

DISSERTATION

GENERALIZED MIXED EFFECTS MODELS FOR ESTIMATING
DEMOGRAPHIC PARAMETERS WITH MARK-RESIGHT DATA

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

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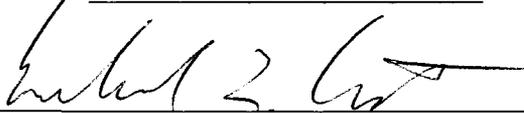
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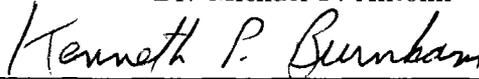
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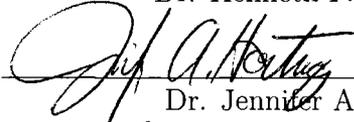
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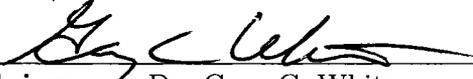
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ABSTRACT OF DISSERTATION
GENERALIZED MIXED EFFECTS MODELS FOR ESTIMATING
DEMOGRAPHIC PARAMETERS WITH MARK-RESIGHT DATA

Mark-resight methods constitute a slightly different type of data than found in traditional mark-recapture, but they are in the same spirit of accounting for imperfect detection towards reliably estimating demographic parameters. Compared to mark-recapture, mark-resight can often be a less expensive and less invasive alternative in long-term population monitoring programs. However, the mark-resight estimators developed to date do not provide a flexible framework allowing the efficient use of covariates in modeling the detection process, information-theoretic model selection and multimodel inference, and the joint estimation of abundance and related demographic parameters. Here I develop a series of mark-resight models for the sampling conditions most often encountered in these studies that address this need for a more generalized framework.

In Chapter 1, I introduce the the logit-normal mixed effects model (LNE) for estimating abundance when sampling is without replacement and the number of marked individuals in the population is known exactly. I compare the model to other mark-resight abundance estimators when applied to mainland New Zealand robin (*Petroica australis*) data recently collected in Eglinton Valley, Fiordland National Park. I also summarize its relative performance in simulation experiments.

It can often be difficult to achieve sampling without replacement or to know the exact number of marked individuals in a population. In Chapter 2, I address these limitations of LNE by introducing the (zero-truncated) Poisson-log normal mixed effects abundance model, (Z)PNE. I demonstrate the use and advantages of (Z)PNE using black-tailed prairie dog (*Cynomys ludovicianus*) data recently collected in Colorado. I also investigate the expected relative performance of the model in simulation experiments.

In Chapter 3, I extend (Z)PNE to a full-likelihood robust design model analogous to that used in mark-recapture for the simultaneous estimation of abundance, apparent survival, and transition probabilities between observable and unobservable states. I illustrate the use of the model with additional New Zealand robin data collected in Fiordland National Park, New Zealand. I also report on a series of simulation experiments evaluating the performance of the model under a variety of sampling conditions.

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Chapter 1

A generalized mixed effects model of abundance for mark-resight data when sampling is without replacement

1.1 Introduction

The mark-resight method for estimating population abundance when the number of marked individuals is known (White and Shenk, 2001; McClintock and White, 2007) may in many circumstances be considered a reliable, cost-effective alternative to traditional mark-recapture or index methods based on counts. Mark-resight is generally most useful for estimating relatively small, closed populations, and because animals only need to be physically captured and marked once prior to resighting sur-

veys, the method is typically less expensive and less invasive than mark-recapture. The various mark-resight estimators available include the Joint Hypergeometric estimator (JHE) (Bartmann et al., 1987), the Minta-Mangel estimator (MME) (Minta and Mangel, 1989), the Immigration/Emigration Joint Hypergeometric estimator (IEJHE) (Neal et al., 1993), Bowden's estimator (BOWE) (Bowden and Kufeld, 1995), and the Beta-Binomial estimator (BBE) (McClintock et al., 2006). These primarily differ in their sampling protocols and means of modeling variability in resighting probabilities. Temporal variation in resighting probabilities is readily handled by all of the estimators, but individual heterogeneity (where sighting probabilities vary among animals) is not. Similar to mark-recapture abundance models, individual heterogeneity has been particularly problematic and often causes biased estimates when not properly accounted for (Otis et al., 1978; Neal et al., 1993).

JHE requires the standard assumptions of mark-resight estimators for the size of a closed population: 1) geographic and demographic closure; 2) no loss of marks; 3) no errors in distinguishing marked and unmarked animals; 4) independently and identically distributed (iid) resighting probabilities for marked and unmarked animals; 5) homogeneity of resighting probabilities within an occasion; and 6) sampling without replacement within occasions (Neal et al., 1993; White and Shenk, 2001). IEJHE requires the same assumptions of JHE, but geographic closure need not be met because the presence of marked animals on the area surveyed is determined explicitly (Neal et al., 1993). BOWE relaxes several assumptions of JHE by allowing temporary movement off the study area, individual heterogeneity, and sampling with replacement (Bowden and Kufeld, 1995). Some study designs, such

as those using camera traps or lacking a defined "occasion," may only be conducted with replacement and necessitate the use of BOWE. MME has similar assumptions to BOWE, but its performance in simulation experiments has proven inferior to the other models allowing individual heterogeneity and its use is not recommended (White, 1993; White and Shenk, 2001). BBE has the same assumptions of BOWE, but sampling must be without replacement. Any heterogeneity model requires that marked animals be individually identifiable, but in some cases this is not feasible and necessitates the use of JHE. If individually identifiable marks are used, both BOWE and BBE tolerate less than 100% individual identification given that the animal is identified as marked (White and Shenk, 2001; Magle et al., 2007). This is a common occurrence in mark-resight studies, and failing to account for unidentified marks will generally result in overestimation of abundance due to underestimation of resighting probabilities. Heterogeneity models also allow demographic closure to be violated via mortality independent of mark status, but abundance estimates produced when this occurs become the population residing in the study area at the beginning of the resighting period. As with IEJHE, when geographic closure is violated via temporary movement off the study area, the interpretation of abundance estimates for the heterogeneity models becomes the total population using the study area, often termed a "super population" (Kendall et al., 1995). For all mark-resight estimators, the assumption of iid resighting probabilities for marked and unmarked individuals is typically considered acceptable when a sufficiently different method is used for selecting the marked individuals (e.g., via helicopter capture) than is used for resighting (e.g., via ground surveys on foot) (White and Shenk, 2001; McClintock

and White, 2007).

JHE is generally contended to be the most precise when its assumptions hold, but confidence interval coverage can fall well below the nominal 95% when individual heterogeneity is moderate to high (Neal et al., 1993; McClintock et al., 2006). BOWE performs well when individual heterogeneity is present, but is not likelihood-based and therefore lacks the benefits of likelihood theory, including information-theoretic model selection and model averaging methods. BBE successfully combines likelihood theory and the ability to model individual heterogeneity. The model may also incorporate a “robust” sampling design, which combines data from both closed and open sampling periods to estimate demographic parameters (Pollock, 1982; Kendall et al., 1995). The “primary” sampling occasions consist of ≥ 2 “secondary” sampling occasions, and the time period for secondary sampling must be short enough for the assumption of closure to be acceptable. The open periods between primary occasions apply to longer intervals of time where closure need not be met. This approach has many advantages in long-term monitoring studies, including the ability to model detection probabilities similarly across time (or groups) for increased efficiency. Under the robust design, BBE has advantages over JHE in the presence of individual heterogeneity and over BOWE in cases where sighting probabilities are similar between primary occasions (McClintock et al., 2006).

When sampling is without replacement, BBE will often outperform other estimators and aid researchers in determining which model is most appropriate, but it is by no means a superlative mark-resight estimator for all situations. Due to the different assumptions and general rigidity of JHE, BOWE, and BBE, researchers

must commit to a particular model based on educated guesswork without rigorous quantitative justification for model selection based on the data. Because there is no quantitative criterion to choose between these estimators, there remains a need for a more generalized framework for mark-resight abundance estimation. Similar to those available for mark-recapture studies, this framework would allow a wide variety of sampling conditions to be parameterized efficiently and provide quantitative justification for model selection regardless of the types and levels of variation encountered in the field. These parameterizations would include complex models utilizing covariates and simpler models where potential sources of variation such as individual heterogeneity may be ignored. By incorporating a more flexible model structure under a generalized framework, the uncertainty that remains in mark-resight model selection would be reduced substantially. In the following section, I introduce a model addressing this need for a more generalized framework when sampling is without replacement. I then apply the model to New Zealand robin (*Petroica australis*) data and compare its performance to the other estimators. Finally, I evaluate the performance of the model based on simulation experiments and discuss the implications for mark-resight model selection.

1.2 The Model

The logit-normal mixed effects mark-resight model (LNE) has the same assumptions of BBE and allows the data to be combined across t primary sampling occasions in a robust sampling design. In order to incorporate heterogeneity parameters into

the model, I will assume marked individuals are individually identifiable. However, unlike BBE and BOWE, LNE does not require individually identifiable marks (although its utility is somewhat diminished without them). A known number of individuals ($n_j, j = \{1, \dots, t\}$) must first be marked at the beginning of interval j , and resighting data are collected during the t closed intervals consisting of k_j ($j = \{1, \dots, t\}$) distinct secondary resighting occasions. The data consist of resightings for marked individual s on secondary occasion i of primary occasion j (δ_{sij}) and the total number of unmarked sightings across all k_j secondary occasions of primary occasion j (T_{u_j}). The δ_{sij} are modeled as independent Bernoulli random variables, where $\delta_{sij} = 1$ if individual s is seen on secondary occasion i of primary occasion j , and $\delta_{sij} = 0$ otherwise. Individual sighting probabilities are approximated as the realization of a logit-normal random variable, where time is modeled as a fixed effect (β_{ij}) and individual heterogeneity as a random effect with mean zero and unknown variance σ_j^2 . The marked individual resighting data have conditional expectation

$$E(\delta_{sij} \mid \sigma_j, Z_{sj}, \beta_{ij}) = p_{sij} = \frac{1}{1 + \exp(-(\sigma_j Z_{sj} + \beta_{ij}))},$$

where $Z_{sj} \stackrel{\text{iid}}{\sim} N(0, 1)$. Therefore, any randomly selected individual s from primary occasion j with latent sightability Z_{sj} has the marginal probability of being seen on secondary occasion i

$$E_{Z_{sj}}(p_{sij}) = p_{ij|s} = \int \frac{1}{1 + \exp(-(\sigma_j z_{sj} + \beta_{ij}))} \phi(z_{sj}) dz_{sj},$$

where $\phi(z_{sj})$ is the standard normal distribution. Time (β_{ij}) could possibly be treated as a random effect, but I chose not to investigate this approach because the number of occasions is generally too small for this to be useful. Under this framework, resighting probabilities may be modeled with no time or heterogeneity effects within secondary occasions ($\beta_{ij} = \theta_j, \sigma_j = 0$), only time effects, only heterogeneity effects, or additive time and heterogeneity effects. Across all marked individuals and secondary occasions, an unconditional likelihood function for σ_j and β_{ij} is

$$L(\sigma_j, \beta_{ij} \mid \delta_{sij}, n_j, k_j) = \prod_{s=1}^{n_j} \int \left[\prod_{i=1}^{k_j} p_{sij}^{\delta_{sij}} (1 - p_{sij})^{(1-\delta_{sij})} \right] \phi(z_{sj}) dz_{sj}. \quad (1.1)$$

Abundance (N) enters the equation by focusing on T_{u_j} and the number of unmarked individuals in the population ($U_j = N_j - n_j$). Using the approach validated for BBE (McClintock et al., 2006), $T_{u_j} \stackrel{\text{ind}}{\sim} N[\mathbb{E}(T_{u_j}), \text{var}(T_{u_j})]$, the approximate likelihood function for N_j is:

$$L(N_j \mid \sigma_j, \beta_{ij}, \delta_{sij}, n_j, k_j, T_{u_j}) = \frac{1}{\sqrt{2\pi \text{var}(T_{u_j})}} \exp \left\{ \frac{-[T_{u_j} - \mathbb{E}(T_{u_j})]^2}{2\text{var}(T_{u_j})} \right\}.$$

Combining the two likelihoods across the t primary occasions yields the LNE likelihood of the general form:

$$L(\mathbf{N}, \boldsymbol{\sigma}, \boldsymbol{\beta} \mid \boldsymbol{\delta}, \mathbf{n}, \mathbf{k}, \mathbf{T}_u) = \prod_{j=1}^t \left\{ \prod_{s=1}^{n_j} \int \left[\prod_{i=1}^{k_j} p_{sij}^{\delta_{sij}} (1 - p_{sij})^{(1-\delta_{sij})} \right] \phi(z_{sj}) dz_{sj} \right\} \\ \times \prod_{j=1}^t \frac{1}{\sqrt{2\pi \text{var}(T_{u_j})}} \exp \left\{ \frac{-[T_{u_j} - \mathbb{E}(T_{u_j})]^2}{2\text{var}(T_{u_j})} \right\}. \quad (1.2)$$

For the simplest model, with no time or individual heterogeneity effects within secondary occasions,

$$E(T_{u_j}) = (N_j - n_j)k_j \frac{1}{1 + \exp(-\theta_j)},$$

and

$$\text{var}(T_{u_j}) = (N_j - n_j)k_j \frac{\exp(\theta_j)}{[1 + \exp(\theta_j)]^2}.$$

For the case of fixed time effects only within secondary occasions,

$$E(T_{u_j}) = (N_j - n_j) \sum_{i=1}^{k_j} \frac{1}{1 + \exp(-\beta_{ij})},$$

$$\text{var}(T_{u_j}) = (N_j - n_j) \sum_{i=1}^{k_j} \frac{\exp(\beta_{ij})}{[1 + \exp(\beta_{ij})]^2}.$$

The individual heterogeneity model with no time effects within secondary occasions has unconditional

$$E(T_{u_j}) = (N_j - n_j)k_j\mu_j,$$

and

$$\text{var}(T_{u_j}) = (N_j - n_j)k_j [\mu_j(1 - \mu_j) + (k_j - 1)(\gamma_j - \mu_j^2)], \quad (1.3)$$

where

$$\mu_j = \int \frac{1}{1 + \exp(-(\sigma_j z_j + \theta_j))} \phi(z_j) dz_j,$$

$$\gamma_j = \int \left[\frac{1}{1 + \exp(-(\sigma_j z_j + \theta_j))} \right]^2 \phi(z_j) dz_j,$$

and $\phi(z_j)$ is the standard normal distribution. For the heterogeneity model with fixed time effects within secondary occasions,

$$E(T_{u_j}) = (N_j - n_j) \sum_{i=1}^{k_j} \mu_{ij},$$

and

$$\text{var}(T_{u_j}) = (N_j - n_j) \left[\sum_{i=1}^{k_j} \mu_{ij}(1 - \mu_{ij}) + \sum_{l \neq i} \sum (\gamma_{lij} - \mu_{lj}\mu_{ij}) \right], \quad (1.4)$$

where

$$\mu_{ij} = \int \frac{1}{1 + \exp(-(\sigma_j z_j + \beta_{ij}))} \phi(z_j) dz_j,$$

and

$$\gamma_{lij} = \int \frac{1}{1 + \exp(-(\sigma_j z_j + \beta_{lj}))} \frac{1}{1 + \exp(-(\sigma_j z_j + \beta_{ij}))} \phi(z_j) dz_j.$$

Interested readers may find the derivations of (1.3) and (1.4) in Appendix A.

LNE may incorporate the number of marked individuals that were identified as marked, but not identified to individual (ϵ_{ij}). These data enter the likelihood in (1.2) via $E(T_{u_j})$ and $\text{var}(T_{u_j})$. For the general case with fixed time effects and individual heterogeneity,

$$E(T_{u_j}) = (N_j - n_j) \sum_{i=1}^{k_j} \mu'_{ij},$$

and

$$\text{var}(T_{u_j}) = (N_j - n_j) \left[\sum_{i=1}^{k_j} \mu'_{ij}(1 - \mu'_{ij}) + \sum_{l \neq i} \sum (\gamma'_{lij} - \mu'_{lj} \mu'_{ij}) \right],$$

where

$$\mu'_{ij} = \int \left[\frac{1}{1 + \exp(-(\sigma_j z_j + \beta_{ij}))} + \frac{\epsilon_{ij}}{n_j} \right] \phi(z_j) dz_j,$$

and

$$\gamma'_{lij} = \int \left[\frac{1}{1 + \exp(-(\sigma_j z_j + \beta_{lj}))} + \frac{\epsilon_{lj}}{n_j} \right] \left[\frac{1}{1 + \exp(-(\sigma_j z_j + \beta_{ij}))} + \frac{\epsilon_{ij}}{n_j} \right] \phi(z_j) dz_j.$$

Similar to BOWE and BBE, with high levels of individual heterogeneity the adjustment to incorporate unidentified marks is reliable when the proportion of unidentified marks remains < 0.10 . When > 0.10 , the resulting underestimates of variances can cause confidence interval coverage of N to fall as low as 88% (White and Shenk,

2001; Magle et al., 2007). When individual heterogeneity is low to moderate, the proportion of unidentified marks can approach 0.20 and still achieve nominal 95% confidence interval coverage (Magle et al., 2007).

Because the integrals in (1.2) do not have a closed form solution, they must be computed numerically. These can be approximated with relative ease using Gaussian-Hermite quadrature (Givens and Hoeting, 2005), with

$$\int \left[\prod_{i=1}^{k_j} p_{sij}^{\delta_{sij}} (1 - p_{sij})^{(1-\delta_{sij})} \right] \phi(z_{sj}) dz_{sj}$$

$$\approx \frac{1}{\sqrt{\pi}} \sum_{m=1}^M w_m \prod_{i=1}^{k_j} \left(\frac{1}{1 + \exp(-(\sqrt{2}\sigma_j v_m + \beta_{ij}))} \right)^{\delta_{sij}}$$

$$\times \left(1 - \frac{1}{1 + \exp(-(\sqrt{2}\sigma_j v_m + \beta_{ij}))} \right)^{1-\delta_{sij}},$$

$$\mu_{ij} \approx \frac{1}{\sqrt{\pi}} \sum_{m=1}^M w_m \frac{1}{1 + \exp(-(\sqrt{2}\sigma_j v_m + \beta_{ij}))},$$

and

$$\gamma_{lij} \approx \frac{1}{\sqrt{\pi}} \sum_{m=1}^M w_m \frac{1}{1 + \exp(-(\sqrt{2}\sigma_j v_m + \beta_{lj}))} \frac{1}{1 + \exp(-(\sqrt{2}\sigma_j v_m + \beta_{ij}))}$$

for tabulated (v_m, w_m) pairs corresponding to M quadrature points (Abramowitz and Stegun, 1964).

1.3 Example: New Zealand Robin

1.3.1 Example Methods

The New Zealand robin (*Petroica australis*) data were collected in March 2005 from $t = 2$ study sites in the Eglington Valley of Fiordland National Park, New Zealand ($44^{\circ}58'S$, $168^{\circ}01'E$). The two sites, Knobs Flat and Walker Creek, consisted of 100 ha grids and were part of an exploratory investigation by the Department of Conservation on the usefulness of this technique for estimating N of endangered populations in the Chatham Islands. Prior to the resighting surveys, as many juvenile and adult birds as possible were captured within the study areas and given individually identifiable bands. Between September 2003 and March 2005, 80 and 79 birds were banded in Knobs Flat and Walker Creek, respectively. Immediately prior to collecting resighting data in March 2005, an independent visual survey was conducted to sample a known "marked" subset ($n_{kf} = 23$, $n_{wc} = 20$) of the previously banded birds. This was necessary because banded birds could have died or emigrated during the extended capture period prior to the resighting surveys. The resighting effort was divided into 7 distinct secondary occasions where the entire area of both study sites was surveyed. Secondary sampling occasions were conducted in the morning and typically required four hours each. The populations were assumed closed during the sampling intervals. On several occasions a marked or banded individual was seen more than once. However, because the extended capture period left few birds unbanded, the researchers believed they could identify double counts and satisfy the assumption of sampling without replacement. Raw estimates of \bar{p} from the

Table 1.1: LNE parameterizations for β_{ij} and σ_j with $t = 2$ primary sampling occasions both consisting of k secondary sampling occasions ($i = 1, \dots, k, j = 1, 2$). Combining the six β_{ij} parameterizations with the five σ_j parameterizations yields 30 possible LNE models with $N_1 \neq N_2$. The number of estimated parameters (not including N_j) in the models range from $K = 1$ for model $\{\beta(\cdot)\sigma(0)\}$ to $K = 2k + 2$ for model $\{\beta(t1, t2)\sigma(\cdot, \cdot)\}$.

Model Notation	Parameterization	K
$\beta(\cdot)$	$\beta_{i1} = \beta_{i2} = \theta$	1
$\beta(\cdot, \cdot)$	$\beta_{i1} = \theta_1, \beta_{i2} = \theta_2$	2
$\beta(t1 = t2)$	$\beta_{i1} = \beta_{i2}$	k
$\beta(t1, \cdot)$	$\beta_{i1} \neq \beta_{i2} = \theta$	$k + 1$
$\beta(\cdot, t2)$	$\beta_{i2} \neq \beta_{i1} = \theta$	$k + 1$
$\beta(t1, t2)$	$\beta_{i1} \neq \beta_{i2}$	$2k$
$\sigma(0)$	$\sigma_1 = \sigma_2 = 0$	0
$\sigma(\cdot)$	$\sigma_1 = \sigma_2$	1
$\sigma(\cdot, 0)$	$\sigma_1 \neq \sigma_2 = 0$	1
$\sigma(0, \cdot)$	$\sigma_2 \neq \sigma_1 = 0$	1
$\sigma(\cdot, \cdot)$	$\sigma_1 \neq \sigma_2$	2

marked populations were 0.40 (SE = 0.04) and 0.41 (SE = 0.04) for Knobs Flat and Walker Creek, respectively. Total unmarked sightings ($T_{u,kf} = 45, T_{u,wc} = 54$) included previously banded birds that were not included in the marked subset.

With $t = 2$ primary occasions both consisting of 7 secondary occasions, there are 30 possible LNE parameterizations with $N_{kf} \neq N_{wc}$ (Table 1.1). The models range in complexity from the simplest no heterogeneity model, $\{\beta(\cdot)\sigma(0)\}$, to the most general time and heterogeneity model, $\{\beta(t1, t2)\sigma(\cdot, \cdot)\}$. The models were easily implemented using the nonlinear mixed-effects model (NLMIXED) maximum likelihood procedure in the SAS System for Windows (SAS Institute, 2002). By default, NLMIXED computes the integrals in (1.1) using adaptive Gaussian quadrature. The integrals in $E(T_{u_j})$ and $\text{var}(T_{u_j})$ must be programmed separately within the procedure, and I found Gaussian-Hermite quadrature with $M = 4$ points to be

an adequate approximation.

I used Akaike’s Information Criterion (AIC_c) (Burnham and Anderson, 2002) and the Bayesian Information Criterion (BIC) (Schwarz, 1978) as a basis for ranking the 30 LNE models and obtaining model-averaged point estimates and unconditional variances with AIC_c and BIC weights (Burnham and Anderson, 2002; Link and Barker, 2006). I defined the effective sample size for AIC_c and BIC calculation as $n = \sum_{j=1}^t n_j k_j + t$. I compared the LNE model-averaged estimates to those of JHE, BOWE, and BBE. BBE estimates were also model-averaged using AIC_c and BIC weights. As “equivalents” to JHE and BOWE, I also compared estimates of the most general LNE and BBE models where all parameters were estimated independently. Logarithm-transformed 95% confidence intervals for BOWE were computed as in Bowden and Kufeld (1995). Confidence intervals for LNE, JHE, and BBE were computed similarly but with the lower bound constrained to be greater than the known number of marked individuals. In comparing the performance of the models, my results focus on the precision of the estimates. Bias is also an important issue, but I was unable to quantify this property because N is unknown for these populations. However, both AIC_c and BIC address the trade-off between bias and precision as a means of model selection.

1.3.2 Example Results

AIC_c and BIC model rankings differed, with AIC_c giving higher weights to the more complex additive models (Table 1.2). BIC rankings suggest mean resighting

Table 1.2: AIC_c and BIC weights for selected LNE models of New Zealand robin abundance in Knobs Flat and Walker Creek study areas in Fiordland National Park, New Zealand. Numbers of estimated parameters include N .

