Open Population Mark-Recapture Models Including Ancillary Sightings

A thesis presented in partial
fulfilment of the requirements
for the degree of
Doctor of Philosophy
in Statistics
at Massey University

Richard J. Barker

1995

BARKER

Massey University Library
Thesis Copyright Form

Title of thesis:

1) ~~(a)~~ I give permission for my thesis to be made available to readers in Massey University Library under conditions determined by the Librarian.

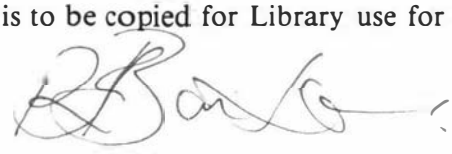
(b) I do not wish my thesis to be made available to readers without my written consent for 3. months.

(2) ~~(a)~~ I agree that my thesis, or a copy, may be sent to another institution under conditions determined by the Librarian.

(b) I do not wish my thesis, or a copy, to be sent to another institution without my written consent for 3. months.

3) ~~(a)~~ I agree that my thesis may be copied for Library use.

(b) I do not wish my thesis to be copied for Library use for 3. months.

Signed 

Date 7 – 11 – 95.

The copyright of this thesis belongs to the author. Readers must sign their name in the space below to show that they recognise this. They are asked to add their permanent address.

NAME AND ADDRESS DATE

Abstract

A model is proposed for a mark-recapture experiment with ancillary observations obtained from marked animals any time between capture periods and throughout the geographic range of the animals. The model allows three types of emigration from the site where recaptures are made: (1) random emigration, where the probability an animal is at risk of capture at i does not depend on whether it was at risk of capture at $i-1$, (2) permanent emigration where animals can leave the area where they are at risk of capture but not return, and (3) Markov emigration, where the probability an animal is at risk of capture at i depends on whether it was at risk of capture at $i-1$. Under random emigration the likelihood function can be factored into a set of conditionally independent binomial terms used to estimate the parameters and a set of conditionally independent multihypergeometric terms that do not involve the parameters. Closed-form maximum likelihood estimators are derived under random emigration for models with age-dependence and a temporary marking effect. Contingency table based goodness-of-fit tests are derived from the multihypergeometric terms in the likelihood function. Contingency table tests of the age-dependence and temporary marking effect models are also derived. Explicit estimators do not appear to exist for permanent or Markov emigration.

It is shown that the estimator suggested by Jolly (*Biometrika* 52:239, 1965), and as a consequence the estimator suggested by Buckland (*Biometrics* 36:419-435, 1980), is only valid if there is no emigration from the study area or if emigration is random. The estimator suggested by Mardekian and McDonald (*Journal of Wildlife Management* 45:484-488, 1981) for joint analysis of recapture and tag-recovery data is also only valid under no emigration or random emigration.

By making appropriate constraints on parameters the models reduce to previously published models including the Jolly-Seber model (with age-dependence and a temporary marking effect), tag-resight models, tag-recovery models, and joint live-recapture/tag-recovery models. Thus, the model provides a common framework for most widely-used mark-recapture models and allows simultaneous analysis of data obtained in several ways. Advantages of the new models include improved

precision of parameter estimates, and the ability to distinguish between different type of emigration. FORTRAN programmes are developed for fitting the models to data with an application to a data set for brown trout (*Salmo trutta*) tagged in spawning tributaries of Lake Brunner, Westland between 1987 and 1991.

Acknowledgements

I thank my supervisors Jeff Hunter, Greg Arnold, and Bryan Manly for their help and encouragement. For support I thank the Statistics Department, Massey University, Hopkins Farming Group and the Hopkins Family Trust, and Manaaki Whenua - Landcare Research. Special thanks to Jim Nichols for his advice and encouragement. Ken Burnham shared a preprint describing his work in developing a model for the joint analysis of live-recapture and tag recovery data and excerpts from an unpublished manuscript describing derivation of sampling variances. Also, extensive comments from Ken Burnham in his examiners report led to many helpful changes in the final draft. Thanks to my parents Valerie Calder and Les Barker for instilling an academic ambition and especially Lynn, Rachael, James and Anna-Claire for putting up with this project.

To John,

whose life's work has made this work possible.

