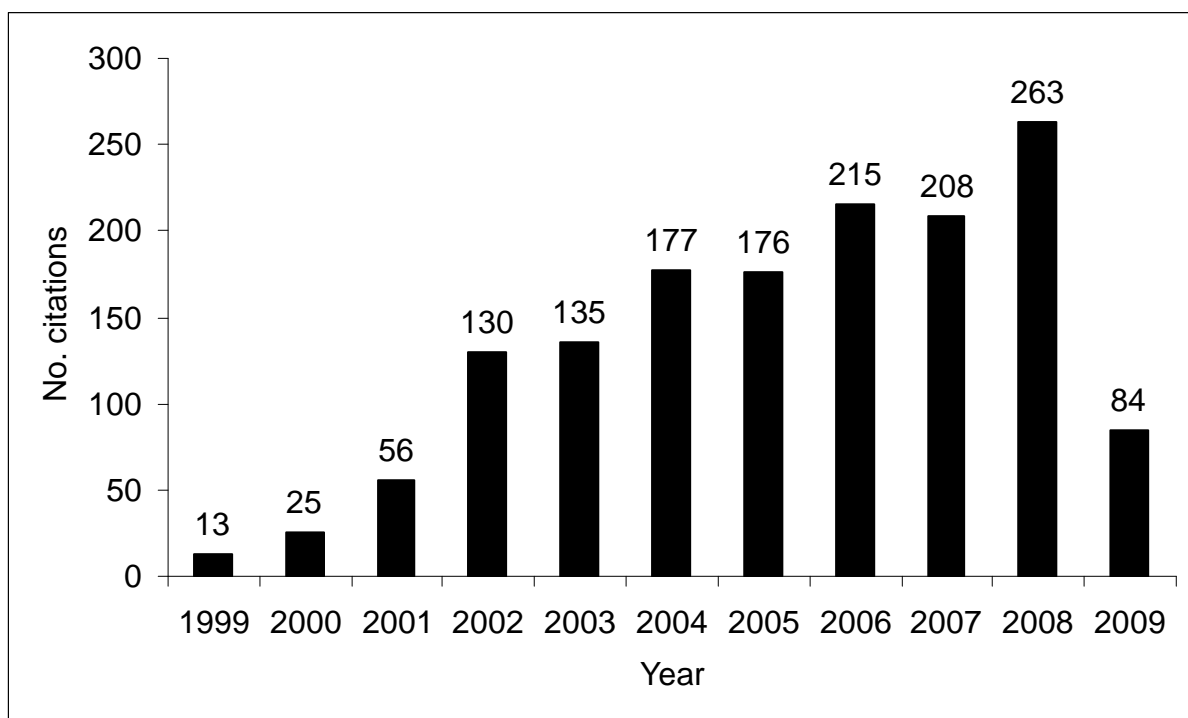


Fig. 6.1. Illustrating the impact of the founding paper for the capture-mark-recapture analytical program MARK (White and Burnham 1999). The number of published papers (up to 08 July 2009), to have cited White and Burnham (1999) *per year* are shown (Scopus®).

The Cormack-Jolly-Seber (CJS) (Cormack 1964; Jolly 1965; Seber 1965) modelling approach for estimating fundamental population parameters (e.g. survival) is central to MARK. Given the complexities of wildlife population systems, the CJS approach requires various assumptions to be made, e.g. (1) that every marked animal present in the population at time (i) has the same probability of recapture (p); (2) Every marked animal in the population immediately after time (i) has the same probability of surviving to time ($i+1$) (Burnham et al. 1987; Lebreton et al. 1992). Although we do not review the multitude of works pertaining to the moderation/elimination of these biases, one assumption, namely individual capture heterogeneity (Lebreton et al. 1992) forms the core of this study. Life history studies using mark-recapture experiments are dependent on, among others, choosing marking methods that do not compromise recapture and survival probability estimates. Unequal catchability or individual capture heterogeneity can have a number of sources, including marker loss and incorrect marker identification (Carothers 1979; Pledger and Efford 1998). Errors associated with: tag-loss, tag visibility and tag readability (including correct colour identification) can compromise individual identification and hence the estimation of vital life-history parameters (e.g. Curtis 2006). We attempt to address the question of marker resighting heterogeneity using program MARK and show how poorly designed experiments can be veiled by incomplete understanding of the software's complexity and functionality. We suggest that such software complexity not only blinds researchers but may also blind journal referees to fundamental flaws in experimental design for two reasons. Firstly, important analytical procedures involved in the correct use of MARK are hidden from the referees of such work. Secondly, referees tend to assume (erroneously) that poor or flawed experimental design has been accounted for by such hidden analytical procedures within the software programme.