Model	AIC _c Weight	No. Est. Parameters	Model	BIC Weight	No. Est. Parameters
$\beta(t1,.)\sigma(.,0)$	0.22	11	$\beta(.)\sigma(0)$	0.61	3
$\beta(t1,.)\sigma(.,.)$	0.14	11	$\beta(.)\sigma(.,0)$	0.15	4
$\beta(.)\sigma(.,0)$	0.09	4	$\beta(.)\sigma(.,.)$	0.14	4
$\beta(t1,.)\sigma(.,.)$	0.08	12	$\beta(.)\sigma(0,.)$	0.04	4
$\beta(.)\sigma(.,.)$	0.08	4	$\beta(.,.)\sigma(0)$	0.03	4
$\beta(t1,.)\sigma(0)$	0.06	10	$\beta(.)\sigma(.,.)$	0.01	5
$\beta(.)\sigma(0)$	0.06	3	$\beta(.,.)\sigma(.,0)$	0.01	5
$\beta(.)\sigma(.,.)$	0.04	5	$\beta(.,.)\sigma(.,.)$	0.01	5
...
$\beta(t1,t2)\sigma(.,.)$	0.00	18	$\beta(t1,.)\sigma(.,0)$	0.00	11
...
$\beta(.,t2)\sigma(0,.)$	0.00	11	$\beta(t1,t2)\sigma(.,.)$	0.00	18

probabilities did not differ between secondary occasions or between the two study areas, but AIC_c rankings provide some evidence of temporal variation in Knobs Flat resighting probabilities. The vast majority of AIC_c weight (85%) was given to models incorporating individual heterogeneity. BIC favored less complex models, with 36% of BIC weight given to those with heterogeneity parameters. The highest ranking BIC model estimates were therefore more precise than those of AIC_c. Estimates for the three-parameter minimum-BIC model, $\{\beta(.)\sigma(0)\}$, were $\hat{\theta} = -0.38$ (SE = 0.12), $\hat{N}_{kf} = 38.7$ (SE = 2.11), and $\hat{N}_{wc} = 38.9$ (SE = 2.37). Heterogeneity and abundance estimates for the 11-parameter minimum-AIC_c model, $\{\beta(t1,.)\sigma(.,0)\}$, were $\hat{\sigma}_{kf} = 0.79$ (SE = 0.28), $\hat{N}_{kf} = 38.7$ (SE = 2.87), and $\hat{N}_{wc} = 38.8$ (SE = 2.74).

In comparing the various estimators, point estimates were very similar regardless of the method used, but precision levels did vary (Table 1.3). The BIC

Table 1.3: Abundance estimates (\hat{N}), percent coefficient of variation (% CV), 95% confidence intervals (CI), and percent confidence interval lengths (% CIL) for Knobs Flat (KF) and Walker Creek (WC) study areas when using the AIC_c model-averaged (modAIC) LNE and BBE, BIC model-averaged (modBIC) LNE and BBE, LNE and BBE with both areas estimated independently, BOWE, and JHE. Estimators are ordered by the smallest average % CV.

Estimator	Study Area	\hat{N}	% CV	95% CI		% CIL
				Lower	Upper	
LNE modBIC	KF	38.7	5.8	34.9	43.7	22.8
	WC	38.9	6.4	34.6	44.4	25.4
JHE	KF	38.4	6.0	34.5	43.5	23.4
	WC	38.9	7.1	34.2	45.1	27.9
BBE modBIC	KF	38.7	6.4	34.6	44.2	24.9
	WC	38.8	7.1	34.1	45.0	28.1
BBE modAIC	KF	38.7	6.6	34.5	44.4	25.7
	WC	38.8	7.2	34.0	45.1	28.5
LNE modAIC	KF	38.7	6.7	34.4	44.5	26.3
	WC	38.8	7.2	34.1	45.2	28.6
BBE	KF	38.7	7.4	34.1	45.2	28.8
	WC	38.8	7.6	33.8	45.4	29.9
LNE	KF	38.7	7.4	34.1	45.2	28.9
	WC	38.8	7.6	33.8	45.4	29.9
BOWE	KF	38.7	7.7	33.0	45.4	32.2
	WC	38.7	7.9	32.8	45.6	33.1

model-averaged LNE and JHE had the highest precision, but given the AIC_c and BIC evidence that individual heterogeneity may be an issue with these data, I believe JHE is underestimating the uncertainty about N and is therefore inappropriate. Model-averaged LNE and BBE results were very similar for these data because both incorporated a robust sampling design and estimated individual heterogeneity parameters. Even when compared to the “equivalent” BBE and LNE models with all parameters estimated independently, BOWE was the least precise of the estimators. Although inferences in this simple example were quite similar regardless of the model used, the model-averaged LNE or BBE appear to be the most appropriate because they were more efficient. Had there been less evidence of heterogeneity, I suspect the AIC_c model-averaged LNE would also have been more efficient than its BBE counterpart because of its ability to incorporate these parameters as deemed necessary by the data.

The use of AIC_c or BIC has received much attention in recent years (Burnham and Anderson, 2004; Link and Barker, 2006). Philosophical issues aside, this example provides no information on the appropriateness of AIC_c or BIC for use with these models. Further, the results from this single data set are not indicative of the expected relative performance of LNE. I therefore conducted simulation experiments to assess the model’s utility in a wide variety of sampling conditions using both AIC_c and BIC.

1.4 Simulation Experiments

1.4.1 Simulation Methods

Simulated data were generated under the assumptions of geographic and demographic closure within secondary resighting occasions, sampling without replacement, iid sighting probabilities for marked and unmarked individuals, 100% mark identification, and no error in distinguishing marked versus unmarked individuals. Individual resighting probabilities were modeled as logit-normal random variables based on an underlying population \bar{p} and individual heterogeneity level (σ_{IH}), but additive temporal variation (σ_{TV}) allowed p_{sij} to vary for each secondary occasion. Because resighting probabilities were modeled using this transformation, input values for \bar{p} , σ_{IH} , and σ_{TV} did not back-transform identically to their original values. McClintock et al. (2006) used the same methods and categorized the realized values for the data-generating parameters. For \bar{p} , the categories were Low ($0.15 < \bar{p} < 0.16$), Medium ($0.30 < \bar{p} < 0.38$), and High ($\bar{p} = 0.50$). The categories for σ_{IH} and σ_{TV} were Low ($0.00 < \sigma < 0.05$), Medium ($0.10 < \sigma < 0.15$), and High ($0.16 < \sigma < 0.26$).

I first generated simulated mark-resight data for $t = 1$ primary sampling occasion. The input parameter values for generating resighting probabilities were all possible combinations of $\bar{p} = \{\text{Low, Medium, High}\}$ and $\sigma_{IH} = \sigma_{TV} = \{\text{Low, Medium, High}\}$. This limited the number of resighting probability scenarios to seven because when $\bar{p} = \text{Low}$, only $\sigma_{IH} = \sigma_{TV} = \text{Low}$ is theoretically possible. Applying these seven resighting probability scenarios to the four sample size classes with $k = 3$ or 5 and $n = 25$ ($N = 100$) or 75 ($N = 500$) totaled 28 simulation scenarios. These scenarios

Table 1.4: Data generating scenarios for simulation experiments with $t = 2$ primary sampling occasions. Number of secondary resighting occasions (k), marked sample size (n), and population abundance (N) were the same for both primary sampling occasions, but mean sighting probability \bar{p} , individual heterogeneity (σ_{IH}), and temporal variation (σ_{TV}) were allowed to vary.

Scenario	k	n	N	\bar{p}_1	$\sigma_{IH(1)}$	$\sigma_{TV(1)}$	\bar{p}_2	$\sigma_{IH(2)}$	$\sigma_{TV(2)}$
A	3	25	100	Low	Low	None	Low	Low	None
B	3	75	500	Med	None	High	Low	None	Low
C	5	25	100	Med	High	Med	Med	High	Med
D	5	25	100	High	Med	None	Med	High	Med
E	5	75	500	Med	Low	High	High	None	High
F	5	75	500	High	Med	Low	High	Med	Low

ranged in sample size from smallest ($k = 3$, $n = 25$, $N = 100$, $\bar{p} = \text{Low}$) to largest ($k = 5$, $n = 75$, $N = 500$, $\bar{p} = \text{High}$) with the variation in \bar{p} determined by the level of $\sigma_{IH} = \sigma_{TV}$.

I next generated data for $t = 2$ primary sampling occasions. With so many possible input parameters determining resighting probabilities and sample sizes, I restricted these simulations to six pseudo-randomly selected scenarios fixing $k_1 = k_2$, $n_1 = n_2$, and $N_1 = N_2$ (Table 1.4). I first designated “small” ($k = 3$, $n = 25$, $N = 100$, $\bar{p} = \text{Low}$), “medium” ($k = 5$, $n = 25$, $N = 100$, $\bar{p} = \text{Medium}$), and “large” ($k = 5$, $n = 75$, $N = 500$, $\bar{p} = \text{High}$) samples. I then randomly assigned $\sigma_{IH(1)} = \sigma_{IH(2)}$ and $\sigma_{TV(1)} = \sigma_{TV(2)}$ from $\{\text{None, Low, Medium, High}\}$ to create three scenarios. For the other three scenarios, all values were randomly selected from $k = \{3, 5\}$, $n = \{25, 75\}$, $\bar{p}_j = \{\text{Low, Medium, High}\}$, $\sigma_{IH(j)} = \{\text{None, Low, Medium, High}\}$, and $\sigma_{TV(j)} = \{\text{None, Low, Medium, High}\}$ with $N_j = 100$ if $n = 25$, and $N_j = 500$ otherwise.

With $t = 1$ primary occasion, there are four possible LNE parameterizations:

1) no time or heterogeneity effects, $\{\beta(\cdot)\sigma(0)\}$, with $K = 3$ parameters; 2) time effects only, $\{\beta(t)\sigma(0)\}$, $K = k + 2$; 3) heterogeneity only, $\{\beta(\cdot)\sigma(\cdot)\}$, $K = 4$; and 4) time and heterogeneity effects, $\{\beta(t)\sigma(\cdot)\}$, $K = k + 3$. With $t = 2$ primary occasions and $k_1 = k_2$, there are 30 possible LNE parameterizations (Table 1.1). If $k_1 \neq k_2$, there are 25 parameterizations because constraining $\beta_{i1} = \beta_{i2}$ is no longer possible. For each of the 1000 replications within a given simulation scenario, I compared the performance of LNE with JHE, BBE, and BOWE. For LNE, I examined both AIC_c and BIC model-averaged parameter estimates. For simulations with 2 primary occasions, I also examined the AIC_c and BIC model-averaged parameter estimates for BBE. AIC_c , BIC, and confidence intervals were computed as in Section 1.3. Model performance was based primarily on percent confidence interval coverage of N , Bias/SE = $E(\hat{N} - N)/SE(\hat{N})$, percent confidence interval length (%CIL = $100(UCI - LCI)/N$), and root mean squared error (RMSE = $\sqrt{\text{Bias}(\hat{N})^2 + \text{var}(\hat{N})}$). Bonferroni intervals with family confidence coefficient $\alpha = 0.05$ (Hocking, 2003) were used to simultaneously compare average estimator coverage, Bias/SE, and % CIL across scenarios. All analyses were performed using NLMIXED as described above and the Interactive Matrix Language (IML) in SAS (SAS Institute, 2002).

1.4.2 Simulation Results

In simulations with 1 primary occasion, bias was not an appreciable problem for any of the estimators, with average Bias/SE across all 28 scenarios < 0.1 for all models (Cochran, 1977) (Table 1.5). BOWE had the highest average point estimate

Table 1.5: Average percent confidence interval coverage, percent confidence interval length (% CIL), and Bias/SE of abundance estimates for BBE, BOWE, JHE, AIC_c model-averaged (modAIC) LNE, and BIC model-averaged (modBIC) LNE across 28 simulated scenarios with $t = 1$ primary sampling occasion.

Estimator	% Coverage		% CIL		Bias/SE	
	Est.	SE	Est.	SE	Est.	SE
BBE	94.1	0.14	42.4	0.11	0.06	0.01
BOWE	94.8	0.13	43.3	0.10	0.03	0.00
JHE	91.6	0.16	37.9	0.10	0.10	0.01
modAIC LNE	93.4	0.15	41.1	0.11	0.07	0.01
modBIC LNE	93.1	0.15	40.6	0.11	0.07	0.01

for coverage and JHE had the lowest % CIL across the seven resighting probability scenarios in all four sample size classes. However, BOWE also had the highest % CIL, and JHE had the lowest coverage across all four sample size classes. No significant differences were observed between the AIC_c or BIC model-averaged LNE approaches. No significant differences in average coverage for the four sample size classes were observed between BOWE and LNE, but average % CILs were significantly lower in all sample size classes for LNE than for BOWE. Overall coverage and % CIL for BBE did not significantly differ from BOWE or LNE. When $\sigma_{IH} = \text{Low}$, no significant difference in average coverage was observed between the approaches. However, JHE and the LNE approaches had significantly smaller % CILs, and the two were not significantly different from one another. BBE tended to have slightly higher RMSEs than the other heterogeneity models, but BOWE had the highest RMSEs with the largest sample sizes. Except with the largest sample sizes, BOWE generally had slightly smaller RMSEs than the LNE approaches. This is attributable to a slight positive bias for LNE with smaller sample sizes, but because Bias/SE

ratios remained small, the LNE approaches still achieved optimal coverage and % CILs.

Across the six scenarios with 2 primary occasions (Table 1.4), BOWE again had the highest average coverage and largest average % CILs. JHE on average had lower coverage and smaller % CILs than the other approaches. Average coverage for the AIC_c model-averaged LNE and BBE were not significantly different than BOWE, but average coverage for the BIC model-averaged LNE and BBE were significantly lower than BOWE. Both LNE and BBE model-averaged approaches produced significantly smaller % CILs than BOWE. Average Bias/SE was only > 0.1 for JHE (Table 1.6). The poorest performance for all approaches was in estimating N_2 of scenario D, where coverage was 87.7% (SE = 1.04) for the AIC_c model-averaged BBE, 82.8% (SE = 1.20) for the BIC model-averaged BBE, 92.3% (SE = 0.84) for BOWE, 80.7% (SE = 1.25) for JHE, 89.0% (SE = 0.99) for the AIC_c model-averaged LNE, and 81.6% (SE = 1.23) for the BIC model-average LNE. In this scenario, coverage was not significantly different between BOWE and the AIC_c model-averaged LNE or BBE, but all other approaches were significantly lower. When $\sigma_{IH(j)} \leq \text{Low}$, no significant differences in average coverage or % CIL were detected between JHE and the AIC_c model-averaged LNE and BBE, but BBE had the highest point estimate for coverage (95.4%, SE = 0.27) and LNE had the smallest point estimate for % CIL (53.7%, SE = 0.46). BIC model-averaged LNE had significantly lower % CILs than JHE with no significant difference in coverage for these low heterogeneity scenarios. With the smallest sample size (scenario A), RMSE was largest for JHE and smallest for the BIC model-averaged BBE. With the largest sample size (scenario F), RMSE

Table 1.6: Average percent confidence interval coverage, percent confidence interval length (% CIL), and Bias/SE of abundance estimates for BOWE, JHE, AIC_c model-averaged (modAIC) LNE and BBE, and BIC model-averaged (modBIC) LNE and BBE across six simulated scenarios with $t = 2$ primary sampling occasions.

Estimator	% Coverage		% CIL		Bias/SE	
	Est.	SE	Est.	SE	Est.	SE
modAIC BBE	94.4	0.21	47.5	0.24	0.07	0.02
modBIC BBE	92.6	0.24	45.0	0.21	0.07	0.04
BOWE	94.5	0.21	50.1	0.23	-0.01	0.01
JHE	89.8	0.27	43.7	0.26	0.13	0.03
modAIC LNE	93.7	0.22	47.1	0.25	0.07	0.02
modBIC LNE	92.0	0.25	43.8	0.21	0.06	0.04

was largest for BOWE and smallest for the BIC model-averaged BBE. For the other scenarios, RMSE was generally largest for BOWE or BBE and smallest for JHE. Although average performance across all scenarios was very similar for LNE and BBE, LNE tended to be more efficient than BBE in scenarios with low levels of heterogeneity and BBE tended to be slightly more efficient when $\bar{p} = \text{Low}$.

1.5 Discussion

With $t = 1$, little difference was observed in LNE performance when using AIC_c or BIC for model-averaged inference. When the number of occasions, marked individuals, and resighting probabilities were all at the lowest levels (scenario A), BOWE did perform better than the maximum likelihood models. A non-parametric model such as BOWE (whose properties are not based on asymptotic theory) may be a less biased approach with such small sample sizes, but precision is so poor that none of the estimators are particularly useful for inferences. With sample sizes suitable for

producing useful levels of precision, LNE was generally a more precise estimator with no significant loss in coverage. Its higher efficiency compared to BBE and BOWE is attributable to LNE's ability to invest in estimating heterogeneity parameters as deemed necessary by the data. With low levels of heterogeneity, LNE had similar coverage and precision to JHE.

With $t = 2$, the advantages of combining data in a robust sampling design were apparent in the increased precision of LNE and BBE. In the few scenarios with low levels of individual heterogeneity, LNE appeared to be more efficient than the other estimators, but not enough scenarios of this type were examined to detect a significant difference. However, based on these results and those from the simulations with 1 primary occasion, I expect that unlike BBE, the model-averaged LNE will be as or more efficient than JHE when heterogeneity levels are low. I also expect these advantages of LNE over the other estimators to be more pronounced with > 2 primary sampling occasions.

Although little difference was found in the use of AIC_c versus BIC with 1 primary occasion, I found a slight advantage in the use of AIC_c in some cases with 2 primary sampling occasions. The tendency of BIC to select less complicated models with small to moderate sample sizes (Burnham and Anderson, 2004; Link and Barker, 2006) was somewhat of a disadvantage in terms of coverage when the population mean resighting probabilities were different. Abundance estimates are particularly sensitive to biases in mean resighting probability estimators, and BIC's greater tendency to "split the difference" in estimating fewer parameters can result in underestimation of N in one primary occasion and overestimation in the other.

I am not suggesting that AIC_c is not susceptible to similar problems with small marked sample sizes, but it did appear to alleviate them more than BIC. For example, in scenario D the “true” generating model had different values for all of the resighting probability input parameters, and all of the estimators failed to achieve nominal coverage in estimating N_2 . As evidence of the criterion “splitting the difference,” Bias/SE for the LNE model-averaged estimates of N_1 and N_2 were 0.35 and -0.26 for BIC, but were 0.11 and 0.02 for AIC_c , respectively. For BBE, these were 0.43 and -0.18 for BIC and 0.21 and 0.00 for AIC_c , respectively. Although coverage was close to nominal for N_1 , coverage for N_2 using the BIC model-averaged approach was significantly lower than its AIC_c counterpart, and the problem appeared more severe for BBE than for LNE. However, this was not an appreciable problem for either approach in simulations with different population mean resighting probabilities and larger sample sizes, such as scenarios B and E. Because the estimation of resighting probability parameters is so critical to estimates of N , I advise against the use of BIC model averaging under sampling conditions similar to those simulated in scenario D. I recommend as a general guideline that researchers carefully compare the estimates obtained via model averaging to those from the most general model where all parameters are estimated independently. If the parameter estimates (particularly N) are quite different, a moderately conservative approach would be to use AIC_c model averaging for inferences. The most conservative approach would be to use the general model. As indicated by the simulations with 1 primary occasion, the use of the most general LNE will typically still be more efficient than BBE and BOWE. When compared with the BIC model-averaged results for scenario D, aver-

age performances were better with the most general LNE and BBE models. Bias/SE for N_1 and N_2 were 0.02 and 0.10 for LNE, and 0.02 and 0.12 for BBE, respectively. Coverage of N_2 was 90.9% (SE = 0.91) and 90.7% (SE = 0.92) with % CILs of 57.8 (SE = 0.69) and 58.0 (SE = 0.68) for LNE and BBE, respectively. Similar to the AIC_c model-averaged results, these coverages were not statistically different from BOWE. Despite being slightly larger than when using AIC_c model averaging, % CILs for the general models were still significantly smaller than BOWE. Although I found it to be a problem with 2 primary occasions, I expect this small sample issue for BIC to be less of a concern in longer-term monitoring studies with > 2 primary occasions.

1.6 Conclusions

In terms of efficiency, I found LNE to be equivalent to or better than the other available mark-resight abundance estimators (with no appreciable loss in coverage) regardless of the sampling conditions. LNE provides researchers a more efficient alternative to JHE capable of incorporating a robust sampling design when individually identifiable marks are not feasible. LNE is more efficient than BOWE or BBE and equivalent to JHE when observed heterogeneity levels are low because it may ignore this variability as deemed appropriate by the data. When heterogeneity levels are high, LNE is more efficient than BOWE and equivalent to BBE because it may incorporate a robust sampling design. When sampling is without replacement, its flexible modeling framework provides quantitative justification for model selection

based on the data, thereby eliminating the need to determine which of JHE, BOWE, or BBE is most appropriate based on educated guesswork. Overlooking philosophical issues, I did identify some potential advantages and disadvantages of using AIC_c or BIC for these models, but little difference in inferences can generally be expected between the two approaches when using model averaging. Although computationally more complicated than the other estimators, I believe the increased complexity that comes with the generalized modeling framework of LNE is justified by its increased efficiency and rigorously defensible means of mark-resight model selection. While not investigated here, the ability of LNE to incorporate environmental or individual covariates in modeling resighting probabilities may further increase its efficiency. However, when sampling must be with replacement, BOWE is still the only reliable option available for these studies. A flexible structure similar to LNE allowing sampling with replacement is still desirable, and I develop such a model in Chapter 2.

Chapter 2

Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown

2.1 Introduction

The mark-resight method for estimating closed population abundance (N) has recently received considerable attention (Bowden and Kufeld, 1995; Miller et al., 1997; White and Shenk, 2001; McClintock et al., 2006; Magle et al., 2007). Compared to traditional mark-recapture (Otis et al., 1978; McClintock and White, 2007), mark-resight can often be a less expensive and less invasive alternative (Minta and Mangel, 1989). The primary advantage of these methods is that animals only need to

be physically captured and marked once, and subsequent data from both marked and unmarked individuals are used for estimating N . This can be appealing to researchers because funds are often limited and capture is generally the most expensive aspect of these studies. Not only can the financial cost of mark-recapture be daunting for long-term population monitoring, but capture is also the most hazardous aspect for the animals. Mark-resight can substantially reduce stress to species because they can be observed at a distance with minimal disturbance after the initial capture. This is of particular importance when working with threatened, endangered, or exceptionally sensitive species.

Despite the possible advantages, one major drawback of mark-resight methods is that the number of marked individuals available for resighting usually needs to be known exactly. This can be difficult to accomplish. It is often believed to be reasonably achieved by capturing and marking individuals immediately prior to resightings and assuming closure between capture and the completion of resighting occasions. When the interval between marking and resighting is of long enough duration for closure to be violated, a more rigorous method of determining the number of marked individuals in the population is through the use of radio-collars equipped with mortality signals (Miller et al., 1997; McClintock and White, 2007). However, many smaller species cannot be fit with these devices, and even if the species is of adequate size, the cost can be prohibitive within the limited budgets typically found in wildlife studies. Even when fit with radio-collars, the battery life of these devices is often limited. This often results in field-readable marks still being present in the population, but without the ability to confirm the exact number of marked

individuals, the interval for application of these methods is essentially restricted to the life-expectancy of the radios. By modifying the Minta-Mangel estimator (Minta and Mangel, 1989), Arnason et al. (1991) developed a mark-resight model for when the number of marked individuals is unknown (ARNE). However, the model has found little application (Casagrande and Beissinger, 1997; Loison et al., 2002) because of several key limitations. These include certain sample size requirements, the assumption of equal and independent sightabilities of individuals, the necessity of 100% marked individual identification, and the inability to combine data across multiple closed sampling periods for more efficient parameter estimation. McClintock et al. (2006) and Magle et al. (2007) demonstrated problems associated with these limitations in other estimators (also see Chapter 1). White (1993) found the performance of the Minta-Mangel estimator to be inadequate in simulation experiments, and I therefore suspect this also applies to ARNE.

Another drawback of most mark-resight estimators is that sampling must be without replacement within distinct resighting surveys that comprise the closed sampling interval of interest (see Chapter 1). Adopting the terminology of the robust sampling design (Kendall et al., 1995), this requires that every individual in the population be sighted at most once within each of the secondary sampling occasions of the closed primary interval(s). In many circumstances, secondary sampling must be with replacement and necessitates the use of Bowden's estimator (BOWE) (Bowden and Kufeld, 1995), the Minta-Mangel estimator, or ARNE. These situations arise when closed primary sampling intervals cannot be divided into distinct secondary occasions where individuals can only be sighted once, such as when studying a highly

mobile species or using camera traps. Although BOWE is a consistent estimator when sampling is with replacement, it is particularly inefficient for long-term monitoring because each N must be estimated independently, i.e., information cannot be borrowed or smoothed across multiple primary sampling occasions.

When sampling is without replacement, I found advantages in the use of the logit-normal mixed effects model (LNE) when compared to the Joint Hypergeometric estimator (Bartmann et al., 1987), BOWE, and the Beta-Binomial estimator (McClintock et al., 2006) by allowing more efficient parameter estimation when combining data across multiple primary sampling occasions (see Chapter 1). Here I develop a model analogous to LNE when sampling is with replacement, the Poisson-log normal mixed effects model (PNE). But unlike LNE, PNE may be modified for when the number of marked individuals is not known exactly, and it therefore addresses two key limitations of other mark-resight estimators. After I introduce the model in the next section, I demonstrate its use on black-tailed prairie dog (*Cynomys ludovicianus*) colonies of north-central Colorado in Section 2.3. In Section 2.4, I report on simulation experiments evaluating the relative performance of the model compared to other estimators. In Section 2.5, I summarize my findings in terms of their implications for abundance estimation in mark-resight studies.

2.2 The Model

The Poisson-log normal mixed effects mark-resight model (PNE) has the same assumptions as BOWE, but data may be combined across t primary sampling occa-

sions in a robust sampling design (Kendall et al., 1995). These assumptions are: 1) geographic and demographic closure during secondary sampling within primary intervals; 2) no loss of marks within each primary interval; 3) no errors in distinguishing marked and unmarked animals; and 4) independently and identically distributed (iid) resighting probabilities for marked and unmarked animals. Marks must be individually identifiable and field-readable. Because marks must be individually identifiable, overdispersion due to resighting rate heterogeneity or lack of independence (e.g., clustering) may be accounted for. The number of marked individuals in the population during sampling may be known exactly or unknown. Given that an individual is identified as marked, PNE may incorporate less than 100% marked individual identification by assuming such events occur randomly within the marked population.