Contents

1 Mark-Recapture Overview 1

1.1 Closed-Population Mark-Recapture Models 3

1.1.1 Petersen estimator 3

1.1.2 Multiple recaptures 4

1.1.3 Generalizations 6

1.1.4 Log-linear models 10

1.1.5 Martingale estimators 11

1.2 Open Populations 11

1.3 Jolly-Seber Model 12

1.3.1 Assumptions and notation 13

1.3.2 Intuitive estimators 15

1.3.3 The Jolly-Seber likelihood 16

1.4 Hypergeometric Formulation of the Jolly-Seber Model 22

1.4.1 Log-linear models 23

1.4.2 Small sample bias 24

1.4.3 Accuracy of Jolly-Seber variance estimates 25

1.4.4 Heterogeneous capture and survival probabilities 26

1.4.5 Special cases of the Jolly-Seber model 28

1.5 Generalizations of the Jolly-Seber Model 31

1.5.1 Stationary Markov movement model 35

1.6 General Multi-Strata Movement Models 36

1.6.1 The Petersen estimator for s strata 36

1.6.2 Open population movement models 37

2 Tag Recovery Models **42**

2.1 Seber-Robson-Youngs Model 42

2.1.1 Notation, assumptions, and data structure 43

2.1.2 Intuitive estimators 45

2.1.3 The tag-return model likelihood 46

2.1.4 Heterogeneous survival and recovery rates 47

2.1.5 Restricted and generalized tag-return models 49

2.1.6 Models allowing heterogeneous survival 53

2.1.7 Ultrastructural models 54

2.2 Joint Live-Recapture and Tag-Return Models 57

2.2.1 The Mardekian-McDonald analysis 57

2.3 Burnham's Model 63

2.4 Live-Recapture Analyses Augmented with Sightings 64

3 Single-Stratum Mark-Recapture Models with Ancillary Observations **66**

3.1 Background 66

3.2 The Experimental Situation, Notation, and Assumptions 67

3.2.1 Notation 68

3.2.2 Assumptions 71

3.2.3 Data structure 72

3.2.4 Random emigration model 76

3.2.5 The likelihood function under random emigration 81

3.2.6 Parameter estimation 92

3.2.7 Asymptotic variances and covariances 94

3.2.8 Goodness-of-fit tests under random emigration 98

3.3 Permanent emigration 104

3.4 Stationary Markov Movement 109

3.5 Losses On Capture 111

3.6 Comparison with Jolly's Solution 114

4 Multi-Strata Mark-Recapture Models with Ancillary Observations 117

4.1 Background 117

4.2 The Age-Dependence Model 117

4.2.1 Assumptions, notation and data structure 118

4.2.2 Random emigration model 120

4.2.3 Distribution of the MSS 127

4.2.4 Maximum likelihood estimators 134

4.2.5 Asymptotic variances and covariances 135

4.2.6 Goodness-of-fit tests under random emigration 138

4.2.7 Testing for age-dependence 141

4.2.8 Age-dependent permanent emigration and Markov movement models 144

4.3 Marking Effect Models 147

4.3.1 Notation and general model under random emigration 147

4.3.2 Test for marking effect 154

4.4 Joint Age-Dependence and Marking Effect Model 155

4.4.1 The probability structure under random emigration 156

4.4.2 The likelihood under random emigration 157

4.4.3 Parameter estimates 163

4.5 Observations Obtained After t 168

4.5.1 Probability structure under random emigration 168

4.5.2 Additional components to the likelihood under random emigration 169

4.5.3 Additional parameter estimates under random emigration . . 172

4.5.4 Additional components to the goodness-of-fit tests 174

4.5.5 Age-dependence and marking effect models under permanent and Markov emigration with $v > t$ 175

5 Modified and Reduced Parameter Models **176**

5.1 Models with No Resightings 176

5.1.1 Benefit of including ancillary observations 182

5.2 Tag-Resight Model 198

5.3 Tag-Resight when Only Young Animals Are Captured 203

5.3.1 Tag-return models 204

5.4 Models with Recaptures and 100% Losses on Observation 207

5.5 Fitting Less than Full Rank Models 211

6 Application - Lake Brunner Trout Tagging 1987-1990 **215**

6.1 One-age Model with no Marking Effect 216

6.1.1 Females 216

6.1.2 Males 218

6.1.3 Comments on the one-age model with no marking effect . . 220

6.2 Age-Dependence and Marking Effect Models 222

6.2.1 Females 223

6.2.2 Males 230

6.3 Discussion 245

7 Discussion **247**

7.1 Benefits of the New Models and Implications for Existing Methods . 247

7.2 Implication for the Design of New Studies 250

7.3 Future Research 251

7.3.1 Direct modelling of capture histories 251

7.3.2 Alternative handling effect models 252

7.3.3 General multi-strata movement model 253

7.3.4 Models with different resighting assumptions 258

7.3.5 Investigations concerning underlying assumptions 259

7.4 Concluding Remarks 260

Bibliography **262**

Appendix 273

List of Tables

1.1 Reduced m-array summary of a mark-recapture data set with t years of capture. 17

1.2 Probability structure for the reduced m-array of Table 1.1 18

1.3 Multivariate reduced m-array for a study with t years of capture. . 39

1.4 Multinomial cell probabilities corresponding to the multivariate m-array of Table 1.3 40

2.1 Recovery array for a tag-recovery experiment with 4 years of release and 6 years of recovery, where $M_{i,j}$ is the number of tag recoveries at time j from animals released at time i. 45