We provide a case study using southern elephant seals to illustrate how an experimental design initiated for purposes other than (but related to) that applied in this study, appeared useable for the detection of variation in marker sightability. Herewith we aim to initiate discussion regarding the potential pitfalls in using sophisticated analytical tools by non-specialist users, and the veiled dangers of such user-friendly programmes. We contend that the illustrated scenario may not be

uncommon in ecological papers reporting on results gleaned from MARK (or other complex CMR software).

Southern elephant seal case study

Pinnipeds are among the more easily marked vertebrates owing to relatively unrestricted access to weaned animals (Bester 1988; McMahon et al. 2006; see Chapter 3 – de Bruyn et al. 2008). Tags, inserted in the flippers of pinnipeds, have been one of the more popular means of marking seals (e.g. Erickson et al. 1993; see Chapter 3 – de Bruyn et al. 2008), however certain errors, such as the loss of tags (e.g. Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009) is associated with this method. To effectively correct for capture heterogeneity in estimates of survival, knowledge of not only tag-loss but also tag sightability are required. The visibility of marks is an important factor in the development and design of animal marks (Trippensee 1941). The CMR dataset of southern elephant seals at Marion Island (spanning two decades) is ideal for investigating the long-term readability of tags. This long-term study has resulted in a plethora of papers on population demography, however, none assessed the possible effect of tag-dependent heterogeneity on results (aside from tag-loss; Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009), although Wilkinson and Bester (1997) did mention the potential for confusion between certain tag colours from field observations. We applied the Cormack-Jolly-Seber (CJS) and associated models (Lebreton et al. 1992) to the long-term mark-resighting data of female southern elephant seals at Marion Island to assess whether tag-dependent heterogeneity, ultimately affecting capture probability, exists in this population.

We chose adult females as study subjects because: (1) there is a comprehensive 19 year CMR dataset available for adult female seals, (2) they are philopatric and return annually to known and well surveyed study beaches, whereas adult males and juveniles of both sexes are less philopatric (Hofmeyr 2000) and (3) females show low and constant tag-loss over time (Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009)

Material and methods

Tagging and resighting of seals

An intensive tagging program of southern elephant seals commenced in 1983 at sub-Antarctic Marion Island (46°54'S, 37°45'E). From 1983 to 1999, 4059 (average: 239 annually, range: 179–344) newly weaned female pups were double tagged in their hindflippers using Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.). The self-piercing tags were uniquely embossed with a three-digit number, and colour-coded to denote the year of application (Table 6.1).

Beaches were checked for tagged seals every seven days during the breeding season (mid-Aug to mid-Nov, all years) and every 10 days during the moulting period (mid-Nov to mid-Apr) from 1983 to 1990. From 1990 the resighting effort every 10 days also extended through the entire non-breeding period (mid-Nov to mid-Aug). For each seal that was resighted, the tag number, tag colour combination (Table 6.1), number of tags remaining (one or two), location and date of the sighting were noted. Two trained observers *per* research season (April to April) were used concurrently to search for tagged seals from 1983 to 2004 (except during 1995, 1996 & 2001 when only one observer was available).

Table 6.1. Tagging regime for different cohorts of southern elephant seals at Marion Island, 1983 - 1999.

Year tagged	Code	Outer tag colour	Inner tag colour
1983	OO	Orange	Orange
1984	BB	Blue	Blue
1985	YY	Yellow	Yellow
1986	RR	Red	Red
1987	PP	Pink	Pink
1988	GW	Green	White
1989	BF	Black	Flame (Bright orange)
1990	LB	Lemon (Pale yellow)	Dark brown
1991	OB	Orange	Royal blue
1992	YP	Yellow	Pink
1993	GR	Green	Red
1994	WB	White	Black
1995	OY	Orange	Yellow
1996	BP	Blue	Pink
1997	WR	White	Red
1998	PO	Pink	Orange
1999	GG	Green	Green

Analysis of tag resightability

To clarify tag resighting heterogeneity by cohort (i.e. colour) multiple resights of each individual within any given year was limited to include only the last resight in each research season. All seals were assumed to age on 15 October, which is the peak adult female haul-out date at Marion Island (Condy 1978). Encounter (resighting) history matrices were constructed for adult female seals (1842 of the 4059 female individuals tagged as weanlings) using the resighting data from the fourth year of life (mean age at first breeding; Pistorius et al. 1999; see Chapter 5) to “death” and treating age three as the “initial release” occasion. In effect, the resighting data available up to 2004 thus allowed 19 years of resighting history for the 1983 cohort (from “initial release” at age 3) and therefore 2 years for the 1999 cohort. These capture-history matrices (depicting absence or presence of individuals per year as 0 or 1 respectively, over time) were condensed to a single input file (staggered, to represent the different “release” occasions for each cohort) for the software package MARK.