I will first assume a known number of individuals ($n_j, j = \{1, \dots, t\}$) are individually marked with field-readable marks and available for resighting at least once during the j th interval of interest. Resighting data are then collected during t primary intervals, each of which is of short enough duration for the assumption of demographic and geographic closure to be satisfied. The resighting data consist of the total number of sightings for marked individual s within interval j ($y_{sj} = \{0, 1, 2, \dots\}, s = \{1, \dots, n_j\}$) and the total number of unmarked sightings during each interval (T_{u_j}). Because PNE does not condition on distinct secondary resighting occasions within the t closed intervals, sampling may occur with or without replacement within secondary occasions. With some similarity to the approach of Rivest and Daigle (2004) for the traditional mark-recapture robust design, the y_{sj}

are modeled as realizations of independent Poisson-log normal random variables, where (on the log scale) the j th mean resighting rate is treated as a fixed effect (θ_j) and individual heterogeneity (a source of overdispersion) as a random effect with mean zero and unknown variance σ_j^2 . The y_{sj} have conditional expectation

$$E(y_{sj} | \sigma_j, Z_{sj}, \theta_j) = \lambda_{sj} = \exp(\sigma_j Z_{sj} + \theta_j),$$

where $Z_{sj} \stackrel{\text{iid}}{\sim} N(0, 1)$. Therefore, any randomly selected individual s from sampling occasion j with latent sightability Z_{sj} has resighting rate with marginal expectation

$$E_{Z_{sj}}(y_{sj}) = \lambda_{j|s} = \int \exp(\sigma_j z_{sj} + \theta_j) \phi(z_{sj}) dz_{sj} = \exp\left(\frac{\sigma_j^2}{2} + \theta_j\right),$$

where $\phi(z_{sj})$ is the standard normal density. I stress that the primary intervals need not be independent with respect to parameters, but they are independent with respect to data. The l primary intervals may therefore be treated as groups if they do not pertain to sequential periods in time (as shown in Section 2.3). Under this generalized framework, resighting rates may be modeled with no time (or group) and no heterogeneity effects between sampling occasions ($\theta_j = \theta$, $\sigma_j = 0$), only time effects, only heterogeneity effects, or additive time and heterogeneity effects. For increased efficiency, these parameters may also be modeled with fixed environmental or individual covariates believed to affect the resighting process, as is demonstrated in Section 2.3. By taking the product across the n_j marked individuals, an uncon-

ditional likelihood function for θ_j and σ_j is

$$L(\sigma_j, \theta_j | y_{sj}, n_j) = \prod_{s=1}^{n_j} \int \frac{\lambda_{sj}^{y_{sj}} \exp(-\lambda_{sj})}{y_{sj}!} \phi(z_{sj}) dz_{sj}. \quad (2.1)$$

For the sake of generality (and at the expense of some additional complexity), I chose to use this formulation instead of the more standard negative binomial model. Under this framework, covariates describing θ and σ may be modeled in a relatively meaningful and intuitive manner. Further, because there is often no detectable individual heterogeneity in mark-resight data, my formulation allows this additional source of variation to be ignored ($\sigma = 0$) for increased efficiency. Similar to the Beta-Binomial estimator (McClintock et al., 2006), using the negative binomial would require that individual heterogeneity always be included in the model, and the incorporation of covariates would not be nearly as straight-forward.

In deriving a joint likelihood that included N , McClintock et al. (2006) assumed $T_{u_j} \stackrel{\text{ind}}{\sim} N[\mathbb{E}(T_{u_j}), \text{var}(T_{u_j})]$ and found this approximation useful (also see Chapter 1). However, because $T_{u_j} \geq 0$, I chose to modify this approximation to a more realistic $T_{u_j} \stackrel{\text{ind}}{\sim} \text{LTN}[\mathbb{E}(T_{u_j}), \text{var}(T_{u_j})]$, where T_{u_j} is left-truncated at zero. The approximate likelihood function for N_j is then:

$$L(N_j | \sigma_j, \theta_j, n_j, T_{u_j}) = \frac{f(T_{u_j})}{\int_0^{\infty} f(T_{u_j}) dT_{u_j}}. \quad (2.2)$$

where $f(T_{u_j})$ is the normal density function with expectation

$$E(T_{u_j}) = (N_j - n_j) \left[\exp\left(\frac{\sigma_j^2}{2} + \theta_j\right) + \frac{\epsilon_j}{n_j} \right] \quad (2.3)$$

and variance

$$\text{var}(T_{u_j}) = (N_j - n_j) \left\{ \exp\left(\frac{\sigma_j^2}{2} + \theta_j\right) + \exp(2\theta_j) [\exp(2\sigma_j^2) - \exp(\sigma_j^2)] + \frac{\epsilon_j}{n_j} \right\} \quad (2.4)$$

where ϵ_j is the total number of marked individuals that were identified as marked, but not identified to individual identity during primary interval j . The derivations of the unconditional (on Z_{sj}) $E(T_{u_j})$ and $\text{var}(T_{u_j})$ formulac for this general case may be found in Appendix B (for the less general case with no individual heterogeneity, $\sigma_j = 0$). Combining (2.1) and (2.2) across the t primary sampling occasions gives the PNE likelihood of the general form:

$$L(\mathbf{N}, \boldsymbol{\sigma}, \boldsymbol{\beta} \mid \mathbf{y}, \mathbf{n}, \mathbf{T}_u) = \prod_{j=1}^t \left[\prod_{s=1}^{n_j} \int \frac{\lambda_{sj}^{y_{sj}} \exp(-\lambda_{sj})}{y_{sj}!} \phi(z_{sj}) dz_{sj} \right] \times \prod_{j=1}^t \frac{f(T_{u_j})}{\int_0^\infty f(T_{u_j}) dT_{u_j}}. \quad (2.5)$$

If n_j is unknown for any interval j , then only marked individuals sighted and individually identified at least once are known to be in the population during this interval, and $y_{sj} = 0$ is no longer observable. In this event, (2.5) may be modified by replacing the contribution of any intervals where n_j is unknown with the zero-truncated PNE (ZPNE). This requires modifying (2.1) to account for the fact that

$y_{sj} = 0$ is no longer observable:

$$L(\sigma_j, \theta_j \mid y_{sj}, n_j^*) = \prod_{s=1}^{n_j^*} \int \frac{\lambda_{sj}^{y_{sj}} \exp(-\lambda_{sj})}{y_{sj}! [1 - \exp(-\lambda_{sj})]} \phi(z_{sj}) dz_{sj}. \quad (2.6)$$

where $y_{sj} = \{1, 2, \dots\}$, n_j^* is the number of marked individuals sighted at least once during interval j , and $1 - \exp(-\lambda_{sj})$ is the probability of being sighted at least once during interval j . Equations (2.3) and (2.4) are then modified by replacing n_j with $n_j^*/[1 - \exp(-\lambda_{j|s})]$.

Point and variance estimates for (Z)PNE may be obtained using maximum likelihood or Bayesian analysis methods. Because the integrals appearing in the likelihoods do not have closed form solutions, they must be computed numerically when using maximum likelihood. The Poisson integrals in (2.1) and (2.6) can be approximated using Gaussian-Hermite quadrature (Givens and Hoeting, 2005), whereby integrals of the form $\int_{-\infty}^{\infty} e^{-v^2} h(v) dv$ may be approximated by $\sum_{m=1}^M w_m h(v_m)$, where M is the number of quadrature points, and (v_m, w_m) are the evaluation nodes and weights corresponding to M . For the Poisson integrals in (2.1),

$$h(v_m) = \frac{\exp(\sqrt{2}\sigma_j v_m + \theta_j)^{y_{sj}} \exp[-\exp(\sqrt{2}\sigma_j v_m + \theta_j)]}{y_{sj}! \sqrt{\pi}}.$$

For the zero-truncated Poisson integrals in (2.6),

$$h(v_m) = \frac{\exp(\sqrt{2}\sigma_j v_m + \theta_j)^{y_{sj}} \exp[-\exp(\sqrt{2}\sigma_j v_m + \theta_j)]}{y_{sj}! \sqrt{\pi} \{1 - \exp[\exp(\sqrt{2}\sigma_j v_m + \theta_j)]\}}.$$

Tables of (v_m, w_m) pairs for ascending values of M are available in texts on numerical

integration (Stroud and Secrest, 1966) or in readily available statistical computing software such as R (Smyth, 2006). The integral for left-truncation of the normal distribution in (2.2) is equal to $1 - \Phi_{T_{u_j}}(0)$, where $\Phi_{T_{u_j}}(0)$ is the normal cumulative distribution function of T_{u_j} evaluated at zero.

2.3 Example: Black-tailed Prairie Dog

2.3.1 Example Methods

As part of the Colorado State University Plague Project (Antolin et al., 2006), mark-resight surveys were conducted on $t = 8$ black-tailed prairie dog (*Cynomys ludovicianus*) colonies in the Pawnee National Grassland of north-central Colorado, USA (40°35'N, 104°45'W). Four colonies (Towns 76a, 82, 83, and 84) in July – September 2005 and four colonies (Towns 70, 76b, 81, and 88) in July – August 2006 were investigated. The colonies ranged in size from 71 acres (Town 76a) to 463 acres (Town 81). Immediately prior to resighting surveys, traps were set at the nearest burrow entrance to randomly selected points within the range of each colony. Captured dogs were fur-dyed on both sides of the midsagittal plane with a unique two-character mark consisting of letters, numbers, and symbols. To aid in the rapid identification of marked versus unmarked animals when only the head was initially visible, a dye “helmet” was also applied to marked individuals. The marking periods generally lasted one week, and 10 – 12 secondary resighting occasions were completed in 1 – 2 weeks on each colony. Resighting surveys were conducted

from stations covering as much of the colony area as possible with the aid of 20x – 60x spotting scopes. Two observers were assigned to each station, with a primary observer tallying marked and unmarked dogs and a secondary observer recording and aiding in individual identification of marked dogs detected by the primary observer. The number of stations required to survey an entire colony ranged from two for the smaller colonies to seven for the larger. The populations were assumed closed during the marking and resighting period. Although the resighting surveys were designed in an attempt to achieve sampling without replacement, on several secondary occasions a marked individual was recorded twice and suggests that, although minimal, sampling of the unmarked individuals was also likely to have been with replacement.

For my maximum likelihood analysis of the combined data from the $t = 8$ colonies using PNE, I evaluated a set of candidate models using both Akaike’s Information Criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson, 2002) and the Bayesian Information Criterion (BIC) (Schwarz, 1978). The effective sample size for AIC_c and BIC calculation was defined as $n = \sum_{j=1}^t n_j + t$. Parameterizations for mean resighting rate θ_j and individual heterogeneity σ_j included constancy across all colonies [represented as $\theta(\cdot)$ and $\sigma(\cdot)$] and complete independence between the eight colonies [$\theta(t)$ and $\sigma(t)$]. By fixing $\sigma_j = 0$, individual heterogeneity may also be ignored [$\sigma(0)$]. Estimating separate N_j for the eight colonies, all combinations of these parameterizations yielded six models, ranging from the simplest 9-parameter model, $\{\theta(\cdot)\sigma(0)N(t)\}$, with colony-constant mean resighting rates and no individual heterogeneity, to the 24-parameter model, $\{\theta(t)\sigma(t)N(t)\}$,

with completely independent mean resighting rates and individual heterogeneity levels for each colony. I also investigated more parsimonious parameterizations for θ_j and σ_j using environmental covariates measured during the surveys. These were modeled as $\theta = \mathbf{X}\boldsymbol{\alpha}$ and $\log(\sigma_j) = \mathbf{z}_j\boldsymbol{\beta}$, where \mathbf{X} is a $t \times (p + 1)$ matrix composed of p covariates (plus an intercept term), $\boldsymbol{\alpha} = (\alpha_0, \alpha_1, \dots, \alpha_p)$ is a $(p + 1) \times 1$ vector of unobservable coefficients corresponding to \mathbf{X} , \mathbf{z}_j is the j th row of a $t \times (q + 1)$ matrix \mathbf{Z} composed of q covariates, and $\boldsymbol{\beta} = (\beta_0, \beta_1, \dots, \beta_q)$ is a $(q + 1) \times 1$ vector of unobservable coefficients corresponding to \mathbf{z}_j . The colony-specific covariates that were measured included area in acres $\times 10^{-2}$ (a), average temperature across surveys (tp), average wind speed across surveys (w), average percent cloud cover across surveys (cl), average prior 24-hour precipitation across surveys (pc), average start time of surveys (s), average length of surveys (tm), and the number of stations required for each colony (st). Other covariates included a linear time trend within years (tr) and dummy variables for year (yr), the presence of cattle during surveys (cw), the presence of predators during surveys (pd), non-research-related human disturbances during surveys (ot), and several colonies (Towns 70, 76a, and 83) identified *a priori* as particularly difficult to survey (df). Maximum likelihood point and variance estimates for $R = 169$ models were obtained using the NLMIXED procedure in SAS 9.1 for Windows (SAS Institute, 2002), and the integrals in (2.5) were programmed within the NLMIXED procedure using the Gaussian quadrature formulae in Section 2.2 with $M = 10$. I calculated model-averaged \hat{N}_j and unconditional variances based on AIC_c and BIC weights of the $R = 169$ models and compared these to estimates from BOWE. Confidence intervals for PNE model-averaged estimates were calcu-

lated as 95% logarithm-transformed normal. Confidence intervals for BOWE were calculated as in Bowden and Kufeld (1995).

I also performed an identical maximum likelihood analysis with ZPNE. Here, I no longer assumed the numbers of marked individuals were known and accordingly zero-truncated the marked individual resighting data. For model selection criteria, the effective sample size for ZPNE was defined as $n = \sum_{j=1}^t n_j^* + t$. Because the data contained considerable numbers of marked individuals resighted but not identified to individual (ϵ_j), I did not believe it reasonable to analyze these data with ARNE for comparative purposes. To incorporate these into the modeling framework of ARNE (thereby preventing overestimation of N_j), one must assume that all ϵ_j were from marked individuals positively identified at least once. Given the relatively large numbers of marked individuals sighted zero times, I did not believe this to be a reasonable assumption.

2.3.2 Example Results

Although not verified by radio-telemetry, the presumed known numbers of individuals captured, marked, and available during resighting surveys were $n_{76a} = 80$, $n_{82} = 66$, $n_{83} = 45$, and $n_{84} = 59$ in 2005, and $n_{70} = 66$, $n_{70b} = 85$, $n_{81} = 82$, and $n_{88} = 53$ in 2006. Mean numbers of marked individual resightings across all secondary occasions were $\bar{y}_{76a} = 2.2$ (SE = 0.3), $\bar{y}_{82} = 3.3$ (SE = 0.3), $\bar{y}_{83} = 3.0$ (SE = 0.3), and $\bar{y}_{84} = 5.2$ (SE = 0.4) in 2005, and $\bar{y}_{70} = 2.7$ (SE = 0.3), $\bar{y}_{76b} = 3.5$ (SE = 0.3), $\bar{y}_{81} = 4.5$ (SE = 0.3), and $\bar{y}_{88} = 6.8$ (SE = 0.4) in 2006. Total numbers of unmarked individual

sightings were $T_{u,76a} = 1764$, $T_{u,82} = 5553$, $T_{u,83} = 6543$, and $T_{u,84} = 4757$ in 2005, and $T_{u,70} = 2820$, $T_{u,76b} = 3150$, $T_{u,81} = 6306$, and $T_{u,88} = 2184$ in 2006. Numbers of resightings that were identified as marked but not to individual were $\epsilon_{76a} = 34$, $\epsilon_{82} = 9$, $\epsilon_{83} = 6$, and $\epsilon_{84} = 1$ in 2005, and $\epsilon_{70} = 24$, $\epsilon_{76b} = 19$, $\epsilon_{81} = 13$, and $\epsilon_{88} = 2$ in 2006.

With 9% of the model weight, the minimum-AIC_c model, $\{\theta(w + pc + a + cw)\sigma(w + pc + a)N(t)\}$, had 17 estimated parameters (Table 2.1). For the mean resighting rate θ , this model contained a negative wind effect ($\hat{\alpha}_w = -1.13$, SE = 0.14), a positive 24-hour precipitation effect ($\hat{\alpha}_{pc} = 0.20$, SE = 0.02), a positive area effect ($\hat{\alpha}_a = 0.13$, SE = 0.03), and a positive cattle effect ($\hat{\alpha}_{cw} = 0.22$, SE = 0.12). For individual heterogeneity σ (on the log scale), the model estimated a positive wind effect ($\hat{\beta}_w = 0.73$, SE = 0.28), a negative 24-hour precipitation effect ($\hat{\beta}_{pc} = -0.24$, SE = 0.09), and a negative area effect ($\hat{\beta}_a = -0.12$, SE = 0.08). With 40% of the model weight, the minimum-BIC model was the 16-parameter model $\{\theta(w + pc + a)\sigma(w + pc + a)N(t)\}$ (Table 2.1). For θ , the model included a negative wind effect ($\hat{\alpha}_w = -0.99$, SE = 0.12), a positive 24-hour precipitation effect ($\hat{\alpha}_{pc} = 0.19$, SE = 0.02), and a positive area effect ($\hat{\alpha}_a = 0.10$, SE = 0.02). For σ , the model contained a positive wind effect ($\hat{\beta}_w = 0.72$, SE = 0.27), a negative 24-hour precipitation effect ($\hat{\beta}_{pc} = -0.25$, SE = 0.10), and a negative area effect ($\hat{\beta}_a = -0.13$, SE = 0.08). Because of the high degree of model selection uncertainty (Table 2.1), selecting only the minimum-AIC_c or -BIC model for inference on N_j is difficult to justify. Point estimates for N_j varied between the AIC_c model-averaged PNE, the BIC model-averaged PNE, and BOWE, but they were not significantly

Table 2.1: AIC_c and BIC weights for selected PNE models of black-tailed prairie dog abundance (N) for $t = 8$ colonies in north-central Colorado. Covariates include colony area (a), presence of cattle (cw), difficult colony (df), other disturbances (ot), 24-hour precipitation (pc), presence of predators (pd), start time of surveys (s), length of surveys (tm), temperature (tp), time trend (tr), and wind (w). Model specific covariates were included for both mean resighting rate and individual heterogeneity (\bullet), mean resighting rate only (θ), or individual heterogeneity only (σ). All models include separate N estimates for the eight colonies. The number of estimated parameters (K) includes N and intercept terms for both θ and σ .

Model														AIC _c		K		Model														BIC		K	
a	cw	df	ot	pc	pd	tm	tp	tr	w	Weight	K	a	s	cw	df	ot	pc	pd	tp	w	Weight	K	a	cw	df	ot	pc	pd	tp	w	Weight	K			
\bullet	θ			\bullet					\bullet	0.09	17	\bullet					\bullet					0.40	16	\bullet							\bullet	0.40	16		
\bullet		θ		\bullet					\bullet	0.07	17	\bullet		θ			\bullet					0.08	17	\bullet							\bullet	0.08	17		
\bullet				\bullet			θ		\bullet	0.06	17	\bullet			θ		\bullet					0.07	17	\bullet							\bullet	0.07	17		
\bullet				\bullet					\bullet	0.05	16	\bullet					\bullet		θ			0.05	17	\bullet							\bullet	0.05	17		
θ			σ	\bullet					θ	0.04	17	θ		θ	σ		\bullet					0.05	16	θ							θ	0.05	16		
\bullet	θ			\bullet				σ	\bullet	0.03	18				\bullet		\bullet					0.05	15	θ							θ	0.05	15		
\bullet	θ		σ	\bullet					\bullet	0.03	18	θ			\bullet	σ	\bullet					0.04	17	θ							θ	0.04	17		
\bullet				\bullet					\bullet	0.03	18	θ			\bullet		\bullet					0.03	16	θ							θ	0.03	16		
θ	θ	σ		\bullet				θ	θ	0.03	17	θ		θ	σ		\bullet					0.02	17	θ							θ	0.02	17		
\bullet				\bullet					\bullet	0.03	17	\bullet		σ			\bullet					0.02	17	\bullet							\bullet	0.02	17		
\bullet	σ			\bullet					\bullet	0.03	18	\bullet			σ		\bullet					0.02	17	\bullet							\bullet	0.02	17		
\bullet				\bullet					\bullet	0.02	18	\bullet					\bullet					0.02	17	\bullet							\bullet	0.02	17		
\bullet				\bullet					\bullet	0.02	18	σ					\bullet					0.02	17	\bullet							\bullet	0.02	17		
\bullet			σ	\bullet					\bullet	0.02	18	σ					\bullet		θ			0.02	17	\bullet							θ	0.02	16		
σ				\bullet					\bullet	0.02	18	θ			\bullet		\bullet					0.01	17	\bullet							σ	0.01	17		
\bullet				\bullet					\bullet	0.02	17	\bullet				σ	\bullet					0.01	16	θ							θ	0.01	16		
θ	σ	\bullet		\bullet					\bullet	0.02	18	θ		σ			θ					0.01	17	θ							\bullet	0.01	17		
σ				\bullet					\bullet	0.02	17	θ			σ		θ					0.00	17	θ							\bullet	0.00	17		

different (Table 2.2). Across all eight colonies, average coefficients of variation were 7.0% for the BIC model-averaged PNE, 7.0% for the AIC_c model-averaged PNE, and 8.0% for BOWE. As a proportion of the point estimates, average confidence interval lengths were 26.5% for the BIC model-averaged PNE, 26.6% for the AIC_c model-averaged PNE, and 32.6% for BOWE. Compared to those of BOWE, PNE percent confidence intervals lengths were smaller for all \hat{N}_j except \hat{N}_{81} .

After zero-truncating the data, the numbers of marked individuals resighted at least once were $n_{76a}^* = 57$, $n_{82}^* = 55$, $n_{83}^* = 39$, and $n_{84}^* = 55$ in 2005, and $n_{70}^* = 56$, $n_{76b}^* = 70$, $n_{81}^* = 75$, and $n_{88}^* = 53$ in 2006. Mean numbers of marked individual resightings across all secondary occasions were $\bar{y}_{76a}^* = 3.1$ (SE = 0.3), $\bar{y}_{82}^* = 3.9$ (SE = 0.3), $\bar{y}_{83}^* = 3.4$ (SE = 0.3), and $\bar{y}_{84}^* = 5.6$ (SE = 0.4) in 2005, and $\bar{y}_{70}^* = 3.2$ (SE = 0.3), $\bar{y}_{76b}^* = 4.2$ (SE = 0.3), $\bar{y}_{81}^* = 4.9$ (SE = 0.3), and $\bar{y}_{88}^* = 6.8$ (SE = 0.4) in 2006. With 11% of the model weight, the minimum- AIC_c model was the 16-parameter $\{\theta(w + pc + s + df)\sigma(pc + df)N(t)\}$ (Table 2.3). For θ , the model included a negative wind effect ($\hat{\alpha}_w = -0.43$, SE = 0.11), a positive 24-hour precipitation effect ($\hat{\alpha}_{pc} = 0.10$, SE = 0.01), a negative start time effect ($\hat{\alpha}_s = -4.60$, SE = 2.85), and a negative difficult-colony effect ($\hat{\alpha}_{df} = -0.46$, SE = 0.12). For σ , there was a negative 24-hour precipitation effect ($\hat{\beta}_{pc} = -0.13$, SE = 0.24) and a positive difficult-colony effect ($\hat{\beta}_{df} = 0.89$, SE = 0.33). With 19% of the model weight, the minimum-BIC model was the 13-parameter $\{\theta(w + pc + df)\sigma(.)N(t)\}$ (Table 2.3). For θ , the model contained a negative wind effect ($\hat{\alpha}_w = -0.46$, SE = 0.11), a positive 24-hour precipitation effect ($\hat{\alpha}_{pc} = 0.09$, SE = 0.02), and a negative difficult-colony effect ($\hat{\alpha}_{df} = -0.23$, SE = 0.08). On the positive real scale, the estimated colony-

Table 2.2: Comparisons of abundance (N) estimates, percent coefficients of variation (% CV), 95% confidence intervals, and percent confidence interval lengths (% CIL) for $t = 8$ black-tailed prairie dog colonies in north-central Colorado from the AIC_c model-averaged PNE (modAIC), BIC model-averaged PNE (modBIC), and Bowden's estimator (BOWE). Models are ordered from smallest to largest by average % CV and % CIL across all colonies.