2.2 Probability structure for the recovery array in Table 2.1 45

2.3 Recovery array for a 2-age tag-recovery experiment with 4 years of release and 5 years of recovery. 50

2.4 Probability structure for the 2-age tag recovery array of Table 2.3 . 51

2.5 Reduced m-array for a mark-recapture study carried out with t years of capture and t years of recovery 63

3.1 Live-recapture reduced m-array for brown trout *Salmo trutta* captured and tagged in Lake Brunner 1987-1990 66

3.2 Capture history codes -adapted from Pollock et al. (1990). 73

3.3 Contributions to the reduced m-array by an animal with capture history 05013 in a study with $t = 5$. 74

3.4 Reduced m-array for a mark-recapture study carried out with t years of capture and ancillary observations of marked animals obtained during the interval $1, t+1$. 75

3.5 Reduced m-array for a hypothetical $t = 4$ mark- recapture study with ancillary observations of animals in the interval $i, i+1$. 76

3.6 Summary statistics for the hypothetical reduced m-array. 76

3.7 Probability structure for animals last released following capture in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and random movement into and out of the area where they are at risk of capture. In this parameterization $p_i^* = F_{i-1}p_i$ and $q_i^* = 1 - p_i^*$. 78

3.8 Probability structure for animals last released following observation in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and random movement into and out of the area where they are at risk of capture. In this parameterization $p_i^* = F_{i-1}p_i$ and $q_i^* = 1 - p_i^*$, and $\delta_i = \frac{1-\theta_i}{\theta_i f_i \rho_i}$. 79

3.9 Parameter estimates and associated standard errors for the hypothetical mark-recapture data. 94

3.10 Example of a 2×2 contingency table for the component 1 goodness-of-fit test 100

3.11 Example of a contingency table for the component 2 goodness-of-fit test at time i. 102

3.12 Example of a 2×2 contingency table for the alternative component 2 goodness-of-fit test. This contingency table tests the random emigration assumption. Note observed after i includes observed in the interval $i, i+1$. 116

4.1 Probability structure under random emigration for age-class 0 animals last released following capture in a 2-age mark-recapture study with t years of capture and ancillary observations of marked animals obtained during the interval $(1, t+1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$ 123

4.2 Probability structure under random emigration for age class 0 animals last released following observation in a 2-age mark-recapture study with t years of capture, and ancillary observations of marked animals obtained during the interval $(1, t+1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1-\theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} \rho_i^{(\nu)}}$ 124

4.3 Probability structure under random emigration for age-class 1 animals last released following capture in a 2-age mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$ 125

4.4 Probability structure under random emigration for age class 1 animals last released following observation in a 2-age mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(1)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1-\theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} \rho_i^{(\nu)}}$ 126

4.5 Example of a contingency table for the component 1 goodness-of-fit test for animals of age $l+1$ at time $i+1$ 139

4.6 Example of a contingency table for the component 2 goodness-of-fit test for animals of age ν at time i $(\nu < l)$. 142

4.7 Example of a contingency table forming one component of the overall tests for age-dependence. 144

4.8 Probability structure under random emigration for mark class 0 animals last released following capture in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$. 150

4.9 Probability structure under random emigration for mark class 0 animals last released following observation (in the first resighting interval) in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and a temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1-\theta_i^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} \rho_i^{(\nu)}}$ 151

4.10 Probability structure under random emigration for mark class 1 animals last released following capture in a mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$. 152

4.11 Probability structure under random emigration for mark class 1 animals last released following observation in a 2-age mark-recapture study with t years of capture, ancillary observations of marked animals obtained during the interval $(1, t+1)$, and temporary marking effect. Note $p_i^{*(\nu)} = F_{i-1}^{(\nu)} p_i^{(\nu)}$ and $q_i^{*(\nu)} = 1 - p_i^{*(\nu)}$, and $\delta_i^{(\nu)} = \frac{1-\theta^{(\nu)}}{\theta_i^{(\nu)} f_i^{(\nu)} \rho_i^{(\nu)}}$. 153