MARK provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model and under several models that appear as special cases of this model (Lebreton et al. 1992). As it was impossible to distinguish between mortality and permanent emigration, we imply apparent rather than absolute survival. The two fundamental parameters of these models are: ϕ_i = the survival probability for all animals between the i th and $(i+1)$ th sample ($i = 1, \dots, k-1$), and ρ_i = the recapture probability for all animals in the i th sample ($i = 2, \dots, k$).

The first step in the mark-recapture analyses involves Goodness-of-Fit (GOF) tests for the CJS model. The median \hat{c} GOF method was used to test the model assumptions including; equal catchability, that marked animals are not missed or marks lost, that every marked animal at time (i) has the same chance of surviving to time ($i+1$), and that all samples are instantaneous between times (i) and ($i+1$) (Lebreton et al. 1992). The most parsimonious model was selected using the small sample corrected Akaike Information Criterion (AIC_c) (Lebreton et al. 1992). Overdispersed data, as a result of violation of one or more of the CJS model assumptions, requires \hat{c} (variance inflation factor) adjustments to AIC_c estimates ($QAIC_c$) for the CJS and nested models. AIC_c model selection was used to test

hypotheses regarding capture heterogeneity of adult female southern elephant seals. Because assessment of survival probabilities were not of primary concern in this study, the findings of Pistorius et al. (1999) were used to depict biologically realistic survival estimates for seals in the models. Models were parameterised using the matrix design in MARK. The encounter history data type is herewith defined and various models can be structured by manipulating numbers in edit boxes within a matrix. In so doing the matrix design depicts a numerical indexing scheme as substitute for the individual survival and recapture (or resighting) values, respectively. Parameter index matrices were structured to be time but not age dependent for survival. Models with capture probability as constant over time but not between cohorts, and as constant over both time and cohort were considered. The lower the AIC_c value, the more parsimonious the model (Burnham and Anderson 1998), and we considered two models to be significantly different when the ΔAIC_c was greater than two (Anderson and Burnham 1999).

Results

The GOF tests indicated some overdispersion in the data set ($\hat{c} = 1.440$) and as a consequence AIC_c values were adjusted accordingly. Relative parsimony supported the fully time dependent CJS model rather than that depicting capture heterogeneity between cohorts (model A) (Table 6.2). Cohort dependent capture heterogeneity in the dataset was not supported and confusion of different coloured tags appears unimportant in the dataset.

Table 6.2. Elimination of nonsignificant effects from the fully time-dependent Cormack-Jolly-Seber (CJS) in modelling recapture probability in adult female southern elephant seals from Marion Island. For each model the Quasi-Akaike Information Criterion ($QAIC_c$), $QAIC_c$ weight, Model Likelihood (mL), number of estimable parameters (NP) and Quasi-Deviance (QDEV) are given. Apparent survival probabilities are referred to as ϕ and recapture probabilities as p . The figures in the model refer to age dependence up to a particular year of life; t – time dependent; c – constant per cohort; _c – constant for all cohorts over time. Model selection based on median $\hat{c} = 1.440$. Model A depicts constant recapture probability within each cohort after age 3; while model B depicts constant recapture probability across all cohorts after age 3.

Model	$QAIC_c$	$QAIC_c$ Weight	mL	NP	QDEV
CJS	8495.034	0.999	1.000	37.000	1734.965
A ($\phi_{\varnothing 3t}; p_{\varnothing 3c}$)	8533.319	0.000	0.000	36.000	1775.273
B ($\phi_{\varnothing 3t}; p_{\varnothing 3_c}$)	8568.029	0.000	0.000	20.000	1842.272

Discussion

We found no significant differences in resight probability among cohorts of adult female southern elephant seals at Marion Island and hence conclude that all seals had the same chance of being resighted during the study. Factors that could potentially affect sightability or accurate individual animal identification can be divided into two broad categories, namely, observer bias and marker bias. Observer bias centres around observer effort and/or ability (e.g. training, visual impairment) on correct mark identification. Marker bias includes a myriad of factors under two main categories; permanent and temporary illegibility. Permanent illegibility factors include worn lettering, marker breakage, marker discolouration, and marker loss. Temporary illegibility factors include soiling, physical obstruction and weather conditions (e.g. light levels). Such a plethora of potential prejudiced variables make studies aimed at quantifying any one factor difficult.