Model	Parameter	Estimate	% CV	95% CI		% CIL
				Lower	Upper	
PNE modBIC	N_{76a}	707.1	8.7	601.6	833.9	32.9
	N_{82}	1698.9	6.4	1506.1	1917.5	24.2
	N_{83}	2131.4	7.4	1853.0	2452.7	28.1
	N_{84}	951.3	7.3	829.0	1093.2	27.8
	N_{70}	923.6	6.9	811.3	1052.9	26.2
	N_{76b}	991.7	7.1	868.0	1134.9	26.9
	N_{81}	1470.2	6.8	1292.9	1673.4	25.9
	N_{88}	370.7	5.3	335.2	410.7	20.4
PNE modAIC	N_{76a}	699.5	9.1	591.9	829.6	34.0
	N_{82}	1715.2	6.7	1511.9	1947.2	25.4
	N_{83}	2176.5	7.6	1887.0	2511.4	28.7
	N_{84}	959.5	7.2	838.6	1099.1	27.2
	N_{70}	951.1	7.1	832.2	1088.6	27.0
	N_{76b}	966.6	7.1	846.0	1106.2	26.9
	N_{81}	1451.5	6.2	1291.2	1633.1	23.6
	N_{88}	370.5	5.3	335.2	410.2	20.2
BOWE	N_{76a}	740.3	10.6	597.6	917.0	43.1
	N_{82}	1690.9	8.1	1436.2	1990.7	32.8
	N_{83}	2137.3	10.9	1712.1	2668.2	44.7
	N_{84}	965.7	6.8	841.6	1108.1	27.6
	N_{70}	965.3	9.4	799.3	1165.7	38.0
	N_{76b}	929.6	7.6	798.4	1082.3	30.5
	N_{81}	1441.4	5.9	1282.1	1620.4	23.5
	N_{88}	370.0	5.1	334.0	409.9	20.5

Table 2.3: AIC_c and BIC weights for selected ZPNE models of black-tailed prairie dog abundance (N) for $t = 8$ colonies in north-central Colorado. Covariates include colony area (a), presence of cattle (cw), difficult colony (df), other disturbances (ot), 24-hour precipitation (pc), presence of predators (pd), start time of surveys (s), temperature (tp), wind (w), and a single intercept for all eight colonies (.). Model specific covariates were included for both mean resighting rate and individual heterogeneity (\bullet), mean resighting rate only (θ), or individual heterogeneity only (σ). All models include separate N estimates for the eight colonies. The number of estimated parameters (K) includes N and intercept terms for both θ and σ .

Model													Model																
AIC _c						K						AIC _c						K											
a	s	cw	df	ot	pc	pd	tp	w	Weight	a	s	cw	df	ot	pc	pd	tp	w	Weight	a	s	cw	df	ot	pc	pd	tp	w	Weight
θ			\bullet		\bullet			θ	0.11	16		θ		θ				θ	0.19	13								θ	σ
θ		θ	σ	\bullet	\bullet			θ	0.07	16		\bullet		\bullet				θ	0.18	15							θ	σ	
θ		σ	\bullet		θ			\bullet	0.07	17		θ		θ				θ	0.1	14							θ	σ	
θ			\bullet		\bullet			θ	0.06	17		θ		\bullet				θ	0.08	16							θ	σ	
θ		\bullet	σ	θ	θ			\bullet	0.04	17		θ		θ			θ	θ	0.07	14							θ	σ	
θ		θ	\bullet		\bullet			θ	0.04	17		θ		θ				θ	0.06	14							θ	σ	
θ		σ	\bullet		θ			\bullet	0.04	17				θ		θ		θ	0.06	14							θ	σ	
θ		σ	\bullet		θ			\bullet	0.03	18				θ		θ		θ	0.06	12							θ	σ	
			\bullet		\bullet			θ	0.03	15		θ		\bullet				θ	0.05	16							θ	σ	
		σ	\bullet		θ			\bullet	0.03	18		θ		\bullet				θ	0.02	16							θ	σ	
θ		θ	σ		\bullet			θ	0.03	17				θ		θ		θ	0.02	13							θ	σ	
θ			\bullet		\bullet			θ	0.03	16		θ		θ				θ	0.02	14							θ	σ	
θ			\bullet		\bullet			θ	0.03	17				σ				θ	0.02	16							θ	σ	
			\bullet		\bullet			θ	0.02	18				σ				\bullet	0.01	16							\bullet	σ	
θ			\bullet		\bullet			\bullet	0.02	18		θ		θ				\bullet	0.01	17							\bullet	σ	
θ		θ	\bullet		\bullet			θ	0.02	18		θ		σ				θ	0.01	17							θ	σ	
θ		θ	\bullet		\bullet			\bullet	0.02	18		θ		θ				θ	0.01	17							θ	σ	
		σ	\bullet		\bullet			θ	0.02	18				θ		θ		θ	0.01	15							θ	σ	
			\bullet		\bullet			θ	0.02	16		θ		θ				\bullet	0.00	17							\bullet	σ	
		σ	\bullet		θ			\bullet	0.02	16		θ		\bullet				θ	0.00	17							θ	σ	
θ		\bullet	σ		\bullet			\bullet	0.01	18		θ		θ				\bullet	0.00	17							\bullet	σ	

Table 2.4: Comparisons of abundance (N) estimates, percent coefficients of variation (% CV), 95% confidence intervals, and percent confidence interval lengths (% CIL) for $t = 8$ black-tailed prairie dog colonies in north-central Colorado from the AIC_c model-averaged ZPNE (modAIC) and BIC model-averaged ZPNE (modBIC). Models are ordered from smallest to largest by average % CV and % CIL across all colonies.

Model	Parameter	Estimate	% CV	95% CI		% CIL
				Lower	Upper	
ZPNE modBIC	N_{76a}	588.0	6.7	518.6	667.9	25.4
	N_{82}	1399.4	8.6	1191.0	1646.1	32.5
	N_{83}	1947.3	7.5	1691.8	2242.4	28.3
	N_{84}	908.0	6.3	805.7	1024.1	24.0
	N_{70}	838.8	6.6	741.2	950.3	24.9
	N_{76b}	793.5	5.2	718.9	876.7	19.9
	N_{81}	1403.5	5.9	1255.2	1570.5	22.5
	N_{88}	375.5	5.6	338.2	417.8	21.2
ZPNE modAIC	N_{76a}	581.3	7.9	501.3	675.7	30.0
	N_{82}	1444.3	8.2	1239.4	1684.5	30.8
	N_{83}	1988.1	7.4	1728.9	2287.0	28.1
	N_{84}	911.9	6.2	811.0	1026.3	23.6
	N_{70}	859.3	6.8	756.1	977.8	25.8
	N_{76b}	789.4	5.5	711.8	876.4	20.9
	N_{81}	1364.4	5.4	1230.8	1513.4	20.7
	N_{88}	374.7	5.1	340.1	413.4	19.6

constant individual heterogeneity level $\hat{\sigma} = 0.28$ (SE = 0.04). Again, the high degree of model selection uncertainty warranted model-averaged point estimates and unconditional variances (Table 2.4). Across all eight colonies, average coefficients of variation were 6.5% for the BIC model-averaged ZPNE and 6.6% for the AIC_c model-averaged ZPNE. Average confidence interval lengths were 24.8% for the BIC model-averaged ZPNE and 24.9% for the AIC_c model-averaged ZPNE. Point estimates for the model-averaged ZPNE tended to be lower than those from PNE and BOWE, but no significant differences were detected.

2.3.3 Example Discussion

In terms of meeting model assumptions, I believe the study design was satisfactory. Closure was likely met by the timing of the surveys and the inclusion of the entire area of each colony. Resighting surveys were performed immediately after application of dye marks such that any loss of marks was unlikely. The dye "helmet" effectively prevented errors in distinguishing between marked and unmarked individuals. Because marked individuals were fur-dyed and therefore differed in appearance from unmarked individuals, the assumption that required careful attention was iid resighting probabilities for marked and unmarked animals. However, I found that by first scanning at low magnification, marked individuals were virtually indistinguishable from unmarked individuals until after they were first sighted, when they were then focused on at higher magnification for identification.

In this example, very little difference was found between (Z)PNE model-averaged estimates using AIC_c or BIC weights. In terms of precision, PNE was demonstrated to be an improvement over individual BOWE estimates. The advantages were most pronounced for colonies such as Town 83, where the marked sample size was lowest. Despite the data being zero-truncated, ZPNE estimates were still more precise than BOWE estimates using the entire data set. It is noteworthy that a significant population increase was detected with PNE and ZPNE for Town 76 from 2005 (76a) to 2006 (76b), but not with BOWE. This further demonstrates the advantages of combining data from multiple primary sampling occasions and using covariates to more easily detect changes in N for long-term monitoring programs.

Based on the AIC_c model-averaged PNE, the average density across all eight colonies $\bar{D} = 7.5$ (SE = 0.21) animals per acre, ranging from 3.1 (SE = 0.19) for Town 81 to 11.2 (SE = 0.75) for Town 82. These are consistent with the estimated densities of other unfragmented colonies in South Dakota (Hoogland, 1995; Severson and Plumb, 1998) and northern Colorado (Antolin et al., 2006). Although Town 76 showed considerable growth in area from 2005 (71 acres) to 2006 (108 acres), no significant change in density was observed with $\hat{D}_{76a} = 9.9$ (SE = 0.90) and $\hat{D}_{76b} = 9.0$ (SE = 0.64). Within one or two years of the resighting surveys, the four colonies with densities > 7 animals per acre (Towns 76, 82, 83, 84) experienced sylvatic plague epizootics generally lasting up to three months until all individuals were dead. Despite having the lowest density, Town 81 also underwent a plague epizootic beginning August 2007. Town 81 was approximately 4 km from Town 76, which may have been the source of the epizootic. Based on observations during the summer of 2007, I further speculate that Town 81 may have increased in density prior to the plague event.

In both analyses, estimated resighting rates were generally lower during high winds, higher following rain events, and higher for larger colonies. I suspect high winds tended to make resightings of individuals more difficult due to shaking of spotting scopes, but it is also possible that prairie dog activity levels were lower during these periods. Rain events in the 24-hours prior to resighting surveys appear to have produced more favorable conditions and increased prairie dog activity. I am unsure why larger towns tended to have higher individual resighting rates, but suspect this may be an artifact of Town 81 having by far the largest area but

also exhibiting the lowest density. This lower density may have resulted in fewer individuals going undetected during survey scans. Although I *a priori* suspected temperature would be an important predictor variable, I found little evidence to support this. For every covariate examined, the direction of the effect was always opposite for θ and σ , indicating that factors which correlated with mean resighting rates were inversely correlated with individual heterogeneity levels.

Although not significantly different, the point estimates for ZPNE tended to be lower than those for PNE and BOWE. On average, ZPNE point estimates were 10% lower than PNE or BOWE. I suspect this was due to more marked individuals being resighted zero times than would be expected under a Poisson distribution. For example, in Town 76a, 23 of $n_{76a} = 80$ marked individuals were never sighted. However, based on 1000 simulated draws of 80 marked individuals using resighting rate parameter estimates from the minimum-AIC_c ZPNE model, an average of only 10.3 (SE = 0.09) individuals would be expected to never be sighted. Such underestimation of the number of marked individuals by ZPNE may result in overestimation of individual resighting rates, which in turn may cause underestimation of N . Although not serious in this example, it is important that researchers applying ZPNE are aware of possible underestimation when a relatively large number of marked individuals are suspected to have never been sighted as a result of substantial heterogeneity.

2.4 Simulation Experiments

2.4.1 Simulation Methods

Because the prairie dog example provides no information on the relative expected performance of PNE and ZPNE compared to BOWE and ARNE, I conducted a limited set of simulation experiments. Data were generated for $t = 3$ primary occasions under the assumptions of geographic and demographic closure within primary sampling occasions, iid sighting probabilities for marked and unmarked individuals, 100% mark identification, and no error in distinguishing marked versus unmarked individuals. The total number of sightings for individual s during primary interval j (y_{sj}) were first modeled as independent Poisson-log normal random variables based on an underlying population $E(y_{sj}) = \bar{\lambda}_j$ and overdispersion due to individual heterogeneity ($\lambda_{\sigma j}$) such that $\text{var}(y_{sj}) = \bar{\lambda}_j + \lambda_{\sigma j}$. In terms of $\bar{\lambda}_j$ and $\lambda_{\sigma j}$,

$$\theta_j = 2 \log(\bar{\lambda}_j) - \frac{\log(\lambda_{\sigma j} + \bar{\lambda}_j^2)}{2},$$

and

$$\sigma_j = \sqrt{\log(\lambda_{\sigma j} + \bar{\lambda}_j^2) - 2 \log(\bar{\lambda}_j)}.$$

When $\lambda_{\sigma j} = 0$, there is no overdispersion due to individual heterogeneity and $\sigma_j = 0$. Based on the input values for $\bar{\lambda}_j$ and $\lambda_{\sigma j}$, the $y_{sj} \stackrel{\text{ind}}{\sim} \text{Poisson}(\lambda_{sj})$ were drawn for the N_j individuals in the population, with $\lambda_{sj} = \exp(\sigma_j z_{sj} + \theta_j)$, $z_{sj} \stackrel{\text{iid}}{\sim} N(0, 1)$, and

Table 2.5: Poisson data generating scenarios for simulation experiments with $t = 3$ primary sampling occasions. For scenarios A, B, and C, all input parameters were randomly selected for each primary occasion from population size $N_j = \{50, 250, 500\}$, proportion of N_j that is marked $p_j = \{0.1, 0.3, 0.5\}$, mean resighting rate $\bar{\lambda}_j = \{1, 3, 5\}$, and overdispersion due to individual heterogeneity $\lambda_{\sigma j} = \{0, \bar{\lambda}_j/2, \bar{\lambda}_j\}$. For scenarios D, E, and F, input parameter values were randomly selected for one primary occasion and used for all three primary occasions.

Scenario	N_1	p_1	$\bar{\lambda}_1$	$\lambda_{\sigma 1}$	N_2	p_2	$\bar{\lambda}_2$	$\lambda_{\sigma 2}$	N_3	p_3	$\bar{\lambda}_3$	$\lambda_{\sigma 3}$
A	50	0.3	3	0	50	0.3	3	1.5	250	0.1	1	0.5
B	500	0.1	5	5	250	0.3	5	0	500	0.1	3	1.5
C	250	0.5	5	2.5	250	0.3	1	0.5	500	0.1	1	0.5
D	50	0.3	5	2.5	50	0.3	5	2.5	50	0.3	5	2.5
E	250	0.1	3	3	250	0.1	3	3	250	0.1	3	3
F	500	0.3	1	0	500	0.3	1	0	500	0.3	1	0

$T_{u_j} = \sum_{s=n_j+1}^{N_j-n_j} y_{sj}$. With so many possible input parameters determining resighting rates and sample sizes, I restricted these simulations to six pseudo-randomly selected data generating scenarios. For three of the scenarios, all input parameters were randomly selected for each primary occasions from $N_j = \{50, 250, 500\}$, proportion of N_j that is marked $p_j = \{0.1, 0.3, 0.5\}$, $\bar{\lambda}_j = \{1, 3, 5\}$, and $\lambda_{\sigma j} = \{0, \bar{\lambda}_j/2, \bar{\lambda}_j\}$. For the other three scenarios, input parameter values were randomly selected for one primary occasion and used for all three primary occasions (Table 2.5). When $N_j = 50$, only $p_j = 0.3$ or 0.5 were allowed.

To examine the robustness of PNE and ZPNE to simulated data under a distribution other than Poisson, I also generated data by modeling resighting rates as the sum of logit-normal random variables. Here, data were generated as if there were k_j distinct secondary sampling occasions without replacement within each primary interval j . Based on an underlying population mean resighting probability $\bar{\mu}_j$ and individual heterogeneity level (σ_{IHj}), additive temporal variation (σ_{TVj}) allowed

μ_{sij} to vary for the s th individual on the i th secondary resighting occasion, such that $y_{sj} = \sum_{i=1}^{k_j} \delta_{sij}$, where $\delta_{sij} \stackrel{\text{ind}}{\sim} \text{Bernoulli}(\mu_{sij})$. Because resighting probabilities were modeled using this transformation, input values for $\bar{\mu}_j$, σ_{IHj} , and σ_{TVj} did not back-transform identically to their original values. McClintock et al. (2006) used similar methods and categorized the realized values for the data-generating parameters (also see Chapter 1). For $\bar{\mu}_j$, the categories were Low ($0.15 < \bar{\mu}_j < 0.16$), Medium ($0.30 < \bar{\mu}_j < 0.38$), and High ($\bar{\mu}_j = 0.50$). The categories for σ_{IHj} and σ_{TVj} were None ($\sigma_j = 0$), Low ($0.00 < \sigma_j < 0.05$), Medium ($0.10 < \sigma_j < 0.15$), and High ($0.16 < \sigma_j < 0.26$). Similar to the simulations using Poisson generated data, six scenarios were pseudo-randomly selected. For three of the scenarios, input parameter values were randomly selected for all three primary sampling occasions from $N_j = \{50, 250, 500\}$, $p_j = \{0.1, 0.3, 0.5\}$, $k_j = \{3, 5, 7\}$, $\bar{\mu}_j = \{\text{Low, Medium, High}\}$, $\sigma_{IHj} = \{\text{None, Low, Medium, High}\}$, and $\sigma_{TVj} = \{\text{None, Low, Medium, High}\}$. For the other three scenarios, input parameter values were randomly selected for one primary occasion and used for all three primary occasions (Table 2.6). When $N_j = 50$, only $p_j = 0.3$ or 0.5 were allowed. When $\bar{\mu}_j = \text{Low}$, σ_{IHj} and σ_{TVj} must be $\leq \text{Low}$.

Each scenario consisted of 1000 simulations where the entire generated data set was applied to PNE and BOWE, and the zero-truncated data set was applied to ZPNE and ARNE. For PNE and ZPNE, all possible time and individual heterogeneity models ($R = 75$, Table 2.7) were implemented using NLMIXED as outlined in Section 2.3. For PNE and ZPNE, AIC_c and BIC model-averaged point estimates, unconditional variances, and confidence intervals were calculated as in Section 2.3. Confidence intervals for BOWE were calculated as in Bowden and Kufeld (1995).

Table 2.6: Logit-normal data generating scenarios for simulation experiments with $t = 3$ primary sampling occasions. For scenarios A, B, and C, all input parameters were randomly selected for each primary occasion from $N_j = \{50, 250, 500\}$, proportion of N_j that is marked $p_j = \{0.1, 0.3, 0.5\}$, number of secondary resighting occasions $k_j = \{3, 5, 7\}$, mean sighting probability $\bar{\mu}_j = \{\text{Low, Medium, High}\}$, individual heterogeneity level $\sigma_{IHj} = \{\text{None, Low, Medium, High}\}$, and temporal variation level $\sigma_{TVj} = \{\text{None, Low, Medium, High}\}$. For scenarios D, E, and F, input parameter values were randomly selected for one primary occasion and used for all three primary occasions.

Scenario	j	N_j	p_j	k_j	$\bar{\mu}_j$	σ_{IHj}	σ_{TVj}
A	1	50	0.3	3	Low	Low	None
A	2	50	0.5	7	High	None	High
A	3	50	0.3	3	Medium	Medium	Low
B	1	500	0.3	7	High	None	High
B	2	500	0.1	7	High	High	High
B	3	500	0.1	5	Low	Low	None
C	1	500	0.1	5	Medium	None	Low
C	2	250	0.1	5	High	Medium	Medium
C	3	50	0.3	7	Medium	Low	None
D	1,2,3	250	0.1	3	Medium	High	Medium
E	1,2,3	500	0.1	7	Low	None	None
F	1,2,3	50	0.3	5	Medium	Medium	Low

Table 2.7: All possible time and individual heterogeneity (Z)PNE parameterizations for θ_j and σ_j with $t = 3$ primary sampling occasions. Combining all permutations of the three θ_j parameterizations and the seven σ_j parameterizations yields $R = 75$ possible models with $N_1 \neq N_2 \neq N_3$ [represented as $N(t)$]. The combined number of parameters (including N_j) in the models range from $K = 4$ for model $\{\theta(\cdot)\sigma(0)N(t)\}$ to $K = 9$ for model $\{\theta(t)\sigma(t)N(t)\}$.

Model Notation	Parameterization	K	No. Permutations
$\theta(\cdot)$	$\theta_a = \theta_b = \theta_c$	1	1
$\theta(2j)$	$\theta_a = \theta_b \neq \theta_c$	2	3
$\theta(t)$	$\theta_a \neq \theta_b \neq \theta_c$	3	1
$\sigma(0)$	$\sigma_d = \sigma_e = \sigma_f = 0$	0	1
$\sigma(\cdot)$	$\sigma_d = \sigma_e = \sigma_f$	1	1
$\sigma(1j_{2=0})$	$\sigma_d \neq \sigma_e = \sigma_f = 0$	1	3
$\sigma(1j_{1=0})$	$\sigma_d = \sigma_e \neq \sigma_f = 0$	1	3
$\sigma(2j_{1=0})$	$\sigma_d \neq \sigma_e \neq \sigma_f = 0$	2	3
$\sigma(2j)$	$\sigma_d = \sigma_e \neq \sigma_f$	2	3
$\sigma(t)$	$\sigma_d \neq \sigma_e \neq \sigma_f$	3	1

Confidence intervals for ARNE were calculated using the inverse cube root transformation of Arnason et al. (1991). The relative performances of the AIC_c and BIC model-averaged (Z)PNE, BOWE, and ARNE were evaluated primarily on average percent confidence interval coverage, average percent confidence interval length (% CIL), and Bias/SE across each scenario of 1000 simulations. Simulations where PNE, ZPNE, or ARNE failed to converge were rare (< 0.6%) and omitted from summary statistics. As described in Arnason et al. (1991), when no marked individual is resighted more than a single time within primary interval j , \hat{N}_j for ARNE is infinite. This is also the case for ZPNE, but is somewhat alleviated by its ability to combine data across multiple primary occasions. Simulations where ARNE or the model-averaged ZPNE estimates were infinite were omitted from summary statistics for these models.

2.4.2 Simulation Results

Across the six scenarios with Poisson generated data (Table 2.8), BOWE (94.6, SE = 0.17) and ARNE (86.2, SE = 0.25) had the highest and lowest average percent coverage, respectively. ARNE had the largest average % CILs (49.0, SE = 0.28) and the BIC model-averaged PNE had the smallest % CILs (37.0, SE = 0.09). Compared to BOWE, both PNE approaches achieved similar coverage but had considerably smaller % CILs. BOWE was unbiased, and PNE generally exhibited a slight positive bias, but Bias/SE for PNE never exceeded 0.25. Although less than the nominal 95%, both ZPNE approaches achieved greater average coverage than ARNE. Average % CILs were smaller for the ZPNE models than for ARNE. Both ARNE and ZPNE generally exhibited a negative bias, but was most severe for ARNE (average Bias/SE = -0.37, SE = 0.10). PNE average percent coverage was lowest for N_3 of Scenario A, at 89.1 (SE = 0.99) using AIC_c model-averaging and 88.7 (SE = 1.01) using BIC model-averaging. BOWE average coverage was lowest for N_3 of Scenario D (93.0, SE = 0.81). ZPNE average percent coverage was lowest for N_2 of Scenario C, at 66.9 (SE = 1.51) using AIC_c model-averaging and 61.5 (SE = 1.56) using BIC model-averaging. ARNE average percent coverage was also lowest for N_2 of Scenario C (64.4, SE = 1.53). For all models, average % CILs were largest for N_3 of Scenario A, at 83.4 (SE = 1.00) for the BIC model-averaged PNE, 84.3 (SE = 1.01) for the AIC_c model-averaged PNE, 94.6 (SE = 1.17) for BOWE, 111.2 (SE = 2.77) for the BIC model-averaged ZPNE, 112.3 (SE = 2.79) for the AIC_c model-averaged ZPNE, and 134.9 (SE = 4.74) for ARNE. No inadmissible cases for

Table 2.8: Average percent confidence interval coverage, percent confidence interval length (% CIL), and Bias/SE of abundance estimates for AIC_c model-averaged (modAIC) PNE and ZPNE, BIC model-averaged (modBIC) PNE and ZPNE, BOWE, and ARNE across six simulated scenarios with data generated under a Poisson distribution.

Model	% Coverage		% CIL		Bias/SE	
	Est.	SE	Est.	SE	Est.	SE
BOWE	94.6	0.17	46.7	0.11	0.00	0.01
PNE modAIC	93.7	0.18	38.9	0.09	0.10	0.02
PNE modBIC	93.2	0.19	37.0	0.09	0.09	0.02
ARNE	86.2	0.25	49.0	0.28	-0.37	0.10
ZPNE modAIC	89.6	0.22	45.1	0.18	-0.18	0.09
ZPNE modBIC	88.3	0.23	42.5	0.18	-0.21	0.11

ARNE or the model-averaged ZPNE where all marked individuals were sighted ≤ 1 time occurred in these scenarios.

Across the six scenarios with logit-normal generated data (Table 2.9), ARNE had the largest average coverage (95.8, SE = 0.15), and the BIC model-averaged ZPNE had the lowest (91.8, SE = 0.21). Average % CILs were smallest and largest for the BIC model-averaged PNE (53.7, SE = 0.32) and ARNE (192.3, SE = 4.16), respectively. Compared to BOWE, both PNE approaches achieved similar coverage but had smaller % CILs. BOWE was again unbiased, and PNE again exhibited a slight positive bias, but Bias/SE for PNE never exceeded 0.25. Compared to ARNE, both ZPNE approaches achieved slightly lower average coverage, but average % CILs were considerably smaller for the ZPNE models. ARNE and ZPNE generally exhibited a positive bias, but was most severe for the BIC model-averaged ZPNE (average Bias/SE = 0.32, SE = 0.09). Both the AIC_c model-averaged PNE and BOWE had their lowest average percent coverage for N_1 of Scenario A, at 88.0

(SE = 1.03) and 93.0 (SE = 0.81), respectively. The BIC model-averaged PNE had its lowest average percent coverage for N_2 of Scenario B (85.7, SE = 1.11). ZPNE average percent coverage was lowest for N_3 of Scenario A using AIC_c model-averaging (89.6, SE = 0.97) and for N_1 of Scenario D using BIC model-averaging (87.9, SE = 1.04). ARNE average percent coverage was lowest for N_1 of Scenario C (91.6, SE = 0.88). Average % CILs were largest for N_1 of Scenario A for BOWE (127.0, SE = 2.58), the BIC model-averaged PNE (127.5, SE = 5.23), the AIC_c model-averaged PNE (134.2, SE = 5.23), and ARNE (1196.1, SE = 47.40). ZPNE average % CILs were largest for N_3 of Scenario A, at 273.6 (SE = 10.41) using AIC_c model-averaging and 274.9 (SE = 10.48) using BIC model-averaging. For N_1 of Scenario A, the combination of $k_1 = 3$ and $\bar{\mu}_1 = \text{Low}$ resulted in 35% and 29% of simulations producing inadmissible estimates for ARNE and the model-averaged ZPNE, respectively. For Scenario D, less than 0.2% of simulations produced inadmissible estimates for ARNE or the model-averaged ZPNE. No other inadmissible cases occurred in the logit-normal scenarios.