5.1 Probability structure for a $t = 4$ two-age Jolly-Seber model with no marking effect under random emigration where $p_i^{*(1)} = F_{i-1}^{(1)} p_i^{(1)}$ and $p_i^{*(0)} = F_{i-1}^{(0)} p_i^{(1)}$. 178

5.2 Probability structure for a $t = 4$ two-age Jolly-Seber model with no marking effect under permanent emigration where $S_i^{*(\nu)} = S_i^{(\nu)} F_i^{(\nu)}$. 179

5.3 Contingency table used to test the "random" vs "permanent" emigration models 180

5.4 Average bias of the capture ($\bar{\hat{p}}_i - \bar{p}$) and survival ($\bar{\hat{S}}_i - \bar{S}$) rate estimators for a $t = 5$ one-age mark recapture experiment with ancillary observations and a population made up of high (p_h) and low (p_l) capture probability individuals ($p_l = \bar{p} - \frac{\Delta_p}{2}$ and $p_h = \bar{p} + \frac{\Delta_p}{2}$), and with $S_i = 0.3$. 194

5.5 Average bias of the capture ($\bar{\hat{p}}_i - \bar{p}$) and survival ($\bar{\hat{S}}_i - \bar{S}$)rate estimators for a $t = 5$ one-age mark recapture experiment with ancillary observations and a population made up of high (p_h) and low (p_l) capture probability individuals ($p_l = \bar{p} - \frac{\Delta_p}{2}$ and $p_h = \bar{p} + \frac{\Delta_p}{2}$), and with $S_i = 0.8$. 196

5.6 Probability structure for a $t = 4$ one-age tag-resight model. All observations are obtained exactly at sampling time i, and observations at i of animals released at i ignored. 198

5.7 Probability structure for a $t = 4$ one-age tag-resight study with a temporary marking response. For animals released at i, class 0 animals are those animals marked at i and class 1 animals are those animals marked before i. Note: $\delta_i^{(\nu)} = \frac{(1-\theta_i^{(\nu)})}{\theta_i^{(\nu)} f_i^{(\nu)}}$ 201

5.8 Probability structure for a $t = 4$ tag-resight study for animals tagged only as young and with observations obtained throughout the interval $i, i+1$. Class 0 animals are young, class 1 animals are adult. 205

5.9 Statistics used by Brownie et al. (1985) for the one-age model without a marking effect and the equivalent ancillary observations model statistics. 206

5.10 Joint live-recapture and tag-recovery array for paradise shelduck tagged in the Wanganui area 1987-1991. 209

5.11 Summary statistics for Wanganui paradise shelduck tagging program 1987-1991. 210

5.12 Parameter estimates for the Wanganui paradise shelduck tagging data 210

5.13 4×2 contingency table testing whether the probability that a member of r_{88} is ever captured or recovered is influenced by whether it was captured in 1988. 211

6.1 Live-recapture and observation array for female brown trout tagged in Lake Brunner spawning tributaries, 1987-1990 and observed by angler captures 1987-1991. 216

6.2 Summary statistics for female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991.217

6.3 Parameter estimates for female brown trout under the one-age model with random emigration and no marking effect. 217

6.4 Live-recapture and observation array for male brown trout tagged in Lake Brunner spawning tributaries, 1987-1990 and observed by angler captures 1987-1991. 218

6.5 Summary statistics for male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 219

6.6 Parameter estimates for male brown trout under the one-age model with no marking effect. 219

6.7 Observed and expected values for the 1988 component 2 contingency table of the random emigration model goodness-of-fit test for males. 221

6.8 Observed and expected values for the 1990 component 2 contingency table of the random emigration goodness-of-fit test for males. 221

6.9 Length classes used to assign Lake Brunner brown trout to age-classes.222

6.10 Age-class 0 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990. 223

6.11 Age-class 1 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990. 224

6.12 Age-class 2 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990. 225
6.13 Age-class 3 component of the 4-age reduced m-array with temporary marking effect for female brown trout tagged in Lake Brunner 1987 - 1990. 226
6.14 Summary statistics for age-class 0 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 227
6.15 Summary statistics for age-class 1 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 228
6.16 Summary statistics for age-class 2 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 228
6.17 Summary statistics for age-class 3 female brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 229
6.18 Parameter estimates for age class 0 females in the 4-age model with temporary marking effect under random emigration. 229
6.19 Parameter estimates for age class 1 females in the 4-age model with temporary marking effect under random emigration. 230
6.20 Parameter estimates for age class 2 females in the 4-age model with temporary marking effect under random emigration. 231
6.21 Parameter estimates for age class 3 females in the 4-age model with temporary marking effect under random emigration. 232
6.22 Parameter estimates, standard errors in parentheses, for age classes 1,2, and 3 from the four age random emigration model with no temporary marking effect for female brown trout tagged in Lake Brunner 1987-1990 233