Although cohort, tag age and tag colour are indistinguishable i.e. confounded in this experimental design, the use of adult females can provide some insight into potential marker confusion issues because the age effect on survival and especially capture probability is known to be minor for this sector of the population (Pistorius et al. 1999, 2004, 2008). Differences observed in recapture probabilities can likely be ascribed to other issues such as temporary emigration from the study site (see Chapter 4). There is corroborating evidence which suggests that confusion in documenting tag colours is of little consequence e.g.: (1) Field workers are tested for colour blindness before appointment. (2) The tag colour combinations are known to the field staff and in all cases only one or two colours have to be identified per seal. (3) Seal sex, age and size often serve as indicators of seal identity once records are checked. (4) Observer bias is reduced by random application of uniquely numbered tags to both sexes within a cohort. (5) We assume that consistently (a) misreading a particular tag and (b) noting it as a specific other tag, is minimized given the design of the resighting schedule that allows multiple resights of the same tags over a relatively short period (one month) of time (see Methods section). (6) At the inception of this mark-resighting program, tag colour combinations (inner and outer tag components) were chosen to minimize the likelihood of confusion between cohorts.

All tags used in this study were manufactured by the same company with the same materials (see Methods section). While it is not known if the manufacturing procedure was identical for each tag or cohort of tags, based on the manufacturers assurance we assume that breakage and inscription wear would be constant amongst tag colours and would follow a similar age related trend. Tag colour should clearly not result in inconsistent tag-loss over time between cohorts (Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009). We expect that certain temporary tag illegibility factors (e.g. physical visual obstruction) would affect resightability of any tags regardless of their colour, while other temporary factors (e.g. soiling) could affect some colours more than others. For example, white tag components exposed to muddy water would appear pinkish. However, the resighting schedule, allows for repeated encounters of individual seals regardless of the state of their tags. Unlike permanent illegibility factors (e.g. tag colour, breakage) that cannot be corrected no matter how often the tag is sighted, temporary illegibility factors (e.g. soiling) would not persist over time and frequency of sighting would eliminate such temporary illegibility problems. We thus disregard temporary illegibility factors as an important source of tag-dependent sighting heterogeneity.

Long-term mark recapture/resighting datasets, particularly for large mammals, are rare and undoubtedly beset with variables, such as temporary emigration, which affect capture heterogeneity in a CMR context. Consequently, analyses based on even the most rigorously designed mark-recapture experiments require certain assumptions to be made. Of course, the species under investigation and the objective of the study will dictate which of the assumptions within the modelling approach will be more crucial than others if models are to be properly assessed. For example, in elephant seals temporary emigration from island study sites can introduce significant confounding arguments without certain assumptions made. Clearly, assuming zero temporary emigration does not make biological sense (also see Chapter 4), while modelling in an “open CMR” context introduces other sources of heterogeneity (Pledger et al. 2003), where further assumptions are required that perhaps do not align with the study scenario. Mitigating against as many of these assumptions as possible is therefore highly desirable for estimating life-history such as survival rigorously. Here we suggest that tag colour confusion and its resulting

effects on estimates of survival in this elephant seal dataset is unlikely, thus, lending confidence to previous estimates of survival based on this dataset (e.g. Pistorius et al. 1999, 2004, 2008; McMahon et al. 2003, 2005).

The Argument

An expanded version of this seal example was originally accepted by two reviewers to be publishable. A third reviewer identified the confounding effect of tag colour, with seal age (and hence tag age and wear) which cannot be teased apart and as a consequence, the manuscript was not acceptable for publication. The only way to overcome the confounding effects of tag colour, seal age and tag age would be to place different coloured tags on seals within the same cohort (year). While this issue is not a CMR or MARK issue but a basic experimental design issue, one referee's expertise in MARK allowed for easy detection of the confounding problem, knowing immediately that the confounding flaw could not be accounted for in the analysis using this software contrary to that assumed by the other reviewers.

We had tried to overcome this issue of the covariates being indistinguishable within the study design by manipulating the PIM tables in MARK to reduce the confounding bias and using only adult females as study subjects (see above). Parameter index matrix (PIM) structuring for model design within MARK is an invisible component of the analytical procedure to manuscript reviewers. While authors describe their model structuring in the results of papers, this does not always translate to the actual PIMs being structured to depict the intended model, particularly if users do not fully understand the PIM manipulation process (White and Burnham 1999). This is especially relevant when complex permutations of biological parameters are envisaged to be at play in a system (see Fig. 6.2 and also Lebreton et al. 1992) and allows for ambiguity when researchers attempt to repeat the methods. Reviewers not familiar with the functionality of MARK may have difficulty in visualising the structuring of PIMs, unless the PIMs are presented as part of the manuscript and thus available for scrutineering. PIMs are bulky additions to manuscripts and as a consequence rarely available to reviewers or readers. This also pertains to the design matrix, which is an additional (and more complex) means to constrain models defined by the PIMs.