2.4.3 Simulation Discussion

When the number of marked individuals was known, PNE generally exhibited advantages over BOWE in terms of coverage and precision regardless of the method used to generate the data. As expected, the advantages were greater with data generated under a Poisson distribution, but PNE performance proved robust with logit-normal data. Because its properties are not based on asymptotics, BOWE

Table 2.9: Average percent confidence interval coverage, percent confidence interval length (% CIL), and Bias/SE of abundance estimates for AIC_c model-averaged (modAIC) PNE and ZPNE, BIC model-averaged (modBIC) PNE and ZPNE, BOWE, and ARNE across six simulated scenarios with data generated under a logit-normal distribution.

Model	% Coverage		% CIL		Bias/SE	
	Est.	SE	Est.	SE	Est.	SE
BOWE	94.6	0.17	58.6	0.21	-0.01	0.01
PNE modAIC	95.5	0.15	55.9	0.32	0.11	0.03
PNE modBIC	94.2	0.17	53.7	0.32	0.11	0.04
ARNE	95.5	0.15	192.3	4.16	0.19	0.08
ZPNE modAIC	93.5	0.19	93.2	0.79	0.31	0.08
ZPNE modBIC	91.8	0.21	89.1	0.78	0.32	0.09

exhibited some advantage in terms of coverage and precision with the poorest logit-normal data sets such as for N_1 in Scenario A where $k_1 = 3$ and $\bar{\mu}_1 = 0.15$. I found little difference between AIC_c and BIC model-averaged results for PNE when using the Poisson or logit-normal data. Despite the slight advantages demonstrated for PNE with data generated under a logit-normal distribution, if one suspects the underlying sampling process is truly without replacement within distinct secondary occasions, the logit-normal mixed effects model (LNE, see Chapter 1) would be the more appropriate choice. Based on simulation experiments (see Chapter 1), I expect LNE to be more precise than PNE when sampling is without replacement, but PNE would perform well and be the more appropriate choice if sampling with replacement were possibly suspected and not confirmed. This may occur when there are relatively few marked individuals, none of which were resighted more than once on a given secondary occasion, but it is unknown whether this is also true for the unmarked individuals.

When the number of marked individuals was unknown, ZPNE exhibited greater coverage and precision than ARNE with the Poisson generated data, but average coverage for both models was less than nominal. With the logit-normal data, ZPNE was considerably more precise than ARNE with near-nominal coverage. Relative to PNE and BOWE, ARNE and ZPNE were less precise with the logit-normal data than with the Poisson data. I found little difference between AIC_c and BIC model-averaged results for ZPNE when using the Poisson data, but did find the AIC_c model-averaged results to be slightly more robust in terms of coverage when using the logit-normal data. With the Poisson data, both ARNE and ZPNE coverage was less than nominal due to a tendency towards negative bias when sample sizes were particularly small. This bias was considerably worse for ARNE when individual heterogeneity was present. With the logit-normal data, ARNE and ZPNE exhibited a positive bias in most scenarios, but were negatively biased when there were high levels of individual heterogeneity. The positive bias was typically more severe for ZPNE, and the negative bias was more severe for ARNE. For the logit-normal scenarios, these biases usually did not cause coverage to fall below nominal for either estimator. However, while the relatively large confidence intervals for ARNE in the logit-normal scenarios allowed the model to achieve adequate coverage when individual heterogeneity levels were high, the poor precision exhibited by ARNE under these circumstances would not be particularly useful for inference.

Overall performance for ARNE and ZPNE was poorest in scenarios containing primary sampling occasions with individual heterogeneity and low numbers of resightings. This occurred in the Poisson simulations for primary occasions where both

$\bar{\lambda}_j = 1$ and $\lambda_{\sigma_j} = 0.5$, and in the logit-normal simulations where $k_j = 3$. In the former case, these input parameter values resulted in relatively large numbers of marked individuals never being resighted. This caused an underestimation of the number of marked individuals and, therefore, N . In the latter case, both overestimation and underestimation of N was observed. Overestimation occurred for N_3 of Scenario A and was likely a result of the highly skewed resighting probability distribution generating fewer marked individuals with $y_{sj} = 0$ than would be expected (based on the resighting frequencies of individuals with $y_{sj} \geq 1$). For N_1 of Scenario A and all primary occasions of Scenario D, the small number of secondary sampling occasions combined with low resighting probabilities or high levels of individual heterogeneity, respectively, resulted in more marked individuals being sighted zero times than would be expected (and underestimation of N). However, average coverage only fell slightly in these scenarios because of large confidence interval lengths. The slight loss in coverage was greater for ZPNE, but the precision of ARNE was extremely poor for these estimates.

When the primary sampling occasions where both $E(y_{sj}) = 1$ and $\text{var}(y_{sj}) = 1.5$ were omitted from summary statistics for the Poisson simulations, average confidence interval coverage across all simulations was improved for the AIC_c model-averaged ZPNE (93.3, SE = 0.20), the BIC model-averaged ZPNE (92.6, SE = 0.21), and ARNE (89.2, SE = 0.25). Average percent confidence interval lengths were reduced for the AIC_c model-averaged ZPNE (39.6, SE = 0.10), the BIC model-averaged ZPNE (37.4, SE = 0.10), and ARNE (42.0, SE = 0.09). The negative average Bias/SE was reduced slightly for ARNE (-0.23, SE = 0.07), but more substantially for the

AIC_c model-averaged ZPNE ($-0.04, SE = 0.05$) and the BIC model-averaged ZPNE ($-0.05, SE = 0.05$). Even with these occasions omitted, the overall performance of ARNE was not greatly improved relative to ZPNE because ARNE estimates tended to be negatively biased when individual heterogeneity levels were moderate to high.

When primary sampling occasions of the logit-normal simulations with $k_j = 3$ were omitted from summary statistics, the average performance of ARNE and ZPNE were both improved, but a considerable advantage in terms of precision was still demonstrated for ZPNE. Average percent coverage was now 94.4 ($SE = 0.20$) for the AIC_c model-averaged ZPNE, 92.9 ($SE = 0.23$) for the BIC model-averaged ZPNE, and 95.5 ($SE = 0.18$) for ARNE. Average % CILs were lowered to 69.2 ($SE = 0.37$) for the AIC_c model-averaged ZPNE, 66.2 ($SE = 0.36$) for the BIC model-averaged ZPNE, and 89.5 ($SE = 1.36$) for ARNE. Average Bias/SEs were still greater than 0.25, at 0.45 ($SE = 0.07$) for the AIC_c model-averaged ZPNE, 0.46 ($SE = 0.08$) for the BIC model-averaged ZPNE, and 0.30 ($SE = 0.09$) for ARNE. Despite a larger Bias/SE after omitting these occasions, ZPNE still achieved greater precision than ARNE with little loss in coverage. In both sets of simulations, the nominal performance of ZPNE when these cases were omitted reiterates the importance of careful study design to help ensure that distributional assumptions and minimal sample size requirements are reasonably satisfied in application.

2.5 Conclusions

Both the black-tailed prairie dog example and the simulation experiments demonstrated clear advantages in the use of PNE or ZPNE when compared to BOWE or ARNE. The generalized modeling framework of (Z)PNE incorporates several key advancements when sampling is with replacement or the number of marks is unknown. These include the use of covariates in modeling resighting rate and individual heterogeneity parameters, information-theoretic model selection and multimodel inference, and the inclusion of unidentified marks towards achieving greater precision with little or no loss in coverage. In these limited simulations, I found PNE and ZPNE to be robust to the data generating process and generally reliable alternatives to BOWE and ARNE, but I note that it is important for researchers to address the possible limitations of small sample sizes or relatively many marked individuals never being resighted when applying (Z)PNE. Similar to the logit-normal mixed effects model (LNE, see Chapter 1), (Z)PNE is computationally more intensive than other estimators. However, I believe this added complexity is justified by the advantages its generalized structure can provide. Further, users not wishing to program the models using standard statistical computing software may implement both LNE and (Z)PNE in the freely available mark-recapture software package Program MARK (available for download at <http://welcome.warnercnr.colostate.edu/~gwhite>). Instructions for implementing the models in MARK may be found in Appendix D.

With the recent introduction of LNE and (Z)PNE, a more flexible and efficient framework for mark-resight abundance estimation is now available for the sampling

conditions most commonly encountered in these studies. I foresee the next logical step for model development in this area to be its extension to a full robust design (Kendall et al., 1995, 1997). By so doing, mark-resight may then be utilized not only for abundance estimation, but also as a less invasive and less expensive method of estimating demographic parameters, such as state-specific survival and transition rates, that help explain the fluctuations in population size commonly observed through long-term monitoring programs. This extension is explored in Chapter 3.

Chapter 3

A less field-intensive robust design for estimating demographic parameters with mark-resight data

3.1 Introduction

Although abundance (N) is invariably of interest in wildlife studies, it provides little information on the forces that drive changes in population size that are commonly observed in long-term monitoring programs. The robust design of Kendall et al. (1995, 1997) provided a means for estimating N , apparent survival probabilities (ϕ), and transition probabilities between observable and unobservable states (ψ^{OU}, ψ^{UO}) from mark-recapture data by combining multinomial likelihoods of the Cormack-Jolly-Seber open population model (Seber, 1982) and closed population abundance models (Otis et al., 1978; Pledger, 2000; Huggins, 1991). Under this framework, N

is estimated for the observable population, the transition probabilities pertain to some super population moving between observable and unobservable states, and ϕ does not differ by state. Sampling consists of t “primary” sampling intervals, each consisting of k_j ($j = \{1, \dots, t\}$) “secondary” sampling occasions. Abundance of the observable population is estimated for the closed period of secondary sampling during each primary interval, and this length of time must be of short enough duration for the assumption of closure to be acceptable. The primary periods between these closed intervals are considered open and used to estimate survival and transition probabilities. Because this “full-likelihood” approach simultaneously utilizes information from the open and closed sampling periods, it possesses advantages in terms of bias and precision over implementing the models separately (Kendall et al., 1995, 1997).

Despite its numerous advantages over other methods (Thompson et al., 1998; Anderson, 2003), two drawbacks of mark-recapture studies are their financial cost and disturbance to animals. Compared to traditional mark-recapture, the mark-resight method (Arnason et al., 1991; Neal et al., 1993; Bowden and Kufeld, 1995; White and Shenk, 2001; McClintock et al., 2006) can often be a less expensive and less invasive alternative (Minta and Mangel, 1989; McClintock and White, 2007). The primary advantage of these methods is that animals only need to be physically captured and marked once, and subsequent sighting data from both marked and unmarked individuals are used for estimation. With limited funds and resources, mark-resight can be appealing to researchers because costs associated with capture are generally the most expensive aspects of mark-recapture studies. Not only can

the financial burden of mark-recapture be discouraging for long-term population monitoring, but capture is also the most hazardous aspect for the animals. If field-readable marks are feasible, mark-resight can substantially reduce stress to species because they can be observed at a distance with minimal disturbance after the initial capture. This can be of particular concern when working with threatened, endangered, or sensitive species.

In Chapters 1 and 2, I introduced generalized mark-resight modeling frameworks in the spirit of traditional mark-recapture (Otis et al., 1978; Coull and Agresti, 1999; Pledger, 2000), including the efficient use of covariates in modeling detection rate and individual heterogeneity parameters, information-theoretic model selection and multimodel inference, and the ability to borrow information across primary intervals for data collected under the robust design. However, the focus of mark-resight methods has to this point been overwhelmingly on the estimation of N . To my knowledge, none of the mark-resight models developed to date have tried to utilize the information these data may contain about demographic parameters in a fashion analogous to mark-recapture. Building on the generalized framework developed in Chapter 2, I extend the model to a full-likelihood robust design, thereby providing a less expensive and less invasive alternative to its mark-recapture predecessor (Kendall et al., 1995, 1997). After introducing the model in the next section, I demonstrate its use in Section 3.3 using New Zealand robin (*Petroica australis*) data collected in Fiordland National Park, New Zealand. In Section 3.4, I report on simulation experiments evaluating the performance of the model under a variety of sampling conditions. In Section 3.5, I summarize my findings in terms of their impli-

cations for demographic parameter estimation in long-term population monitoring programs.

3.2 The Model

The robust design Poisson-log normal mixed effects mark-resight model (RDPNE) has the same basic assumptions of the abundance model developed in Chapter 2, but it utilizes information from the open sampling periods to estimate apparent survival and transition probabilities between observable and unobservable states. These assumptions are: 1) geographic and demographic closure during secondary sampling within primary intervals; 2) no loss of marks; 3) no errors in distinguishing marked and unmarked animals; and 4) independently and identically distributed (iid) resighting probabilities for marked and unmarked animals. The usual assumptions of the Cormack-Jolly-Seber model also apply (Seber, 1982). Marks must be individually identifiable and field-readable. Because marks must be individually identifiable, it is possible to account for overdispersion due to resighting rate heterogeneity or lack of independence. The number of marked individuals in the population during sampling may be known exactly or unknown. Given that an individual is identified as marked, RDPNE may incorporate less than 100% marked individual identification by assuming such events occur randomly within the marked population.

I will assume some number of individuals with permanent field-readable marks are available for resighting during t sequential primary sampling intervals of interest. Each primary sampling interval consists of secondary sampling occasions

during which the population is assumed closed. Sampling within secondary occasions may be with or without replacement (i.e., individuals may be sighted more than once within a secondary occasion). This differs from the traditional mark-recapture model of Kendall et al. (1995, 1997) because secondary occasions need not be distinct, and consideration is given only to some closed period of sampling for each primary interval. If the number of marked individuals in the population (n_j) is known exactly during primary interval j ($j = \{1, \dots, t\}$), the resighting data for this interval consist of the total number of sightings for marked individual s ($y_{sj} = \{0, 1, 2, \dots\}$, $s = \{1, \dots, n_j\}$) and the total number of unmarked sightings (T_{u_j}). Typically, the number of marks is known exactly only when radio-collars are used (McClintock and White, 2007) or all marking occurs immediately prior to the onset of secondary sampling. In the latter case, it is often reasonable to assume no mortality or movement between marking and the closed resighting period (see Chapter 2). If the exact number of marks is unknown during primary interval j , then some number of marked individuals are resighted at least once (n_j^*), and the resighting data consist of the total number of sightings for these individuals ($y_{sj} = \{1, 2, \dots\}$, $s = \{1, \dots, n_j^*\}$) and T_{u_j} . Often times a marked individual is sighted, but not identified to individual identity. Because ignoring these data would generally result in overestimation of N , the total number of times this occurs during interval j ($\epsilon_j = \{0, 1, 2, \dots\}$) is also incorporated into the model.

When the number of marks in the population is known exactly during primary interval j , the y_{sj} 's ($s = \{1, \dots, n_j\}$) are modeled as realizations of independent Poisson-log normal random variables. If the number of marks is unknown, the y_{sj} 's

($s = \{1, \dots, n_j^*\}$) are modeled as realizations of independent zero-truncated Poisson-log normal random variables. On the log scale, mean resighting rate (θ_j) is treated as a fixed effect and individual heterogeneity (a source of overdispersion) as a random effect with mean zero and unknown variance σ_j^2 . The y_{sj} 's have conditional expectation

$$E(y_{sj} \mid \sigma_j, Z_{sj}, \theta_j) = \lambda_{sj} = \exp(\sigma_j Z_{sj} + \theta_j),$$

where $Z_{sj} \stackrel{\text{iid}}{\sim} N(0, 1)$. For increased efficiency, θ_j and σ_j may be modeled with fixed environmental or individual covariates believed to affect the resighting process, as is demonstrated in Section 3.3 and in Chapter 2. By taking the product across the n_j or n_j^* marked individuals for each primary interval, an unconditional likelihood function for θ_j , σ_j , and N_j is

$$\begin{aligned} L(\mathbf{N}, \boldsymbol{\sigma}, \boldsymbol{\theta} \mid \mathbf{y}, \mathbf{n}, \mathbf{T}_u) \\ = \prod_{j=1}^t \left\{ \prod_{s=1}^{n_j} \int \frac{\lambda_{sj}^{y_{sj}} \exp(-\lambda_{sj}) I_j}{y_{sj}!} \phi(z_{sj}) dz_{sj} + \prod_{s=1}^{n_j^*} \int \frac{\lambda_{sj}^{y_{sj}} \exp(-\lambda_{sj}) (1 - I_j)}{y_{sj}! [1 - \exp(-\lambda_{sj})]} \phi(z_{sj}) dz_{sj} \right\} \\ \times \prod_{j=1}^t \frac{f(T_{u_j})}{\int_0^\infty f(T_{u_j}) dT_{u_j}}. \end{aligned} \quad (3.1)$$

where I_j is an indicator for when the the number of marks is known ($I_j = 1$) or unknown ($I_j = 0$) for primary interval j , $\phi(z_{sj})$ is the standard normal density,

$f(T_{u_j})$ is the normal density with expectation

$$\begin{aligned} E(T_{u_j}) &= \left[N_j - n_j I_j - \frac{n_j^*(1 - I_j)}{1 - \exp(-\lambda_{j|s})} \right] \\ &\quad \times \left[\exp\left(\frac{\sigma_j^2}{2} + \theta_j\right) + \frac{\epsilon_j}{n_j I_j + \frac{n_j^*(1 - I_j)}{1 - \exp(-\lambda_{j|s})}} \right] \end{aligned} \quad (3.2)$$

and variance

$$\begin{aligned} \text{var}(T_{u_j}) &= \left[N_j - n_j I_j - \frac{n_j^*(1 - I_j)}{1 - \exp(-\lambda_{j|s})} \right] \\ &\quad \times \left\{ \exp\left(\frac{\sigma_j^2}{2} + \theta_j\right) + \exp(2\theta_j) [\exp(2\sigma_j^2) - \exp(\sigma_j^2)] + \frac{\epsilon_j}{n_j I_j + \frac{n_j^*(1 - I_j)}{1 - \exp(-\lambda_{j|s})}} \right\}. \end{aligned} \quad (3.3)$$

and

$$\lambda_{j|s} = E_{Z_{sj}}(y_{sj}) = \int \exp(\sigma_j z_{sj} + \theta_j) \phi(z_{sj}) dz_{sj} = \exp\left(\frac{\sigma_j^2}{2} + \theta_j\right).$$

Full details on the derivation of this likelihood may be found in Chapter 2, with the only difference being that the data are no longer considered independent between primary intervals under RDPNE. It remains that the data need not be independent with respect to parameters.

To model the sampling process for the open periods between primary sampling intervals, I combine (3.1) with the first-order Markovian emigration likelihood “ L_{1b} ”

introduced by Kendall et al. (1997):

$$L(\mathbf{N}, \boldsymbol{\sigma}, \boldsymbol{\theta}, \boldsymbol{\phi}, \boldsymbol{\psi}^{OU}, \boldsymbol{\psi}^{UO} \mid \mathbf{y}, \mathbf{n}, \mathbf{T}_u) = L(\mathbf{N}, \boldsymbol{\sigma}, \boldsymbol{\theta} \mid \mathbf{y}, \mathbf{n}, \mathbf{T}_u) L_{1b}. \quad (3.4)$$

As in the models of Kendall et al. (1995, 1997), the open L_{1b} portion of this full likelihood ignores the timing and frequencies of encounters during secondary sampling occasions, considering only whether or not the individual was encountered at any time during primary interval j . By utilizing information from both open and closed sampling periods, this provides a means for jointly estimating N_j , θ_j , σ_j , the probability that an individual alive and in the super population during interval j survives and remains in the super population to interval $j + 1$ (ϕ_j , $j = \{1, \dots, t - 1\}$), and the transition probabilities between observable and unobservable states for individuals alive and in the super population from interval j to $j + 1$ (ψ_j^{OU} , $j = \{1, \dots, t - 1\}$ and ψ_j^{UO} , $j = \{2, \dots, t - 1\}$). These transition probabilities are the same as γ'' and $1 - \gamma'$, respectively, of Kendall et al. (1997) when used in the context of temporary emigration from a single study area, but they don't necessarily need to describe state transitions in space. They may describe any transitions between observable and unobservable states, such as observable "breeding" and unobservable "nonbreeding" states (Kendall and Nichols, 2002). However, a fundamental assumption of this modeling approach is that apparent survival probabilities are the same for all individuals in the super population and, therefore, do not differ by state.

Even with modest t , the multinomial cell probabilities under L_{1b} in (3.4) can become quite complicated, and interested readers are referred to Appendix C and

Kendall et al. (1997) for a more detailed explanation of the likelihood. Suffice it to say that the L_{1b} in (3.4) is identical to that of Kendall et al. (1997), but in my model the open and closed portions of the full likelihood are linked via the probability of being encountered at least once during primary interval j (p_j^*) under the Poisson-log normal model. This contrasts with the p_j^* derived from the closed capture multinomial model in Kendall et al. (1995, 1997) or the loglinear model in Rivest and Daigle (2004). Here I use the term encounter (instead of resight) because in mark-resight methodology, marked or unmarked individuals may be encountered through sightings, but individuals may also be encountered through captures (e.g., for marking) during the open periods. If a capture event were to occur immediately prior to the onset of a closed primary interval, any of the captured individuals that were not subsequently resighted may be reasonably assumed to have been present. When n_j is known, these individuals constitute the marked individuals with $y_{sj} = 0$. However, when n_j is unknown these individuals do not contribute to the Poisson portion of the likelihood, but because they were known to have been present, this information can be used in the open portion of the likelihood. I define c_j as the total number of individuals captured immediately prior to primary interval j (and therefore assumed to be present in the population during this interval), but not resighted. Then $c_j^* = n_j^* + c_j$ is the total number of marked individuals encountered at least once (via capture or resighting) for primary occasion j , and

$$p_j^* = \frac{c_j^*}{n_j}.$$

Thus, if n_j is known exactly, then all available marked individuals have been encountered and $p_j^* = 1$. Otherwise, $n_j = n_j^*/[1 - \exp(-\lambda_{j|s})]$. If n_j is unknown and there are no encounters from capture events immediately prior to closed interval j (i.e., $c_j^* = n_j^*$) then $p_j^* = 1 - \exp(-\lambda_{j|s})$, the probability of being resighted at least once during primary interval j under the zero-truncated Poisson-log normal model.

Point and variance estimates for RDPNE may be obtained using maximum likelihood or Bayesian analysis methods. Because the integrals appearing in the likelihood do not have closed form solutions, they must be computed numerically when using maximum likelihood (see Chapter 2). The model may be implemented using standard statistical computing software, but this can become quite complicated and tedious as the number of primary intervals increases. The model has therefore been incorporated into the freely available mark-recapture software package Program MARK (White and Burnham, 1999). Instructions for implementing the model in MARK may be found in Appendix D.

I note that in application, if the number of marked individuals is known exactly for all primary intervals, there is no advantage to using the full-likelihood approach proposed here. This would apply if all marked individuals were fit with radio-collars, and the fates of these individuals were therefore known. Under these circumstances, it would be better to ignore temporary emigration and apparent survival altogether by using the known fate data from the marked individuals to estimate survival rates directly (Pollock et al., 1989). This could be done in conjunction with an analysis using the Poisson-log normal (see Chapter 2) or logit-normal (see Chapter 1) models to obtain abundance estimates.

3.3 Example: New Zealand Robin

3.3.1 Example Methods

Between March 2005 and August 2007, the New Zealand Department of Conservation investigated the utility of mark-resight methodology for monitoring New Zealand robin (*Petroica australis*) populations on three study areas in the Eglinton Valley of Fiordland National Park, New Zealand (44°58'S, 168°01'E). This exploratory investigation was initiated to assess whether the technique may be used to monitor the endangered populations of the closely related species (*Petroica traversi*) inhabiting the Chatham Islands. The three sites (Knobs Flat, Smithy, and Walker Creek) consisted of 100 ha grids and were visited in March (post-breeding) and August (pre-breeding) of each year, but data collection did not begin in Smithy until August 2005. Therefore, there were 6 primary intervals for both Knobs Flat and Walker Creek, but only 5 primary intervals for Smithy. Between September 2003 and August 2007, as many juvenile and adult birds as possible were captured within the sites and given individually identifiable bands. These capture events took place continuously throughout the breeding season and intermittently prior to primary sampling intervals. Because banded birds could have died or permanently emigrated during this extended capture period, the exact number of marked individuals in each population was unknown for every primary interval. At the time of capture, the sex and age class of each individual was recorded. The primary intervals were divided into 8 – 10 distinct secondary occasions where the entire area of each site was surveyed. Secondary sampling was conducted in the morning and typ-

ically required four hours for each occasion. The populations were assumed closed during primary sampling intervals. Sampling was with replacement because marked individuals were resighted more than once on several secondary occasions. Stoat (*Mustela erminea*) and possum (*Trichosurus vulpecula*) control occurred at low levels on all three study areas for the duration of the study. Additionally, ship rat (*Rattus rattus*) control was conducted on Walker Creek from June 2006 until April 2007, thereby overlapping two primary sampling intervals (August 2006 and March 2007).