6.23 Results of contingency table tests for age- dependence and temporary marking effect. Model 1: no age-dependence and no marking effect; Model 2a marking effect but no age-dependence; Model 2b: age-dependence but no marking effect; Model 3: age-dependence and marking effect. 234
6.24 Reduced m-array with temporary marking effect for age-class 0 male brown trout tagged in Lake Brunner 1987 - 1990. 235
6.25 Reduced m-array with temporary marking effect for age-class 1 male brown trout tagged in Lake Brunner 1987 - 1990. 236
6.26 Reduced m-array with temporary marking effect for age-class 2 male brown trout tagged in Lake Brunner 1987 - 1990. 237
6.27 Reduced m-array with temporary marking effect for age-class 3 male brown trout tagged in Lake Brunner 1987 - 1990. 238
6.28 Summary statistics for age-class 0 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 239
6.29 Summary statistics for age-class 1 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 239
6.30 Summary statistics for age-class 2 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 240
6.31 Summary statistics for age-class 3 male brown trout tagged in spawning tributaries of Lake Brunner 1987-1990 and observed by anglers 1987-1991. 240
6.32 Parameter estimates for age-class 0 males under the 4-age model with temporary marking effect under random emigration fitted to the male data. 241

6.33 Parameter estimates for age-class 1 males under the 4-age model with temporary marking effect under random emigration fitted to the male data. 241
6.34 Parameter estimates for age-class 2 males under the 4-age model with temporary marking effect under random emigration fitted to the male data. 242
6.35 Parameter estimates for age-class 3 males under the 4-age model with temporary marking effect under random emigration fitted to the male data. 243
6.36 Results of contingency table tests for age- dependence and temporary marking effect for males. Model 1: no age- dependence and no marking effect; Model 2a marking effect but no age-dependence; Model 2b: age-dependence but no marking effect; Model 3: age-dependence and marking effect. 243
6.37 Parameter estimates, standard errors in parentheses, for the age-independent random emigration model with temporary marking effect in capture probabilities for male brown trout tagged in Lake Brunner 1987-1990 244

7.1 Multivariate reduced m-array for a mark-recapture study beginning at time 1 with t capture periods and ancillary observations of marked animals obtained during the interval $1, t+1$. 256

List of Figures

1.1 Overview of the main classes of mark-recapture models and their inter-relationships. Adapted from Pollock et al. (1990). 2

5.1 Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 5$ and $S_i = 0.3$ (Relative efficiency = $\frac{Var(\hat{S}_i^{JS})}{Var(\hat{S}_i)}$). 184

5.2 Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 5$ and $S_i = 0.5$ (Relative efficiency = $\frac{Var(\hat{S}_i^{JS})}{Var(\hat{S}_i)}$). 185

5.3 Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 5$ and $S_i = 0.8$ (Relative efficiency = $\frac{Var(\hat{S}_i^{JS})}{Var(\hat{S}_i)}$). 186

5.4 Relative asymptotic efficiency of the survival rate estimator of the one-age mark recapture model with ancillary observations relative to the Jolly-Seber model with $t = 10$ and various survival and capture probabilities (Relative efficiency = $\frac{Var(\hat{S}_i^{JS})}{Var(\hat{S}_i)}$). 187

5.5 Average asymptotic bias of $\hat{p}_i^*$ relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individuals. $\Delta_p = p_h - p_l$, t=5, $S_i = 0.3$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\hat{p}_i^{*JS} - \bar{p}}$, P =$\bar{p}$). 190

5.6 Average asymptotic bias of $\hat{p}_i^*$ relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individual. $\Delta_p = p_h - p_l$, t=5, $S_i = 0.8$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\hat{p}_i^{*JS} - \bar{p}}$, P =$\bar{p}$). 191

5.7 Average asymptotic bias of $\hat{S}_i^*$ relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individual. $\Delta_p = p_h - p_l$, t=5, $S_i = 0.3$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\hat{p}_i^{*JS} - \bar{p}}$, P =$\bar{p}$). 192

5.8 Average asymptotic bias of $\hat{S}_i^*$ relative to the Jolly-Seber model in a one-age study where the population comprises high (p_h) and low (p_l) capture probability individual. $\Delta_p = p_h - p_l$, t=5, $S_i = 0.8$, and $f = 0.2$ (A), 0.4 (B), 0.6 (C), and 0.8 (D). (Relative bias = $\frac{\hat{p}_i^* - \bar{p}}{\hat{p}_i^{*JS} - \bar{p}}$, P =$\bar{p}$). 193