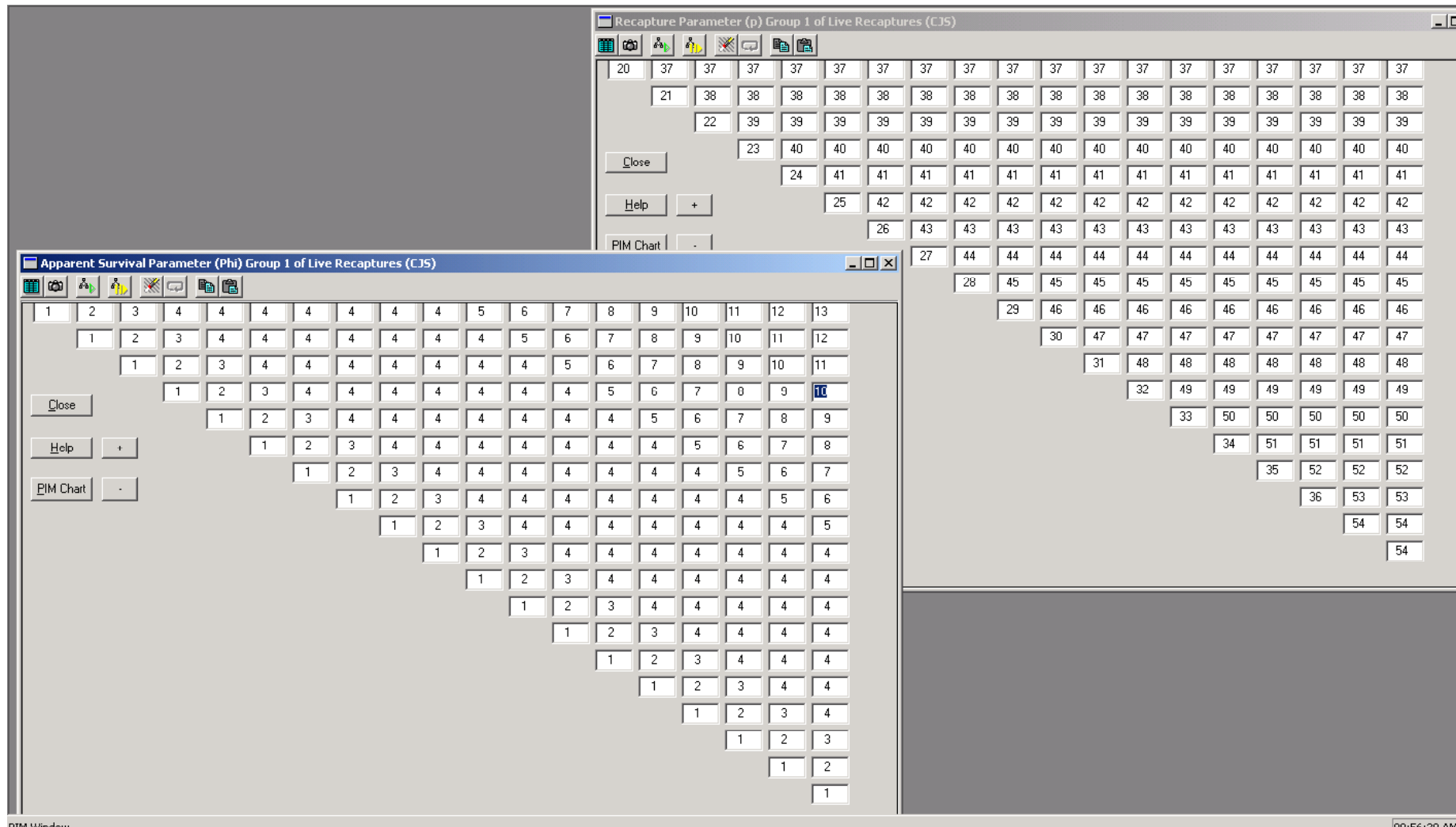


Fig. 6.2. An example of a more complex Parameter Index Matrix (PIM) setup for survival and recapture estimation of one group (e.g. sex) of animals from different cohorts over a temporal scale, within the Program MARK (White and Burnham 1999).