To aid in evaluating the relative performance of the mark-resight abundance estimates, intensive territory mapping was conducted during most primary intervals of each site to produce an independent estimate of the minimum number known alive (MNA). These MNAs were believed to be reasonably close to the actual population sizes within each site, but they required considerably greater field effort to obtain relative to the mark-resight methodology. The Department of Conservation was primarily interested in determining whether mark-resight may be a reliable and more cost-efficient alternative to territory mapping.

I performed a joint RDPNE maximum likelihood analysis for these three groups using Program MARK (White and Burnham, 1999). Covariates examined included sex, age class at time of capture (juvenile or adult), study area, time, breeding season, and rat control on Walker Creek. Three covariate models for rat control on Walker Creek were examined: 1) an immediate and constant effect during the entire program (rat_1); 2) no immediate effect with a delayed effect thereafter (rat_2); and 3) an immediate effect with a variable effect thereafter (rat_{12}). I also investi-

gated models under completely random emigration, $\psi^{OU} = 1 - \psi^{UO}$, (Kendall et al., 1997) and models ignoring individual heterogeneity ($\sigma = 0$) or temporary emigration ($\psi^{OU} = 1 - \psi^{UO} = 0$) altogether. Because the duration of the open periods was four months between March and August surveys and seven months between August and March surveys, the open period parameters refer to four-month intervals. I first modeled the resighting rate parameters under the most general (but identifiable) time- and group-dependent structure for N and the open period parameters. To make all parameters identifiable, I followed the suggestion of Kendall et al. (1997) and constrained the final $\psi_{t-2}^{OU} = \psi_{t-1}^{OU}$ and $\psi_{t-2}^{UO} = \psi_{t-1}^{UO}$ for each site. I then investigated various models for θ and σ . As a means for model selection, Program MARK by default utilizes Akaike's Information Criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson, 2002). This allows multimodel inference based on AIC_c weights using an effective sample size I defined as $\sum_{j=1}^t \{n_j I_j + n_j^*(1 - I_j)\} + t$. For the combined data set, $t = 17$ and $I_j = 0$. I proceeded by first selecting the model structure for θ and σ best supported by AIC_c and then using only this structure for investigating more parsimonious models for ϕ , ψ^{OU} , and ψ^{UO} . Lastly, I investigated various combinations of the best supported structures for the open period parameters with any other structures for θ and σ that had received relatively strong AIC_c support. I computed model-averaged parameter estimates and unconditional variances based on AIC_c weights and calculated confidence intervals as 95% logarithm-transformed normal for N and 95% logit-transformed normal for the open period parameters. The minimum lower bound for all N_j was n_j^* .

3.3.2 Example Results

Across the 6 primary intervals for Knobs Flat and Walker Creek, 65 and 45 marked individuals, respectively, were resighted at least once. Across the 5 primary intervals for the Smithy site, 39 marked individuals were resighted at least once. Across the $t = 17$ total primary intervals, the effective sample size $\sum_{j=1}^t \{n_j I_j + n_j^* (1 - I_j)\} + t = 378$. Across all primary intervals, the average numbers of resightings for the n_j^* marked individuals observed at least once were 2.9, 2.6, and 3.0 for Knobs Flat, Smithy, and Walker Creek, respectively. The total numbers of unmarked individuals resighted across all secondary occasions of each primary interval ranged from $T_{u_j} = 4$ to 45 for Knobs Flat, 6 to 28 for Smithy, and 1 to 57 for Walker Creek, with the lower numbers typically occurring during winter (August). Small numbers of marked individuals were identified as marked but not to individual identity, ranging from $\epsilon_j = 0$ to 6 across all sites and primary intervals.

The model structure for resighting rate parameters best supported by AIC_c included breeding season, age, sex, and rat_1 terms for θ , and a breeding season term for σ . No other structures for θ and σ were an improvement when combined with the open period parameter structure best supported by AIC_c . With 19% of the AIC_c weight, the 29-parameter minimum- AIC_c model included an age effect with a delayed effect of rat control (rat_2) on apparent survival, and a season effect under completely random emigration for ψ^{OU} and ψ^{UO} (Table 3.1). For mean resighting rate θ , negative effects (on the log scale) were found for pre-breeding primary intervals in August (-0.21 , $SE = 0.09$), individuals first captured as adults

Table 3.1: AIC_c weights for selected RDPNE models of apparent survival and transition rates for New Zealand robin populations on three study areas in Fiordland National Park, New Zealand. Covariates include age class, study area, rat control, season, sex, and intercept only (.). Three covariate models for rat control were examined, including an immediate and constant effect during the entire program (rat_1), no immediate effect with a delayed effect thereafter (rat_2), and an immediate effect with a variable effect thereafter (rat_{12}). Models where certain parameters were assumed to have no effect (0) were also investigated. Model specific covariates were included for apparent survival only (ϕ), transition rates under completely random temporary emigration only (ψ), transition rates under unconstrained temporary emigration only (ψ_u), or both apparent survival and transition rates under completely random temporary emigration (\bullet). All models include separate abundance (N) estimates for each primary interval of each study area. Unless otherwise noted, all models include age, rat_1 , season, and sex effects on mean resighting rate (θ), and season effects on individual heterogeneity (σ). The number of estimated parameters (K) includes N , θ , σ , and intercept terms.

		Model							AIC_c	K
age	area	rat_1	rat_2	rat_{12}	season	sex	.	0	Weight	
ϕ			ϕ		ψ				0.19	29
ϕ	ϕ		ϕ		ψ				0.15	31
ϕ	ϕ				ψ				0.13	30
ϕ		ϕ			ψ				0.08	29
ϕ				ϕ	ψ				0.07	30
ϕ	ϕ		ϕ				ψ		0.06	30
ϕ			ϕ				ψ		0.06	28
ϕ					ψ				0.06	28
ϕ			ϕ		ψ_u				0.03	31
\bullet			ϕ						0.02	29
ϕ			ϕ				ψ_u		0.02	29
ϕ			ϕ			ψ			0.02	29
ϕ			\bullet						0.02	29
ϕ			ϕ					ψ	0.02	27
ϕ	ψ		ϕ						0.02	30
			ϕ		ψ				0.01	28
					ψ	ϕ			0.01	28
					ψ		ϕ		0.01	27
ϕ			ϕ		ψ			σ	0.00	27
		ϕ			ψ				0.00	28
				ϕ	ψ				0.00	29
							\bullet		0.00	26
					\bullet				0.00	28
	ϕ				ψ				0.00	29
	ϕ		ϕ		ψ				0.00	30

($-0.16, SE = 0.08$), and females ($-0.43, SE = 0.10$). An immediate and constant positive effect (on the log scale) was found on θ for Walker Creek during rat control ($0.34, SE = 0.10$). For all three study areas, $\hat{\sigma} = 0.47$ ($SE = 0.09$) during pre-breeding primary intervals in August and $\hat{\sigma} = 0.00$ ($SE = 0.02$) during post-breeding primary intervals in March. Virtually no support (0% of AIC_c weight) was given to the same minimum- AIC_c model assuming no individual heterogeneity (Table 3.1).

Model-averaged parameter and unconditional variance estimates suggest fluctuating population sizes (Figure 3.1) and relatively constant apparent survival rates for adults and juveniles on the three study areas until rat control was initiated on Walker Creek (Figure 3.2). During the period of rat control on Walker Creek, a significant increase in population size was detected. Both Knobs Flat and Smithy exhibited significant population declines through the course of the study. With the exception of Knobs Flat from August 2006 to March 2007, all study areas exhibited increases in population size from pre-breeding to post-breeding. Confidence intervals for abundance estimates were greater than or included the MNAs from territory mapping in every case except for Knobs Flat and Walker Creek in August 2006 (Figure 3.1). The weight of evidence strongly favored the completely random emigration hypothesis with very little support for the same minimum- AIC_c model assuming no temporary emigration or unconstrained temporary emigration, both with $< 3.5\%$ of the AIC_c weight (Table 3.1). Using the mean values for individual covariates, model-averaged estimates of transition rates for Smithy and Knobs Flat were $\hat{\psi}^{OU} = 0.10$ ($SE = 0.05$) and $\hat{\psi}^{UO} = 0.86$ ($SE = 0.18$) post- to pre-breeding, and $\hat{\psi}^{OU} = 0.02$ ($SE = 0.05$) and $\hat{\psi}^{UO} = 0.98$ ($SE = 0.17$) pre- to post-breeding. For Walker

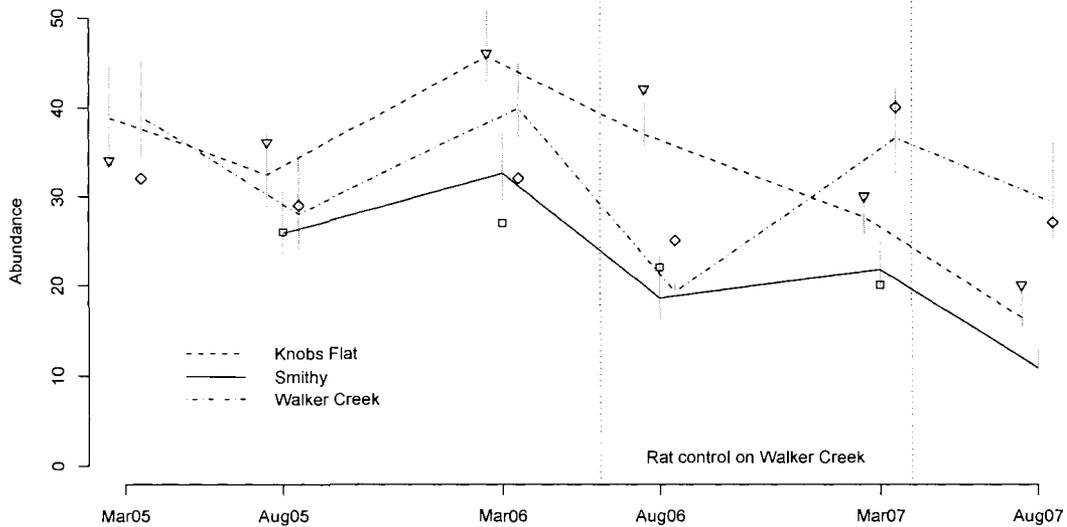


Figure 3.1: Mark-resight abundance estimates and 95% confidence intervals between March 2005 and August 2007 for three New Zealand robin populations (Knobs Flat, Smithy, and Walker Creek) in Fiordland National Park, New Zealand. Point symbols (∇ = Knobs Flat, \square = Smithy, \diamond = Walker Creek) indicate the minimum number known alive based on territory mapping that was independent of the mark-resight methodology. Vertical hashed lines indicate a period of rat control on the Walker Creek study area.

Creek, $\hat{\psi}^{OU} = 0.10$ (SE = 0.06) and $\hat{\psi}^{UO} = 0.87$ (SE = 0.18) post- to pre-breeding, and $\hat{\psi}^{OU} = 0.02$ (SE = 0.04) and $\hat{\psi}^{UO} = 0.98$ (SE = 0.17) pre- to post-breeding.

3.3.3 Example Discussion

As also found in Chapter 2, covariates that correlated with θ were inversely correlated with σ when both were included in a given model. Mean resighting rates were typically lower with higher levels of individual heterogeneity during pre-breeding. Regardless of breeding interval, females exhibited lower mean resighting rates. Individuals captured as juveniles tended to have higher mean resighting rates than

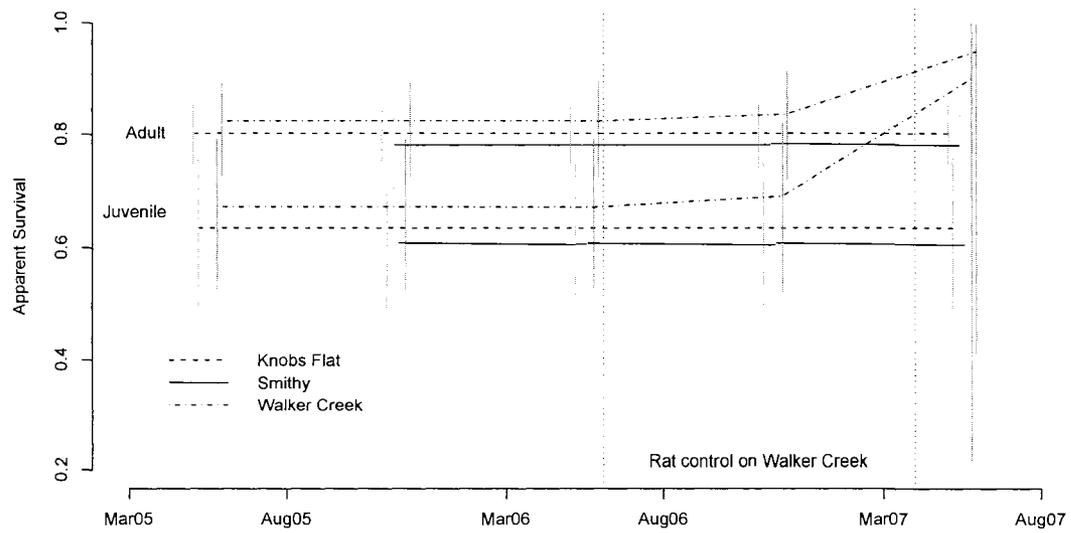


Figure 3.2: Four-month apparent survival estimates and 95% confidence intervals between March 2005 and August 2007 for three New Zealand robin populations (Knobs Flat, Smithy, and Walker Creek) in Fiordland National Park, New Zealand. Estimates are a function of age at time of first capture (adult or juvenile). Vertical hashed lines indicate a period of rat control on the Walker Creek study area.

individuals captured as adults. Mean resighting rates were higher during rat control on Walker Creek. The population increase exhibited by Walker Creek during the rat control program (during which neither Knobs Flat or Smithy showed increases) suggests rat control on the Chatham Islands may be effective and warrants further investigation.

With average four-month apparent survival estimates near 0.78 (SE = 0.02) for the three study areas until rat control was initiated on Walker Creek, the populations tended to decline over the winter months post- to pre-breeding, but usually exhibited increases pre- to post-breeding. I found some evidence of lower survival for individuals first captured as juveniles compared to those first captured as adults. The evidence for an increase in apparent survival for the Walker Creek population during and immediately following the rat control program suggests the population increase pre- to post-breeding and the less dramatic decrease post- to pre-breeding during this period may be attributable not only to increased recruitment, but also to higher survival or lower permanent emigration of the juvenile and adult population. For all three study areas, individuals were more likely to temporarily emigrate from post- to pre-breeding. Still, temporary emigration rates were relatively low, suggesting that any other emigration from the study areas was permanent. Estimates of transition rates, particularly for ψ^{UO} , were the least precise of all parameters. This lower precision is consistent with the findings of Kendall et al. (1997).

When compared to the independent MNAs obtained through territory mapping, the mark-resight estimates were closely correlated and provide a degree of validation for this methodology. Based on these data, it appears mark-resight would be a

reliable and more cost-efficient alternative to territory mapping (or mark-recapture) for monitoring the endangered populations inhabiting the Chatham Islands. However, in August 2006, the mark-resight estimates for Knobs Flat and Walker Creek were significantly lower than the MNAs. This may be a result of breeding starting earlier than usual in this particular year. With mostly breeding and non-breeding males being detected while breeding females remained on nests, I suspect some severe undetected heterogeneity may have been introduced, thereby causing the RDPNE to underestimate abundance. Because of this potential risk when using the model, the timing of studies should always be designed to maximize resighting rates and minimize individual heterogeneity whenever possible. These issues are addressed in greater detail in Chapter 2 and in the next section.

3.4 Simulation Experiments

3.4.1 Simulation Methods

In Chapter 2, I investigated the properties of the (zero-truncated) Poisson-log normal model for abundance estimation and generally found its performance to be nominal (or near-nominal) under a variety of simulated sampling conditions. Kendall et al. (1995, 1997) performed simulations evaluating their mark-recapture robust design model and also found its performance to be satisfactory. Given these results, it follows that the component of RDPNE that deserves special attention is its ability to adequately estimate the probability of being encountered at least once during pri-

primary intervals, p_j^* , and therefore properly model the open period sampling process. I therefore performed a series of simulation experiments examining the large-sample properties of RDPNE for comparison to the simulations of Kendall et al. (1995, 1997).

Data were generated for a single population with $t = 4$ primary sampling occasions under the assumptions of geographic and demographic closure within primary intervals, iid sighting probabilities for marked and unmarked individuals, 100% mark identification, and no error in distinguishing marked versus unmarked individuals. I assumed an initial super population of 500 observable individuals with time-dependent ϕ_j ($j = \{1, \dots, t-1\}$), ψ_j^{OU} ($j = \{1, \dots, t-1\}$), and ψ_j^{UO} ($j = \{2, \dots, t-1\}$). I also assumed no additions to the super population through births or immigration so that the population (and marked sample) size would decline through time. For the members of the super population that were observable, the total number of sightings for individual s during primary interval j (y_{sj}) were modeled as independent Poisson-log normal random variables based on an underlying population $E(y_{sj}) = \bar{\lambda}_j$ and overdispersion due to individual heterogeneity ($\lambda_{\sigma j}$) such that $\text{var}(y_{sj}) = \bar{\lambda}_j + \lambda_{\sigma j}$. In terms of $\bar{\lambda}_j$ and $\lambda_{\sigma j}$,

$$\theta_j = 2 \log(\bar{\lambda}_j) - \frac{\log(\lambda_{\sigma j} + \bar{\lambda}_j^2)}{2},$$

and

$$\sigma_j = \sqrt{\log(\lambda_{\sigma j} + \bar{\lambda}_j^2) - 2 \log(\bar{\lambda}_j)}.$$

When $\lambda_{\sigma_j} = 0$, there is no overdispersion due to individual heterogeneity and $\sigma_j = 0$. Based on the input values for $\bar{\lambda}_j$ and λ_{σ_j} , the $y_{sj} \stackrel{\text{ind}}{\sim} \text{Poisson}(\lambda_{sj})$ were drawn for the N_j observable individuals in the population, with $\lambda_{sj} = \exp(\sigma_j z_{sj} + \theta_j)$, $z_{sj} \stackrel{\text{iid}}{\sim} \text{N}(0, 1)$, and $T_{u_j} = \sum_{s=n_j+1}^{N_j} y_{sj}$.

To facilitate comparisons with the simulations of Kendall et al. (1997) where $p_j^* = 0.64$, individuals in the super population were marked immediately prior to the first primary interval with probability $m = 0.64$. No marking occurred thereafter, so as the overall population size decreased, the proportion of marked individuals available for resighting remained approximately equal to m for each interval. The number of marks was known for the first primary interval but unknown for the other intervals. The generating model was fully time-dependent for each of the model parameters, and three transition conditions were investigated. As in Kendall et al. (1997), these conditions were $\psi_j^{OU} = 1 - \psi_j^{UO}$ (completely random emigration), $\psi_j^{OU} > 1 - \psi_j^{UO}$, and $\psi_j^{OU} < 1 - \psi_j^{UO}$. To aid in assessing the relative performance of the model (without loss of generality under the fully time-dependent model), the set of parameter values for $\bar{\lambda}_j$, λ_{σ_j} , ψ_j , ψ_j^{OU} , and ψ_j^{UO} were kept the same for each primary interval. I specified a relatively high mean resighting rate ($\bar{\lambda}_j = 5$), and a scenario with ($\lambda_{\sigma_j} = 2.5$) and without ($\lambda_{\sigma_j} = 0$) individual heterogeneity was examined for each of the three conditions. The other data-generating values were $\phi_j = 0.8$, $\psi_j^{OU} = 1 - \psi_j^{UO} = 0.2$ (under random emigration), $\psi_j^{OU} = 0.3$ and $\psi_j^{UO} = 0.8$ (when $\psi_j^{OU} > 1 - \psi_j^{UO}$), and $\psi_j^{OU} = 0.2$ and $\psi_j^{UO} = 0.7$ (when $\psi_j^{OU} < 1 - \psi_j^{UO}$). Each of these six scenarios was independently replicated 1000 times.

I performed a maximum likelihood analysis of each generated data set using

the NLPQN subroutine in the SAS System for Windows (SAS Institute, 2002). Because ϕ_{t-1} , ψ_{t-1}^{OU} , and ψ_{t-1}^{UO} are confounded under the fully time-dependent model, I followed the suggestion of Kendall et al. (1997) to make all estimated parameters identifiable by constraining $\psi_{t-2}^{OU} = \psi_{t-1}^{OU}$ and $\psi_{t-2}^{UO} = \psi_{t-1}^{UO}$ with all other estimated parameters fully time-dependent. To investigate the effects of unmodeled heterogeneity on parameter estimates, I also analyzed the data generated with individual heterogeneity under this constrained model assuming no heterogeneity ($\sigma_j = 0$). I evaluated model performance primarily on Bias/SE and percent coefficient of variation for the parameters of interest. I also examined percent confidence interval coverage of the true parameter values. Confidence intervals for N_j were calculated as 95% logarithm-transformed normal with the minimum lower bound set at the minimum number of marked individuals known to be in the population during interval j . Confidence intervals for ϕ , ψ^{OU} , and ψ^{UO} were calculated as 95% logit-transformed normal.

3.4.2 Simulation Results and Discussion

In terms of Bias/SE, precision, and confidence interval coverage, the performance of N , ϕ , ψ^{OU} , and ψ^{UO} estimators varied between the transition and individual heterogeneity scenarios (Table 3.2). Because the number of marks was only known for the first primary interval, N_1 estimates tended to be the least biased and most precise relative to the other abundance estimates. The relative precision of abundance estimates decreased through time as the marked sample size decreased. Because of the

way the data were generated, the transition conditions had no effect on N_1 , but the other abundance estimates tended to be slightly less precise when $\psi^{OU} > 1 - \psi^{UO}$. No trends were found for the effects of the three transition conditions on bias and coverage of abundance estimates. All abundance estimates were relatively unbiased with nominal coverage when there was no individual heterogeneity in resighting rates. Estimates for N_1 remained relatively unbiased with nominal coverage when individual heterogeneity was present and included in the model, but a slight negative bias was found for the other abundance estimates. This resulted in lower coverage for these parameters, but never falling below 91.4%. When individual heterogeneity was present but not included in the model, N_1 estimates remained relatively unbiased, but variance underestimation resulted in lower coverage of this parameter. When the number of marks was unknown, unmodeled heterogeneity caused abundance estimates to be more negatively biased with coverage falling as low as 84.3%.

Apparent survival estimates were relatively unbiased with nominal coverage across all transition conditions and individual heterogeneity scenarios. Under completely random emigration ($\psi^{OU} = 1 - \psi^{UO}$), survival estimates tended to be most precise. Little difference was generally found between survival estimates when $\psi^{OU} < 1 - \psi^{UO}$ or $\psi^{OU} > 1 - \psi^{UO}$, but $\hat{\phi}_3$ was noticeably less precise when $\psi^{OU} > 1 - \psi^{UO}$. Transition probability estimates were generally less precise than the other estimated parameters, particularly when $\psi^{OU} < 1 - \psi^{UO}$. These findings are consistent with those in the previous section and those of Kendall et al. (1997). Individual heterogeneity did not appear to affect the precision and coverage of ψ^{OU} and ψ^{UO} ,

Table 3.2: Average bias divided by standard error (B/SE), percent coefficient of variation (CV), and percent confidence interval coverage (Cover) for estimates of abundance (N), apparent survival (ϕ), and transition probabilities between observable and unobservable states (ψ^{OU} and ψ^{UO}) from simulation experiments consisting of $t = 4$ primary intervals under three conditions for transitions (ψ): $\psi^{OU} < 1 - \psi^{UO}$ ($<$), $\psi^{OU} > 1 - \psi^{UO}$ ($>$), and completely random emigration $\psi^{OU} = 1 - \psi^{UO}$ ($=$). These three conditions include scenarios without individual heterogeneity, with individual heterogeneity, and with unmodeled individual heterogeneity. To make all estimated parameters identifiable, I constrained $\psi_{t-2}^{OU} = \psi_{t-1}^{OU}$ ($\psi_{2=3}^{OU}$) and $\psi_{t-2}^{UO} = \psi_{t-1}^{UO}$ ($\psi_{2=3}^{UO}$) with all other parameters fully time-dependent.

Parm.	ψ	No Ind. Het.			With Ind. Het.			Unmodeled Ind. Het.		
		B/SE	CV	Cover	B/SE	CV	Cover	B/SE	CV	Cover
N_1	$<$	0.0	1.5	94.7	0.0	1.8	94.5	0.1	1.5	89.2
	$>$	0.0	1.5	94.7	0.0	1.8	94.8	0.1	1.5	88.3
	$=$	0.0	1.5	94.5	0.0	1.8	95.2	0.0	1.5	89.3
N_2	$<$	0.0	1.9	94.8	-0.4	2.4	92.0	-0.5	1.9	84.5
	$>$	0.0	2.1	94.1	-0.3	2.5	92.7	-0.4	2.1	87.6
	$=$	0.0	1.9	95.5	-0.3	2.4	92.5	-0.5	1.9	84.3
N_3	$<$	0.1	2.2	94.5	-0.2	2.7	91.4	-0.3	2.2	85.1
	$>$	0.1	2.3	94.1	-0.2	2.8	93.4	-0.5	2.3	86.8
	$=$	0.0	2.2	94.9	-0.2	2.6	92.8	-0.3	2.2	87.3
N_4	$<$	0.0	2.4	93.5	-0.2	3.0	92.5	-0.4	2.4	85.9
	$>$	0.0	2.5	95.3	-0.3	3.1	92.6	-0.3	2.6	87.9
	$=$	0.0	2.4	94.0	-0.2	2.9	92.5	-0.4	2.4	86.9
ϕ_1	$<$	0.2	4.0	97.2	0.1	4.1	97.0	0.1	4.0	97.1
	$>$	0.1	3.9	95.5	0.0	4.0	95.4	0.0	4.0	95.6
	$=$	0.1	3.5	95.7	0.0	3.6	96.1	0.0	3.6	95.3
ϕ_2	$<$	0.1	5.9	95.9	0.1	6.0	93.9	0.1	5.9	95.8
	$>$	0.0	5.7	95.2	0.1	5.9	96.6	0.0	5.9	96.3
	$=$	0.0	4.9	96.0	0.0	5.1	95.7	0.0	5.1	95.2
ϕ_3	$<$	0.1	7.1	95.6	0.1	7.1	95.6	0.0	7.1	95.3
	$>$	0.0	7.4	94.6	0.0	7.6	95.1	0.0	7.6	94.7
	$=$	0.1	6.5	96.3	0.0	6.6	95.0	0.1	6.6	96.5
ψ_1^{OU}	$<$	0.1	16.7	96.0	0.3	16.3	94.8	0.3	16.3	95.1
	$>$	0.0	11.5	96.3	0.2	11.3	94.7	0.2	11.3	94.5
	$=$	0.0	15.2	95.2	0.3	14.8	94.0	0.3	14.9	95.0
$\psi_{2=3}^{OU}$	$<$	0.1	21.2	96.6	0.2	20.7	95.8	0.2	20.7	95.1
	$>$	0.0	13.2	94.1	0.2	13.1	93.8	0.2	13.1	94.4
	$=$	0.1	18.1	95.4	0.2	18.0	95.3	0.3	17.7	94.8
$\psi_{2=3}^{UO}$	$<$	-0.1	17.9	98.5	-0.1	17.8	97.9	-0.1	17.4	97.9
	$>$	0.0	9.4	98.0	-0.2	9.9	96.5	-0.2	9.8	96.7
	$=$	0.0	11.7	99.1	-0.1	11.9	98.5	-0.1	12.0	97.9

although it may have induced a slight positive and negative bias for these estimates, respectively (Table 3.2).

Based on these large-sample simulations, it appears p_j^* works adequately in modeling the open periods for estimating ϕ , ψ^{OU} , and ψ^{UO} . As expected, I found little effect of individual heterogeneity on these estimates, but (as more thoroughly investigated in Chapter 2) severe heterogeneity can result in underestimation of abundance estimates when the number of marks is unknown, and it is important that heterogeneity be modeled under these circumstances for more reliable inferences on abundance. I suggest that individual heterogeneity models always be investigated and compared to those that do not include individual heterogeneity, as demonstrated in Section 3.3. I further stress that practitioners carefully design studies to minimize severe individual heterogeneity whenever possible.

3.5 Conclusions

When permanent field-readable marks are feasible, I have proposed a full-likelihood approach for estimating abundance, apparent survival, and transition rates between observable and unobservable states for mark-resight data that is analogous to that using traditional mark-recapture data. I found the model to perform similarly to its mark-recapture counterpart in large-sample simulation experiments. However, as with the mark-recapture model, the proposed approach is “data-hungry” and requires that practitioners employ careful study design in order to meet minimum sample size requirements for useful estimation of parameters. To facilitate this practice,

the simulation capability for this model has been implemented in Program MARK (White and Burnham, 1999). Practitioners may therefore design and analyze studies under RDPNE using MARK and circumvent computer programming altogether. MARK is downloadable at <http://welcome.warnercnr.colostate.edu/~gwhite>, and documentation for implementing the model may be found in the help files that accompany the program (see Appendix D).

I envision this full-likelihood approach to be utilized when the number of marked individuals may only be known for the first (or first several) primary intervals. Under this scenario, some known number of marks may first be introduced into the population, but after sufficient time some marks will no longer be in the population and the exact number would thereafter be unknown. A second scenario where this approach would be particularly useful would be when continuous marking has been occurring over a long period of time and the exact number of marks in the population is never known (as was the case for the New Zealand robin example in Section 3.3). Under either of these two scenarios, this full-likelihood mark-resight approach enables researchers to design long-term monitoring programs that minimize expenses and disturbances associated with capture while still providing a means for simultaneously estimating abundance, apparent survival, and transition rates that was previously only available using traditional mark-recapture methods. Further developments in this area include extending the model to multiple states (Brownie et al., 1993) or to incorporate both live and dead encounters (Barker, 1997).

Appendix A

Derivation of the variances for total unmarked sightings under the logit-normal model

If by definition the sightings of the $N-n$ unmarked individuals (any primary occasion j) are independent over individuals and conditionally (on Z_s) independent over occasions, then

$$T_u = \sum_{s=1}^{N-n} \sum_{i=1}^k \delta_{si} = \sum_{s=1}^{N-n} T_s.$$

Hence,

$$\text{var}(T_u) = (N - n) \text{var} \left(\sum_{i=1}^k \delta_{si} \right) = (N - n) \text{var}(T_s).$$

The general variance formula for any individual s is

$$\begin{aligned} \text{var}(T_s) &= \mathbf{E}_Z [\text{var}(T_s | Z)] + \text{var}_Z [\mathbf{E}_{T_s}(T_s | Z)] \\ &= \mathbf{E}_Z \left[\sum_{i=1}^k p_{si}(1 - p_{si}) \right] + \text{var}_Z \left(\sum_{i=1}^k p_{si} \right) \\ &= \mathbf{E}_Z \left[\sum_{i=1}^k p_{si}(1 - p_{si}) \right] + \sum_{l=1}^k \sum_{i=1}^k \text{cov}_Z(p_{sl}, p_{si}). \end{aligned} \quad (\text{A.1})$$

For (1.3), with no fixed time effects (A.1) becomes

$$\begin{aligned} \text{var}(T_s) &= \mathbf{E}_Z [kp_s(1 - p_s)] + k^2 \text{var}_Z(p_s) \\ &= k\mu - k\mathbf{E}_Z(p_s^2) + k^2 [\mathbf{E}_Z(p_s^2) - \mu^2], \end{aligned}$$

where

$$\gamma = \mathbf{E}_Z(p_s^2) = \int \left[\frac{1}{1 + \exp(-(\sigma z_s + \theta))} \right]^2 \phi(z_s) dz_s.$$

Hence,

$$\begin{aligned} \text{var}(T_s) &= k\mu - k\gamma + k^2(\gamma - \mu^2) \\ &= k[\mu(1 - \mu) + (k - 1)(\gamma - \mu^2)], \end{aligned}$$

and

$$\text{var}(T_u) = (N - n)k [\mu(1 - \mu) + (k - 1)(\gamma - \mu^2)].$$

For (1.4), with fixed time effects (A.1) becomes

$$\begin{aligned} \text{var}(T_s) &= \sum_{i=1}^k \mathbb{E}_Z [p_{si}(1 - p_{si})] + \sum_{l=1}^k \sum_{i=1}^k [\mathbb{E}_Z(p_{sl}, p_{si}) - \mu_l \mu_i] \\ &= \sum_{i=1}^k \mu_i(1 - \mu_i) + \sum_{l \neq i} \sum (\gamma_{li} - \mu_l \mu_i), \end{aligned}$$

and

$$\text{var}(T_u) = (N - n) \left[\sum_{i=1}^k \mu_i(1 - \mu_i) + \sum_{l \neq i} \sum (\gamma_{li} - \mu_l \mu_i) \right].$$

Appendix B

Derivation of the expectation and variance for total unmarked sightings under the Poisson-log normal model

If by definition the sightings of the $N - n$ unmarked individuals (any primary interval j) are independent, then $T_u = \sum_{s=1}^{N-n} y_s$. Hence, $E(T_u) = (N - n)E(y_s)$, and $\text{var}(T_u) =$

$(N - n)\text{var}(y_s)$. The general formulac, unconditional on Z_s for any individual s , are

$$E_Z(y_s) = \int \lambda_s \phi(z_s) dz_s = \int \exp(\sigma z_s + \theta) \phi(z_s) dz_s = \exp\left(\frac{\sigma^2}{2} + \theta\right),$$

and

$$\begin{aligned} \text{var}_Z(y_s) &= E_Z[\text{var}(y_s | Z)] + \text{var}_Z[E(y_s | Z)] \\ &= E_Z(\lambda_s) + \text{var}_Z(\lambda_s) \\ &= E_Z(\lambda_s) + E_Z(\lambda_s^2) - E_Z(\lambda_s)^2 \\ &= \int [\exp(\sigma z_s + \theta) + \exp(\sigma z_s + \theta)^2] \phi(z_s) dz_s - \left[\int \exp(\sigma z_s + \theta) \phi(z_s) dz_s \right]^2 \\ &= \exp\left(\frac{\sigma^2}{2} + \theta\right) + \exp(2\theta + 2\sigma^2) - \exp(2\theta + \sigma^2), \end{aligned}$$

where $\phi(z_s)$ is the standard normal density. Therefore, after inflating $E_Z(y_s)$ and $\text{var}_Z(y_s)$ by the (average) number of times the n marked individuals were sighted but not identified to individual identity (c),

$$E(T_u) = (N - n) \left[\exp\left(\frac{\sigma^2}{2} + \theta\right) + \frac{c}{n} \right],$$

and

$$\text{var}(T_u) = (N - n) \left\{ \exp\left(\frac{\sigma^2}{2} + \theta\right) + \exp(2\theta) [\exp(2\sigma^2) - \exp(\sigma^2)] + \frac{c}{n} \right\}.$$

Appendix C

The first-order Markovian temporary emigration likelihood of Kendall et al. (1997)

Building on the notation of Kendall et al. (1995, 1997) and that introduced in Chapter 3, let

m_{hi} = the number of animals encountered (via capture or resighting) in primary interval i ($i = \{2, 3, \dots, t\}$) that were last encountered in primary interval h ($h = \{1, 2, \dots, i - 1\}$), and

r_j = the number of the c_j^* marked individuals encountered during primary interval

j that were encountered again in some subsequent primary interval.

Likelihood L_{1b} in Equation (3.4) becomes quite complex with large t , but using matrix notation with

$$\mathbf{f}_j = \begin{bmatrix} \psi_j^{OU} \\ (1 - \psi_j^{OU})(1 - p_{j+1}^*) \end{bmatrix}^T,$$

$$\mathbf{d}_j = \begin{bmatrix} \psi_j^{UO} \\ 1 - \psi_j^{OU} \end{bmatrix},$$

and

$$\mathbf{G}_j = \begin{bmatrix} 1 - \psi_j^{UO} & \psi_j^{UO}(1 - p_{j+1}^*) \\ \psi_j^{OU} & (1 - \psi_j^{OU})(1 - p_{j+1}^*) \end{bmatrix},$$

the general pattern for arbitrary $h < i \leq t$ is

$$\begin{aligned} L_{1b} &= \prod_{j=1}^{t-1} \binom{c_j^*}{m_{j,j+1}, \dots, m_{jt}} [\phi_j (1 - \psi_j^{OU}) p_{j+1}^*]^{m_{j,j+1}} [\phi_j \mathbf{f}_j \phi_{j+1} \mathbf{d}_{j+1} p_{j+2}^*]^{m_{j,j+2}} \\ &\quad \times [\phi_j \mathbf{f}_j \phi_{j+1} \mathbf{G}_{j+1} \phi_{j+2} \mathbf{d}_{j+2} p_{j+3}^*]^{m_{j,j+3}} \\ &\quad \times [\phi_j \mathbf{f}_j \phi_{j+1} \mathbf{G}_{j+1} \phi_{j+2} \mathbf{G}_{j+2} \phi_{j+3} \mathbf{d}_{j+3} p_{j+4}^*]^{m_{j,j+4}} \dots \\ &\quad \times [\phi_j \mathbf{f}_j \phi_{j+1} \mathbf{G}_{j+1} \phi_{j+2} \mathbf{G}_{j+2} \dots \phi_{t-2} \mathbf{G}_{t-2} \phi_{t-1} \mathbf{d}_{t-1} p_t^*]^{m_{j,t}} (1 - \Pi_j)^{c_j^* - r_j} \end{aligned}$$

where Π_j is the sum of the $t - j$ multinomial cell probabilities (in square brackets) corresponding to $m_{j,j+1}, \dots, m_{jt}$.

Appendix D

Estimating demographic parameters using the mark-resight data type in Program MARK

Mark-resight methods constitute a slightly different type of data than found in traditional mark-recapture, but they are in the same spirit of accounting for imperfect detection towards reliably estimating demographic parameters (see White and Shenk, 2001 for a thorough explanation of how these data are collected and Chapters 1-3 for full details of the models). Like the other mark-recapture models in MARK, this approach models encounters (resightings) of marked individuals, but they also

incorporate additional data via sightings of unmarked individuals into the estimation framework. Mark-resight data may be used to estimate abundance (N) in a fashion analogous to the closed capture models of Otis et al. (1978). When sampling is under the robust design, mark-resight data may be used to estimate abundance, apparent survival, and transition rates between observable and unobservable states in a fashion analogous to the closed capture robust design models of Kendall et al. (1995, 1997). These models assume some individuals have been marked prior to sampling, and sampling occasions consist of resighting surveys (instead of capture periods). The main advantage of this approach is that it is generally less invasive and less expensive than traditional mark-recapture, but it requires that the number of marked individuals in the population during resightings be known exactly or can at least be reliably estimated. Adopting the same terminology of the robust design (Kendall et al., 1995, 1997), the approach may combine data from both closed and open sampling periods. The open periods refer to the resighting process between primary intervals, where each primary interval consists of secondary resighting occasions. The time periods between the secondary resighting occasions of a primary interval must be of short enough duration for the assumption of closure to be satisfied. Marks may be added to the population at any time during the open periods, but no marks may be added during the closed periods. If sampling within the secondary occasions is without replacement (i.e., any single individual may only be sighted once per distinct secondary occasion) and the number of marked individuals in the population available for resighting is known exactly, then the mixed logit-normal mark-resight models may be employed (see Chapter 1). Alternatively, if sampling

within secondary occasions is with replacement or the exact number of marked individuals in the population is unknown, the Poisson-log normal mark resight model may be used (see Chapter 2). If permanent field-readable marks are used but the number of marks is not known for all primary intervals, then mark-resight data collected under the closed robust design may be analyzed with the Poisson-log normal model in a fashion analogous to the regular mark-recapture robust design for estimating apparent survival (ϕ), transition rates between observable and unobservable states (γ'' and γ'), and N (see Chapter 3).

These models were developed as reliable and more efficient alternatives to the mark-resight models previously available in Program NOREMARK (White, 1996). Similar to other mark-recapture models, they provide a framework for information-theoretic model selection and multimodel inference based on AIC (Burnham and Anderson, 2002), and the utilization of individual or environmental covariates on parameters. However, because the nature of mark-resight data is somewhat different than that of mark-recapture, a different format for the input files has been developed to address this. Explanations of the various models and their MARK input file formats are detailed below. The input and results files referenced here accompany the program (available at <http://welcome.warnercnr.colostate.edu/~gwhite>). Following the explanations of the models and their MARK input files, some general suggestions are provided for performing an analysis with these models in MARK.

D.1 The mixed logit-normal mark-resight model

To be used when sampling is without replacement within secondary sampling occasions and the number of marked individuals in the population available for resighting is known exactly. Marks may or may not be individually identifiable. See Chapter 1 for full details.

Data:

t = the number of primary sampling intervals

k_j = the number of secondary sampling occasions (without replacement) during primary interval j

n_j = the exact number of marked individuals in the population during primary interval j

$m_{ij} = \sum_{s=1}^{n_j} \delta_{sij}$ = total number of marked individual sightings during secondary occasion i of primary interval j

T_{uj} = total number of unmarked individual sightings during primary interval j

δ_{sij} = Bernoulli random variable indicating sighting ($\delta_{sij} = 1$) or no sighting ($\delta_{sij} = 0$) of marked individual s on secondary occasion i of primary interval j (this only applies when individually identifiable marks are used)

ϵ_{ij} = total number of marks seen that were not identified to individual during secondary occasion i of primary interval j (this only applies when individually identifiable marks are used)

Parameters:

N_j = population size or abundance during primary interval j

p_{ij} = intercept (on logit scale) for mean resighting probability of secondary occasion i during primary interval j . Note that this parameter was referred to as β_{ij} in Chapter 1. If there is no individual heterogeneity ($\sigma_j = 0$), once back-transformed from the logit scale the real parameter estimate can be interpreted as the mean resighting probability

σ_j^2 = individual heterogeneity level (on the logit scale) during primary interval j (i.e., the variance of a random individual heterogeneity effect with mean zero)

D.1.1 No individually identifiable marks

If a known number of marks are in the population, but the marks are not individually identifiable, then the data for the mixed logit-normal model are t , k_j , n_j , m_{ij} , and T_{uj} . These are the same data as for the Joint Hypergeometric estimator (JHE) previously available in Program NOREMARK (White, 1996), but the mixed logit-normal model can be a more efficient alternative because it can borrow information about resighting probabilities across primary intervals (see Chapter 1). Note that because no information is known about individual identities, individual heterogeneity models cannot be evaluated with these data (i.e., $\sigma_j = 0$) and the probability of any individual being resighted on secondary occasion i of primary interval j is p_{ij} .

Suppose there is only one group and $t = 3$, $k_j = 4$, $n_1 = 30$, $n_2 = 33$, $n_3 = 32$, $m_{11} = 8$, $m_{21} = 9$, $m_{31} = 10$, $m_{41} = 5$, $m_{12} = 11$, $m_{22} = 10$, $m_{32} = 18$, $m_{42} = 9$, $m_{13} = 5$,

$m_{23} = 10$, $m_{33} = 13$, $m_{43} = 8$, $T_{u1} = 96$, $T_{u2} = 68$, and $T_{u3} = 59$.

Although no individual identities are known, these data may be summarized into artificial individual encounter histories similar to those of the mark-recapture robust design. The total number of unmarked individuals seen (T_{u_j}) must be entered after the encounter histories under the heading “Unmarked Seen Group=1” such that the resulting input file would be:

```

/* No Individual Marks 1 group */
/* 12 occasions, 3 primary, 4 secondary each */

/* Begin Input File */

111111111111 5;
111011110111 3;
011011110110 1;
001011100110 1;
000010100010 1;
000000100010 2;
000000100000 5;
000000000000 12;
....00000000 2;
....0000.... 1;

Unmarked Seen Group=1;
96 68 59;

/* End Input File */

```

Notice the sums of the encounter history columns (when multiplied by the corresponding frequency) equal m_{ij} and the sums of the frequencies with non-missing entries (i.e., not “...”) for each primary interval equals n_j . If this single group data were split into two groups, such that $n_1 = 17$, $n_2 = 19$, $n_3 = 18$, $m_{11} = 6$, $m_{21} = 6$, $m_{31} = 7$, $m_{41} = 4$, $m_{12} = 5$, $m_{22} = 5$, $m_{32} = 11$, $m_{42} = 5$, $m_{13} = 3$, $m_{23} = 7$, $m_{33} = 7$, $m_{43} = 7$, $T_{u1} = 48$, $T_{u2} = 40$, and $T_{u3} = 20$ for the first group, and $n_1 = 13$, $n_2 = 14$, $n_3 = 14$, $m_{11} = 2$, $m_{21} = 3$, $m_{31} = 3$, $m_{41} = 1$, $m_{12} = 6$, $m_{22} = 5$, $m_{32} = 7$, $m_{42} = 4$,

$m_{13} = 2$, $m_{23} = 3$, $m_{33} = 6$, $m_{43} = 1$, $T_{u1} = 48$, $T_{u2} = 28$, and $T_{u3} = 39$ for the second group, a possible input file would be:

```

/* No Individual Marks 2 groups */
/* 12 occasions, 3 primary, 4 secondary each */

/* Begin Input File */

111111111111 3 0;
111111110111 1 0;
111011110111 1 0;
111000100111 1 0;
001000100111 1 0;
000000100000 4 0;
000000000000 6 0;
....00000000 1 0;
....1111.... 1 0;
111111111111 0 1;
111011111110 0 1;
011011110110 0 1;
000011110010 0 1;
000011100010 0 1;
000010100010 0 1;
000000100000 0 1;
000000000000 0 6;
....00000000 0 1;

Unmarked Seen Group=1;
48 40 20;

Unmarked Seen Group=2;
48 28 39;

/* End Input File */

```

Notice here that the single group data has simply been split up into two group data. The encounter histories are followed by group frequencies just as in other MARK input files for mark-recapture encounter histories. The twist is that the unmarked data must be entered separately for each group. Again, the sums of the encounter history columns (when multiplied by the corresponding group frequencies) equals

m_{ij} for each group, and the sums of the frequencies with non-missing entries (i.e., not "...") for each primary interval equals n_j for each group.

The analysis using these input data (Logit_NoIndividualMarks_OneGroup.inp) yielded the following results for the time-constant ($p_{ij} = p, \sigma_j = 0$) model in MARK:

Real Function Parameters of {p(.) sigma(.)=0 N(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval		
			Lower	Upper	
1:p Session 1	0.3052632	0.0236241	0.2610167	0.3534229	
2:sigma Session 1	0.0000000	0.0000000	0.0000000	0.0000000	Fixed
3:N Session 1	108.62069	9.0417052	92.800732	128.42580	
4:N Session 2	88.689653	7.0894111	76.435814	104.40047	
5:N Session 3	80.318964	6.4400883	69.253239	94.671659	

Note that σ_j must be fixed to zero for these data because heterogeneity models do not apply when marks are not individually identifiable. This is because no information is known about individual resighting rates, and the above encounter histories are artificial in that they don't actually refer to a real individual's encounter history (these artificial encounter histories are just a convenient and consistent way to enter the data into MARK). Because there is no individual heterogeneity in the model, the real parameter estimate of p may be interpreted as the overall mean resighting probability (0.31 in this case).

D.1.2 Individually identifiable marks

If marks are individually identifiable, encounter histories are constructed just as for robust design mark-recapture data with the tk_j possible encounters representing δ_{sij} for individual s during secondary occasion i of primary interval j . However, now it is possible to have an individual identified as marked, but not to individual identity. A marked individual may be encountered but not be identified to individual when the mark was seen but the unique pattern or characters that identify the individual were obscured or too far away to read. These are the same data as could be used for

Bowden's estimator (Bowden and Kufeld, 1995) in Program NOREMARK (White, 1996), but the logit-normal model can be more efficient because information about resighting probabilities may be borrowed across primary intervals, and it does not require investment in individual heterogeneity parameters unless deemed necessary by the data (see Chapter 1). If an individual was not known to be in the population during any primary interval j , then missing values (.) are included for all k_j secondary occasions of that interval in the encounter history. The total number of marks seen but not identified to individual during secondary occasion i of primary interval j (ϵ_{ij}) are entered sequentially ($\epsilon_{11}, \epsilon_{21}, \dots, \epsilon_{k_1 1}, \dots, \epsilon_{1t}, \epsilon_{2t}, \dots, \epsilon_{k_t t}$) with each entry separated by a space. Using the data from the previous single group example but with $\epsilon = (0, 0, 0, 0, 1, 1, 1, 0, 0, 3, 0, 1)$ entered after the unmarked data under the heading "Marked Unidentified Group=1;", one possible input file would be:

```

/* Individual Marks 1 Group */
/* 12 occasions, 3 primary, 4 secondary each */

/* Begin Input File */

001001000011 1;
000000100110 1;
010000000110 1;
0000..... 1;
...01101101 1;
000010000000 1;
001100100000 1;
001011100011 1;
000010000010 1;
010001100000 1;
000000000010 1;
001010010110 1;
101000100000 1;
...01001110 1;
010000100000 1;
11001000... 1;
000100000000 1;
100000101011 1;

```

```

000011010000 1;
000100000000 1;
111000100001 1;
010000111001 1;
101000110000 1;
100001100010 1;
....00010000 1;
101000010010 1;
0000..... 1;
010000101000 1;
000110100000 1;
011000000000 1;
010011110010 1;
000010110000 1;
101100000001 1;
....00010110 1;
....11100100 1;

Unmarked Seen Group=1;
96 68 59;

Marked Unidentified Group=1;
0 0 0 0 1 1 1 0 0 3 0 1;

/* End Input File */

```

Note that the sums of each column $\sum_{s=1}^{n_j} \delta_{sij} = m_{ij} - \epsilon_{ij}$. The last two encounter histories are for individuals that were not marked and known to be in the population until immediately prior to the second primary interval. The fourth encounter history from the top represents an individual who was marked and known to be in the population during the first primary interval (when it was resighted 0 times), but known to have not been marked and in the population during the second or third primary intervals. This could be because the individual was known to have died, emigrated, or lost its mark. Similar to other MARK input files, the encounter histories may pertain to multiple groups and include individual covariates. Splitting the above data into two groups, the above input file could look like:

```

/* Individual Marks 2 Groups */

```

```
/* 12 occasions, 3 primary, 4 secondary each */
```

```
/* Begin Input File */
```

```
001001000011 0 1;  
000000100110 1 0;  
010000000110 1 0;  
0000..... 1 0;  
....01101101 1 0;  
000010000000 0 1;  
001100100000 1 0;  
001011100011 0 1;  
000010000010 0 1;  
010001100000 0 1;  
000000000010 0 1;  
001010010110 1 0;  
101000100000 1 0;  
....01001110 1 0;  
010000100000 1 0;  
11001000.... 1 0;  
000100000000 1 0;  
100000101011 1 0;  
000011010000 1 0;  
000100000000 0 1;  
111000100001 1 0;  
010000111001 0 1;  
101000110000 1 0;  
100001100010 0 1;  
....00010000 0 1;  
101000010010 0 1;  
0000..... 0 1;  
010000101000 0 1;  
000110100000 1 0;  
011000000000 1 0;  
010011110010 1 0;  
000010110000 0 1;  
101100000001 1 0;  
....00010110 1 0;  
....11100100 0 1;
```

```
Unmarked Seen Group=1;  
48 40 20;
```

```
Unmarked Seen Group=2;  
48 28 39;
```

```

Marked Unidentified Group=1;
0 0 0 0 0 1 1 0 0 1 0 1;

Marked Unidentified Group=2;
0 0 0 0 1 0 0 0 0 2 0 0;

/* End Input File */

```

Notice the encounter histories are followed by group frequencies the same way as they are in all other MARK input files.