The approach to model construction in MARK essentially encompasses three steps (excluding additive effects/ covariate inclusive hypotheses), greatly simplified as follows (specific details in White and Burnham 1999). First, the collected data is condensed to biologically meaningful 0's (absence) and 1's (presence), to be used as input files for MARK. Secondly, the user interacts with these input files via PIMs, i.e. the parameter space for a data type is defined in the PIMs. At this stage the user structures various models by manipulating numbers in edit boxes within a matrix (Fig. 6.2), i.e. substituting a numerical indexing scheme for the individual survival and recapture (or resighting) values, respectively. Thirdly, these models are then weighted according to quality of fit and precision by way of Information Criterion, usually Akaike's, but sometimes Bayesian (Burnham and Anderson 2004). The most parsimonious model, i.e. the model that best describes the quality of fit (deviance) of the data as related to the number of estimable parameters (precision) (Lebreton et al. 1992), is then used to draw biological conclusions from. Because, the analytical steps are "hidden" within the programme some referees erroneously assume that fundamental experimental design imperfections may have been taken into consideration within these "hidden" steps. The recent advent of "online supplementary material" for journals could provide an avenue for publication of some of these previously "hidden" steps and help to alleviate this problem.

Multitudes of published works have their origin within a mark-recapture framework, but in many cases the published study was not initially envisaged to arise from the CMR data. Indeed this broad applicability is one of the fundamental strengths of CMR experiments. However, CMR experiments are not all things, to all studies all of the time and do have limitations as shown here. Thus understanding the limitations of original experimental design is crucial to effective data analyses. It is our aim here to highlight the need for researchers to think very carefully about their data and not to assume too readily that sound design for one study, albeit a study of very broad scope as is the case in CMR studies, will satisfy all the needs for a related study e.g. the quantification of tag colouration of recapture as described above. The need for careful experimental design in biological studies is clear and well established (e.g. Anderson 2001). However, strong experimental design and a solid analytical foundation do not always guarantee unbiased results in the face of user-friendly, yet sophisticated analytical software as described here. Ecologists and

wildlife managers are increasingly required to provide rapid answers and input into global ecological problems, and often answers are sought from datasets that are not specifically structured to address that specific question. A case in point is a published study by Loehle et al. (2005) that used radiotelemetry experiments for assessing survival (Franklin et al. 2006). Several MARK experts critiqued the Loehle et al. (2005) study, identifying conceptual errors of the details of the analytical procedures (Franklin et al. 2006). They therefore addressed the two issues raised here; that of conceptually opaque use of powerful analytical tools and poor research design. Given the two examples highlighted here (Loehle et al. 2005, this study) it follows that there is a likelihood of at least some of the >1400 published papers citing MARK (Fig. 6.1) containing flaws due to poor study design and/or an inadequate understanding of software/programme functionality. The latter study and our example of SES illustrates the need for researchers to consider carefully their study design prior to commencement of field work and to be visionary in how studies are designed i.e. to trawl the current state of knowledge carefully and thoroughly to identify knowledge gaps which can be addressed. Researchers also need to be cautious when using new software packages and have a responsibility to fully understand how they work before submitting work for peer review.

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CHAPTER SEVEN: **GENERAL CONCLUSION**

Synthesis

The long-term Marion Island southern elephant seal mark-recapture programme has provided an authoritative foundation for understanding the population dynamics of a long-lived marine top-predator. Extensive mark-recapture and population trend analyses over the past decade have elucidated much about the life history traits and their demographic consequences in this species. Notwithstanding these advancements, important facets of the regulation of the Marion Island population have remained contentious. Particularly, the roles of juvenile (McMahon et al. 2003, 2005) and adult female survival (Pistorius et al. 1999a, 2004, 2008a) in the recent recovery of the population from decline to increase (McMahon et al. 2009), has fuelled considerable debate. The exact timing of population trend inflexion (1994 or 1997/8) has also seen continuing debate (Pistorius et al. 1999b, 2001; Bradshaw et al. 2002; McMahon et al. 2009). The nature of the drivers of these life history parameters, and ultimate population trends, have been explored and density dependent and density independent regulating factors have been proposed (Pistorius et al. 2001, 2008b; Bradshaw et al. 2002; McMahon et al. 2009) to be important in the Marion Island population. However, given the complexity of the relationship between these intrinsic and extrinsic population regulating drivers (de Little et al. 2007), researchers must guard against oversimplification in their efforts to explain these drivers (McMahon et al. 2008). To heed such caution the need arises for holistic approaches to life history studies, whereby numerous ecological factors are explored and field methodology improvements are sought to further explicate relevant ecological parameters.

Individual body condition and its established relationship with various life history processes require methodology that allows for accurate body condition estimation. In seals the relevant measure of body condition, central to further understanding of population demography, is mass (e.g. Proffitt et al. 2007). In Chapter two the importance of body mass estimation in seal population demographic studies are acknowledged and the current challenges elucidated. Building on the foundation of photogrammetric work that has been done on seals, I aimed to

establish a photogrammetric method for body mass estimation that would be widely applicable to phocids (and potentially other vertebrates) in a range of field scenarios. By focusing attention on the substrate surrounding the seal to create a three-dimensional space within which the seal shape can then be 'built', rather than building a model based solely on features of the seal itself, a robust and widely applicable method resulted. Consequently, this novel three-dimensional photogrammetric method for estimation of body volume and mass can be implemented in areas hitherto impossible with existing weighing or photogrammetric methods. In so doing, body mass estimates of large samples of individuals over extensive study areas can now be achieved with obvious incentive to future covariate analyses in demographic studies. The field effort required to weigh seals for providing a benchmark to test the photogrammetric techniques against, highlighted some challenges associated with chemical immobilisation. While the current protocol on Marion Island is sufficient for our needs, I was interested in examining if improvements, specifically related to the recovery time experienced by immobilised seals, could be made. A prospective experimental protocol was thus structured and is presented in Appendix one.

The ability to relate the body mass of any particular individual to genetically related individuals (e.g. mother and pup) has palpable advantages in demographic research. However, to model body mass as a covariate with survival or reproductive effort as related to kin, one first needs to be able to identify appreciable numbers of related individuals over time. To address this current gap in the long-term mark-recapture experiment at Marion Island was the specific aim of Chapter three. The polygynous breeding system of southern elephant seals results in crowded breeding harems on beaches, making access to individuals difficult. Compounding the difficulty of access to individuals is the inability to identify the mothers of pups once they have weaned and moved out of crowded harems, because adult females abruptly break the maternal tie to their then weaned pups. Consequently, a repeatable procedure involving; a quick intrusion into the harem, placement of a marker on an unweaned pup, identification of the mother, and withdrawal from the harem is required. Supersmall® Dalton lamb tags proved to be the most effective marker type for use in harems smaller than 60 cows (maximum for Marion Island harems). In the testing phase of this temporary marking technique more than half of all known aged mother's

pups could be marked prior to weaning. Clearly, a continuation of this field effort over time, will provide a large sample of relatedness information applicable to cumulative studies of for example, maternal investment, inbreeding avoidance and sociality at haul-out sites.

Methodological advances within a mammalian mark-recapture framework (Chapters two and three) are unfortunately initially constrained by the lag-time involved in accumulating sufficient temporal samples. The opportunities for such advancements would however not have been highlighted, had there not existed a long-term dataset that could be built upon. Therefore, the 25-year longitudinal mark-resighting southern elephant seal dataset at Marion Island remains extremely valuable for demographic studies even without these latest accompaniments. In Chapter four this dataset is used to assess the survivorship schedule of elephant seals at this locality to extend upon the 15-year mark-recapture dataset used by Pistorius et al. (1999a). In Appendix two, we addressed tag-loss for the entire 25-year mark-recapture experiment, for correction of survival estimates presented in Chapters four and five. A comparable approach to the Pistorius et al. (1999a) study was adopted in Chapter four, given the pivotal role that study played in the subsequent demographic discussion of this population of seals, and for re-assessment of the survivorship conclusions drawn from that study. The Pistorius et al. (1999a) study did not, however, correctly address the extra-binomial variation observed in the data, although this possibly would not have altered the conclusions drawn there. However, in Chapter four, extra-binomial variation in the current dataset was too large to ignore and was thus adjusted as a parallel analysis to the unadjusted analysis. These overdispersed results indicated departures of the data from particularly the “recapture homogeneity” assumption. This finding initiated discussion of the hitherto assumed “negligible” migration of elephant seals into and out of this population, both temporarily and permanently. Notwithstanding this extra-binomial variation in the data for most cohorts, meaningful survival estimates could be gleaned from program MARK. Blurred distinction in categorisation of age-classes and demographic terminology seems to have augmented some of the contention related to earlier findings for this population. The additional 10 years of marking and resighting data used here elucidated the relative importance of juvenile and adult female survival in regulation of this population. A comparative increase in juvenile

survival appears to have preceded an increase in adult female survival, lending support to the McMahon et al. (2003, 2005) contention that this sector was important in the population recovery. However, this change in survivorship appeared to be centred around three-year olds (a proportion of which pup every year – Bester and Wilkinson 1994) that were classified as adult females by Pistorius et al. (1999a, 2004, 2008a), but as part of the juvenile age-group according to McMahon et al. (2003, 2005). Similarly, an apparent inflexion in survival rates around 1994 would have coincided with a population trend inflexion around 1997/1998 if a lag-time from all increased juvenile survival (1st, 2nd and 3rd year age-classes) around 1994 related to increased survival (thus breeding potential) of 4th, 5th and 6th year adult females around 1998. Notwithstanding the important findings reported, a multistate modelling approach with an ‘unobservable’ state should be considered to further clarify survivorship findings. The addition of environmental covariates in model design would further improve our knowledge of regulation in this population. In particular, seal movement (and survival) relationships with Southern Oscillation Index, Antarctic circumpolar waves, frontal system shifts and pack ice extent, among others, could enhance our understanding of the importance of extrinsic population drivers. While not within the scope of this thesis, the findings gleaned here can improve future assessments of southern elephant seal biology and indeed general mammalian population ecology in establishing the relative importance of environmental and biological covariates on these populations. A hasty leap into assessments of the importance of environmental covariates in population regulation, without a clear understanding of fundamental life-history parameters in the context of the relevant population/species is risky. Unless hypotheses regarding the fundamental biological traits of the species are quantitatively assessed, erroneous assumptions could become entrained in the published literature and in time are accepted as truth, as illustrated in Chapter five.

In Chapter five, attention was directed at the adult female sector of the population to gain a clearer understanding of the potential influence of longevity, fertility and senescence on population demography. Predicted longevity estimates of adult females based on survival estimates gleaned from Chapter four, indicated that a far greater number of post 20-year old individuals should persist than has been observed. This is likely a function of the large number of young animals from the

increasing post 1994 period of the population included in the estimates, and it remains to be seen if such a large number of very old individuals will persist within the next decade if the population trend remains relatively stable. The commonly preferred state-dependent modelling approach was used to investigate senescence. Analogous with the Pistorius and Bester (2002) study, there was no evidence for actuarial senescence in this population of southern elephant seals, despite a much larger sample of aged individuals. Contrary to the previous study's findings however, reproductive senescence was evident in post 12-year old individuals. Additionally, females primiparous at age three indicated reduced breeding success later in life compared with four- and five-year old primiparous individuals. This suggests that while survivorship of young adult females (3-, 4- and 5-year-olds) may have increased (Chapter four), allowing a greater absolute number of females to breed (thereby augmenting population growth) these animals reduce their breeding efforts in later life and those that became primiparous at age three even more so. The "prudent parent" hypothesis predicts that a female will invest somatically before investing in offspring, and this seems to apply to southern elephant seals, with significant implications on population growth as compared to per capita foraging pressure. Contrary to assumptions hitherto expressed, southern elephant seals do not generally breed every year after primiparity and this is unrelated to age at primiparity. Conclusions of numerous previous papers have in part rested upon some of these assumptions and will need re-evaluation.

The complexity in identification of the drivers of elephant seal population regulation necessitates extensive research questions based on various facets of seal ecology. In light thereof, the resident Marion Island killer whale population has been identified as a potentially important top-down driver of the southern elephant seal population. However, very little is known about this population of killer whales and no work has been done on their sociality and the importance of their prey preferences on this social organisation. We thus initiated a fundamental sociality study to launch subsequent studies of prey preference, temporal and spatial predation rates and killer whale population dynamics. The preliminary results pertaining to the sociality of killer whales here (Appendix 3) will hopefully initiate studies to address the relative importance of killer whales as drivers of elephant seal populations.

Chapter six was in fact intended as an antecedent to chapters four, five and Appendix two in the analytical process. Initially, I attempted to establish if confusion in identification of markers attached to different cohorts of elephant seals was evident in this mark-recapture programme. However, during the process of analyses, further literature perusal and in the course of professional discussions it became evident that the analyses were confounded to address this research question. I considered the intricacies of the analytical procedure and realised that my unfortunate lack of prescience may in fact serve as a cautionary discussion for ecologists as users of complex analytical software. This Chapter can therefore be seen as the “Ph” in “PhD”. The recognition of appropriate experimental design in mark-recapture experiments in the face of sophisticated software packages is illustrated. Meticulous perusal of available literature and careful thought of the available data and the software to be used is discussed.

This entire thesis has been structured with the additional purpose of illuminating potential future research directions in life history studies and population demographic research.

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