Because marks are individually identifiable, individual heterogeneity models may be explored with these data. Here, individual heterogeneity is modeled as a random effect with mean zero and unknown variance σ_j^2 . These input data (Logit_IndividualMarks_OneGroup.inp) yielded the following results for the time-constant individual heterogeneity ($p_{ij} = p, \sigma_j = \sigma$) model in MARK:

Real Function Parameters of {p(.) sigma(.) N(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p Session 1	0.2754701	0.0276547	0.2246760	0.3328182
2:sigma Session 1	0.5272687	0.2579346	0.2126915	1.3071155
3:N Session 1	113.66936	10.635869	95.282220	137.23536
4:N Session 2	87.914774	7.1303186	75.621226	103.75424
5:N Session 3	78.370038	6.1915138	67.733970	92.171887

The time-constant model with no heterogeneity ($p_{ij} = p, \sigma_j = 0$) yields:

Real Function Parameters of {p(.) sigma(.)=0 N(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval		
			Lower	Upper	
1:p Session 1	0.2868421	0.0232018	0.2435938	0.3343745	
2:sigma Session 1	0.0000000	0.0000000	0.0000000	0.0000000	Fixed
3:N Session 1	113.66972	9.8898399	96.420546	135.39844	
4:N Session 2	92.266052	7.7342427	78.939944	109.45775	
5:N Session 3	83.422016	7.0187109	71.400363	99.111660	

As before, when $\sigma_j = 0$, the real parameter estimate of p may be interpreted as the overall mean resighting probability ignoring unidentified marks (0.29 in this

case). Notice that these results are different than the results from the same model when there were no individually identifiable marks. This is because the two versions (individually identifiable marks or not) of the mixed-logit normal model are only comparable when all marks are correctly identified to individual and σ_j is fixed to zero. Further, if one finds very little support for individual heterogeneity models (based on AIC_c) and has relatively many unidentified marks, it may be better to analyze the data as if there were no individually identifiable marks to begin with.

D.2 The Poisson-log normal mark-resight model

For use when the number of marked individuals in the population may be unknown or sampling is with replacement within secondary sampling occasions (or there is no concept of a distinct secondary sampling occasion without replacement). Marks must be individually identifiable. See Chapters 2 and 3 for full details.

Data:

t = the number of primary sampling intervals (may be through time, groups, or time and groups)

n_j = the exact number of marked individuals in the population during primary interval j

n_j^* = total number of marked individuals resighted at least once and known to be in the population

c_j = total number of individuals captured (c.g., for marking) immediately prior to primary interval j and therefore assumed to be present in the population during primary interval j , but not resighted during primary interval j

$c_j^* = n_j^* + c_j$ = total number of marked individuals captured immediately prior to primary interval j or resighted at least once during primary interval j . When

the number of marks is known exactly, $c_j^* = n_j$. When the number of marks is unknown this is the minimum number of marked individuals known to be in the population

y_{sj} = Poisson random variable for the total number of times individual s was resighted during primary interval j

ϵ_j = total number of times an individual was sighted and identified as marked, but not identified to individual identity during primary interval j

T_{uj} = total unmarked individual sightings during primary interval j

Parameters:

N = population size or abundance

α_j = intercept (on log scale) for mean resighting rate during primary interval j . Note that this parameter was referred to as θ_j in Chapters 2 and 3. If there is no individual heterogeneity ($\sigma_j = 0$), once back-transformed from the log scale this parameter can be interpreted as the mean resighting rate for the entire population

σ_j^2 = individual heterogeneity level (on the log scale) during primary interval j , i.e., the additional variance due to a random individual heterogeneity effect with mean zero

ϕ_j = apparent survival between primary intervals j and $j + 1$, $j = \{1, \dots, t - 1\}$

γ_j'' = probability of transitioning from an observable state at time j (e.g., on the study area) to an unobservable state at time $j + 1$ (e.g., off the study area), $j = \{1, \dots, t - 1\}$. This is equivalent to transition probability ψ_j^{OU} of Kendall and Nichols (2002)

γ'_j = probability of remaining at an unobservable state at time $j + 1$ (e.g., off the study area) when at an unobservable state at time j , $j = \{2, \dots, t - 1\}$. This is equivalent to $1 - \psi_j^{UO}$ of Kendall and Nichols (2002)

D.2.1 Closed resightings only

If interest is only in abundance estimates for t groups (or t time intervals for a single group with few or no marked individuals in common across the intervals), then the mark-resight Poisson-log normal model may be used in a fashion analogous to the closed mark-recapture models of Otis et al. (1978). In contrast to the closed mark-recapture models of Otis et al. (1978), individual covariates may be used in modeling resighting rates. However, because the data consist of the total number of times each marked individual in group j was resighted, the encounter histories must be modified to reflect this different type of encounter data. If the number of marks is known exactly, then n_j , y_{sj} , ϵ_j and T_{uj} are the same data used for Bowden's estimator (Bowden and Kufeld, 1995) in NOREMARK (White, 1996), but the Poisson-log normal model will generally be more efficient because information about resighting rates may be borrowed across groups (see Chapter 2). The number of marks available for each of the t groups may be known or unknown. The input file must contain the encounter histories containing the y_{sj} resightings, the frequencies and group(s) to which each encounter history pertains, the T_{uj} unmarked sightings and group(s) to which they pertain, the ϵ_j unidentified marks and the group(s) to which they pertain, and whether or not the number of marks is known exactly for each group. Instead of the familiar 0's and 1's of other MARK encounter histories, these histories simply contain the y_{sj} for each marked individual s in group j . Two character spaces are allocated to allow $y_{sj} > 9$. Note that this coding does not allow $y_{sj} > 99$. For reasons that will become clear in the next section covering the robust design Poisson-log normal model, entries for which $y_{sj} = 0$ are entered using '+0' instead of '00'.

Further, (unlike the logit-normal model and mark-recapture robust design), because the Poisson-log normal model does not condition on distinct secondary resighting occasions, the number of encounter occasions entered into MARK when creating a new analysis is the number of primary occasions (1 in this case). For instance, suppose in a very simple example that there were $t = 2$ groups with known $n_1 = n_2 = 3$ and $y_{11} = 2, y_{21} = 3, y_{31} = 0, y_{12} = 0, y_{22} = 0, y_{32} = 12, T_{u_1} = 11, T_{u_2} = 5, \epsilon_1 = 2,$ and $\epsilon_2 = 3$. The resulting input file would be:

```

/* Poisson log-normal mark-resight */
/* Occasions=1 groups=2 */

/* Begin Input File */

02 1 0;
03 1 0;
+0 1 0;
+0 0 1;
+0 0 1;
12 0 1;

Unmarked Seen Group=1;
11;

Unmarked Seen Group=2;
5;

Marked Unidentified Group=1;
2;

Marked Unidentified Group=2;
3;

Known Marks Group=1;
3;

Known Marks Group=2;
3;

/* End Input File */

```

The columns following the encounter histories are the frequencies for the two groups, just as would be done in other MARK encounter history files. Under “Unmarked Seen”, the T_{uj} are entered separately for each group. The “Marked Unidentified” data (ϵ_j) are entered in the same fashion separately for each group. Similarly, the “Known Marks” headings contain the n_j for each group.

Using the same example, but now with the number of marks being unknown for the second group, the input file must be modified to reflect that n_2 is unknown and $y_{s2} = 0$ is no longer observed:

```

/* Poisson log-normal mark-resight */
/* occasions=1 groups=2 */

/* Begin Input File */

02 1 0;
03 1 0;
+0 1 0;
12 0 1;

Unmarked Seen Group=1;
11;

Unmarked Seen Group=2;
5;

Marked Unidentified Group=1;
2;

Marked Unidentified Group=2;
3;

Known Marks Group=1;
3;

Known Marks Group=2;
0;

/* End Input File */

```

Here, the encounter histories for $y_{12} = 0$ and $y_{22} = 0$ have been removed because they cannot be observed if the number of marked individuals in the population (n_2) is unknown. Further, under “Known Marks;” there is now a “0” for the second group. By including a “0” for the second group’s “Known Marks”, MARK knows the number of marks is unknown and will use the zero-truncated Poisson-log normal model.

It is possible that the number of marks may be unknown for a given group, but some marking was conducted immediately prior to the primary sampling interval of interest. Here, some additional information is known about the minimum number of marks in the population because those (previously marked or newly marked) individuals captured during the marking period are known to have been present and available for resighting (even if they were not resighted during the interval of interest). Suppose this were the case in the above example, such that the second individual of the second group was captured and marked immediately prior to resighting surveys but never resighted. This information (although not used in the zero-truncated likelihood) may be included in the encounter history file to make the lower bound for $N_2 \geq c_2^*$:

```

/* Poisson log-normal mark-resight */
/* occasions=1 groups=2 */

/* Begin Input File */

02 1 0;
03 1 0;
+0 1 0;
+0 0 1;
12 0 1;

Unmarked Seen Group=1;
11;

Unmarked Seen Group=2;
5;

```

```

Marked Unidentified Group=1;
2;

Marked Unidentified Group=2;
3;

Known Marks Group=1;
3;

Known Marks Group=2;
0;

/* End Input File */

```

Because the “Known Marks;” is still “0” for the second group, MARK knows the actual number of marks is unknown and to use the zero-truncated model for the second group, but $c_2^* = 2$ (instead of $n_2^* = 1$) will be used in establishing the lower bound for N_2 . When the number of marks is unknown, the information provided by such encounters via capture events will become more useful when considering the robust design Poisson-log normal model in the next section.

Now to analyze a more realistic $l = 2$ data set where the number of marks was known for the first group but not for the second. No marking occurred immediately prior to resighting surveys for the second group, so $c_2^* = n_2^*$, and therefore no ‘+0’ encounter histories are included for the second group. For these data, $n_1 = 60$, $T_{u_1} = 1237$, $\epsilon_1 = 10$, $n_2^* = 33$, $T_{u_2} = 588$, and $\epsilon_2 = 5$:

```

/* Poisson log-normal mark-resight */
/* Occasions=1 groups=2 */

/* Begin Input File */

02 1 0;
03 1 0;
03 1 0;
01 1 0;
01 1 0;

```

01 1 0;
02 1 0;
09 1 0;
05 1 0;
01 1 0;
01 1 0;
01 1 0;
03 1 0;
03 1 0;
02 1 0;
06 1 0;
04 1 0;
02 1 0;
03 1 0;
01 1 0;
02 1 0;
01 1 0;
03 1 0;
04 1 0;
03 1 0;
03 1 0;
05 1 0;
03 1 0;
04 1 0;
04 1 0;
+0 1 0;
04 1 0;
01 1 0;
03 1 0;
02 1 0;
01 1 0;
03 1 0;
02 1 0;
03 1 0;
05 1 0;
06 1 0;
03 1 0;
01 1 0;
04 1 0;
07 1 0;
03 1 0;
+0 1 0;
06 1 0;
+0 1 0;
04 1 0;

+0 1 0;
02 1 0;
02 1 0;
02 1 0;
02 1 0;
05 1 0;
02 1 0;
01 1 0;
04 1 0;
+0 1 0;
02 0 1;
02 0 1;
04 0 1;
01 0 1;
02 0 1;
01 0 1;
01 0 1;
01 0 1;
04 0 1;
03 0 1;
01 0 1;
05 0 1;
02 0 1;
02 0 1;
05 0 1;
02 0 1;
01 0 1;
05 0 1;
01 0 1;
02 0 1;
07 0 1;
01 0 1;
03 0 1;
05 0 1;
03 0 1;
03 0 1;
04 0 1;
02 0 1;
03 0 1;
05 0 1;
02 0 1;
02 0 1;
02 0 1;

Unmarked Seen Group=1;

```

1237;

Unmarked Seen Group=2;
588;

Marked Unidentified Group=1;
10;

Marked Unidentified Group=2;
5;

Known Marks Group=1;
60;

Known Marks Group=2;
0;

/* End Input File */

```

The analysis for these data (Poisson_TwoGroups.inp) yielded the following results for the most general model:

Real Function Parameters of {alpha(g) sigma(g) N(g)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:alpha	2.620091	0.2495220	2.1309460	3.1090722
2:alpha	2.3579937	0.3661278	1.6403831	3.0756042
3:sigma	0.2909827	0.1386550	0.0990465	0.6050691
4:sigma	0.2694048	0.2560261	0.0279997	0.8251843
5:N	486.55517	37.472530	353.10901	500.00133
6:N	260.59714	30.369020	168.07386	287.12042

Here are the results for the model with no group effects on α_j or σ_j :

Real Function Parameters of {alpha(.) sigma(.) N(g)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:alpha	2.5330927	0.2049978	2.1312970	2.9348883
2:sigma	0.2857660	0.1216583	0.1284121	0.6359386
3:N	500.94650	32.963465	440.92617	570.42389
4:N	244.56021	17.524220	212.90589	281.78407

Here are the results for the model with no group effect on α_j and $\sigma_j = 0$:

Real Function Parameters of {alpha(.) sigma(.)=0 N(g)}

Parameter	Estimate	Standard Error	95% Confidence Interval		
			Lower	Upper	
1:alpha	2.6488893	0.1731506	2.3095142	2.9882644	
2:sigma	0.0000000	0.0000000	0.0000000	0.0000000	Fixed
3:N	499.34483	29.766676	444.76851	561.66238	
4:N	243.77627	15.823866	214.97302	277.13858	

Note that to run models without individual heterogeneity, σ_j must be fixed to zero. When $\sigma_j = 0$, then the real parameter estimate for α may be interpreted as the mean resighting rate for all individuals. In this case, the marked individuals for both groups were resighted an average of 2.65 times during the single primary interval.

D.2.2 Full-likelihood robust design

If interest is in apparent survival, transition rates, and abundance for one or more groups through time, then a mark-resight robust design analogous to the mark-recapture robust design of Kendall et al. (1995, 1997) may be employed. In contrast to the modeling of recapture probabilities in the mark-recapture robust design utilizing the closed capture models of Otis et al. (1978), the mark-resight robust design may incorporate individual covariates in modeling resighting rates. The input files are similar to those from the previous Closed Resightings model, but now individuals with permanent field-readable marks may be encountered through time across t primary sampling intervals in a robust design. For instance, if an individual s was encountered $y_{s1} = 4$ times during the first primary interval and $y_{s2} = 2$ times during the second primary interval, then the encounter history would be ‘0402’. Each encounter history will contain $2t$ characters, again allowing two characters for each y_{sj} . Because the number of marks can be known or unknown for any given primary interval, the primary intervals must again be identified as such under the “Known Marks” heading in the input file. In the individual encounter histories, a ‘+0’ indicates that the individual was known to be a marked individual available for

resighting during primary interval j but never resighted. Therefore, when the number of marks is unknown, the total number of '+0' entries during primary interval j is equal to c_j as defined above. A '-0' indicates a previously encountered individual that was not encountered (via capture OR resighting) during primary interval j , and only applies when the number of marks is unknown (i.e., when the number of marks is known a '-0' is impossible). Lastly, a '..' indicates a marked individual who has not yet been encountered prior to and during primary interval j OR an individual that is known to no longer be in the marked population (due to removal, mortality, or permanent emigration) during and after primary interval j . As in the regular CJS model in MARK, any '..' contributes no information to the estimation of parameters. When n_j is known, '+0' contributes information towards estimation of survival, transition rates, resighting rates, and abundance. When n_j is unknown, '+0' contributes information towards estimating survival and transition rates, but makes no contribution to the estimation of resighting rates or abundance (but it does affect the minimum lower bound for N_j as described in the previous section). A '-0' contributes no information to the estimation of resighting rates or abundance (it is only a valid entry when the number of marks is unknown), and is equivalent to a '0' in the regular CJS encounter history for MARK. It therefore only contributes to the estimation of survival and transition rates. As before, the encounter histories are followed by group frequencies in the usual MARK input file. The entries for "Unmarked Seen", "Marked Unidentified", and "Known Marks" are the same as described earlier and are entered separately for each group. In the following example input file with a single group and $t = 4$ primary intervals, the number of marks are known for the first and second primary intervals, but unknown for the third and fourth. Because the model does not condition on distinct secondary resighting occasions, the number of encounters that are input into MARK is equal to the number of primary occasions ($t = 4$ in this case). Capturing for marking occurred immediately

prior to the first, second, and third occasion, but not the fourth occasion, so $n_4^* = c_4^*$. Here, $n_1 = 45$, $T_{u_1} = 1380$, $\epsilon_1 = 8$, $n_2 = 67$, $T_{u_2} = 1120$, $\epsilon_2 = 10$, $n_3^* = 56$, $T_{u_3} = 1041$, $\epsilon_3 = 9$, $n_4^* = 52$, $T_{u_4} = 948$, and $c_4 = 11$:

```

/* Poisson log-normal Mark-resight */
/* 4 occasions, 1 group */

/* Begin Input File */

....+002 1;
..06-0-0 1;
04060202 1;
+0010402 1;
070602-0 1;
04020606 1;
..020101 1;
060602-0 1;
..04-004 1;
040401-0 1;
03010103 1;
02030503 1;
..03+0-0 1;
070503-0 1;
04+00104 1;
01010401 1;
06060103 1;
02010602 1;
..0403-0 1;
..020306 1;
020202-0 1;
..050201 1;
02010103 1;
031002-0 1;
+0+00704 1;
01030102 1;
01010302 1;
..02-0-0 1;
..020210 1;
020301-0 1;
02+00503 1;
02+0+0-0 1;
02020302 1;
..080201 1;

```

..040603 1;
030304-0 1;
02020202 1;
..030107 1;
04050402 1;
+0050101 1;
..030605 1;
05+00101 1;
..04-003 1;
06020204 1;
..03-004 1;
..010201 1;
04+00303 1;
04040204 1;
01+00201 1;
0403-004 1;
01+00103 1;
..020307 1;
01060701 1;
..040101 1;
03040301 1;
..0404-0 1;
03050101 1;
05040202 1;
03010202 1;
05+00302 1;
01020202 1;
01+0+0-0 1;
01070202 1;
..050105 1;
02040205 1;
02010301 1;
..03-010 1;
..01+0-0 1;

Unmarked Seen Group=1;
1380 1120 1041 948;

Marked Unidentified Group=1;
8 10 9 11;

Known Marks Group=1;
45 67 0 0;

/* End Input File */

The first encounter history indicates this individual was not captured for marking until immediately prior to the third primary occasion, and the '+0' for the third occasion indicates that it was not resighted (although known to be a marked individual available for resighting during this occasion). This individual was then resighted twice during the fourth occasion. The second encounter history from the top indicates that this individual was only known to be marked and in the population during the second primary occasion (when it was resighted 6 times). Because the number of marks is known for the first primary interval, this individual must have been marked between the first and second primary intervals. As indicated by '-0', this individual was never encountered again when the number of marks was unknown during the third and fourth primary intervals. The third encounter history from the top indicates an individual who was known to be marked and available for resighting for all $t = 4$ occasions. The '+0' entry for the first primary occasion indicates that it was known to be marked and available for resighting, but never resighted. This individual was then resighted one, four, and two times during the second, third, and fourth intervals, respectively. The final encounter history describes an individual that was not marked until immediately prior to the second primary occasion, and during the second occasion it was resighted one time. It was then captured immediately prior to (but never resighted during) the third occasion. Because the number of marks was unknown for the third occasion, this '+0' primarily contributes information to the estimation of survival and transition rates (as described in the previous section). As indicated by '-0' this individual was then never resighted during the fourth occasion (and could not have been captured immediately prior to the occasion because no capturing took place). Because no individuals were captured (e.g., for marking) immediately prior to the fourth occasion (and the number of marked individuals was unknown), no '+0' appears in the entries for this occasion. Because no marked

individuals were known to have left the population (due to removal, mortality, or permanent emigration), no ‘.’ entries appear after an individual’s first encounter. The “Unmarked Seen;” entry tells MARK that 1380 unmarked sightings occurred during the first primary interval, 1120 during the second, 1041 during the third, and 948 during the fourth. The “Marked Unidentified” entry follows the same pattern. The “Known Marks” entry tells MARK that n_j is known for the first and second primary intervals ($n_1 = 46$, $n_2 = 60$), but unknown for the third and fourth (as indicated by ‘0’ for these occasions).

As a simple two group example, suppose for the first group that $n_1 = 10$, $T_{u_1} = 800$, $\epsilon_1 = 4$, $n_2 = 14$, $T_{u_2} = 950$, $\epsilon_2 = 2$, $n_3^* = 11$, $T_{u_3} = 500$, $\epsilon_3 = 6$, $n_4^* = 8$, $T_{u_4} = 1201$, and $\epsilon_4 = 3$. For the second group, $n_1 = 11$, $T_{u_1} = 459$, $\epsilon_1 = 2$, $n_2^* = 14$, $T_{u_2} = 782$, $\epsilon_2 = 5$, $n_3^* = 15$, $T_{u_3} = 256$, $\epsilon_3 = 0$, $n_4^* = 11$, $T_{u_4} = 921$, and $\epsilon_4 = 1$. With capturing (e.g., for marking) occurring for both groups immediately prior to the first and second occasions, a possible input file would be:

```
/* Poisson log-normal Mark-resight */
/* 4 occasions, 2 groups */

/* Begin Input File */
04060202 1 0;
..06-0-0 1 0;
+0010402 1 0;
070602-0 1 0;
04020606 1 0;
..020101 1 0;
060602-0 1 0;
..04-004 1 0;
040401-0 1 0;
03010103 1 0;
02030503 1 0;
..03-0-0 1 0;
070503-0 1 0;
04+00104 1 0;
01010401 0 1;
06060103 0 1;
02010602 0 1;
```

```

..0403-0 0 1;
..020306 0 1;
020202-0 0 1;
..050201 0 1;
02010103 0 1;
031002-0 0 1;
+0-00704 0 1;
01030102 0 1;
01010302 0 1;
..02-0-0 0 1;
..020210 0 1;
020301-0 0 1;
02+00503 0 1;

Unmarked Seen Group=1;
800 950 500 1201;

Unmarked Seen Group=2;
459 782 256 921;

Marked Unidentified Group=1;
4 2 6 3;

Marked Unidentified Group=2;
2 5 0 1;

Known Marks Group=1;
10 14 0 0;

Known Marks Group=2;
11 0 0 0;

/* End Input File */

```

Here, the encounter histories are followed by two columns for group frequencies in the usual MARK input file manner. The entries for “Unmarked Seen”, “Marked Unidentified”, and “Known Marks” are entered separately for each group. The entries under “Known Marks” tell MARK that the number of marks was known for the first and second primary occasions of the first group ($n_1 = 10$, $n_2 = 14$) and for only the first primary occasion of the second group ($n_1 = 11$). Again, no ‘-0’ can

appear for a primary occasion where the number of marks is unknown. Notice that a '+0' appears in the encounter history for the last individual of the second group, but that the number of marks for this primary occasion was unknown. This indicates that this individual happened to be caught (e.g., during marking) immediately prior to the second primary occasion, but was never resighted. Hence, for the second group during the second primary interval, $n_2^* = 14$ and $c_2^* = 15$.

An analysis using the single group data (Poisson_RobustDesign_OneGroup.inp) yielded the following results for the random emigration model $\{\phi(.)\gamma''(.) = \gamma'(.)\alpha(t)\sigma(t)N(t)\}$:

Real Function Parameters of {Phi(.) gamma''(.)=gamma'(.). alpha(t) sigma(t) N(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:alpha	2.7533589	0.2906413	2.2400523	3.3842895
2:alpha	2.6391370	0.2712789	2.1587110	3.2264830
3:alpha	2.1023124	0.2757290	1.6275392	2.7155828
4:alpha	2.1101662	0.3295252	1.5566457	2.8605104
5:sigma	0.2552927	0.1727985	0.0766079	0.8507524
6:sigma	0.4688073	0.1132659	0.2939316	0.7477258
7:sigma	0.4099264	0.1555193	0.1997845	0.8411045
8:sigma	0.5489796	0.1274057	0.3504234	0.8600414
9:N	501.60001	43.560257	423.88945	595.24906
10:N	428.88089	35.134127	366.30696	504.53669
11:N	489.22506	46.107464	407.96411	589.51777
12:N	410.18201	45.453163	331.58621	510.87225
13:Phi	0.9857400	0.0182539	0.8443149	0.9988663
14:Gamma''	0.0552755	0.0364728	0.0146651	0.1870013

For model $\{\phi(.)\gamma''(.) = \gamma'(.)\alpha(.)\sigma(.)N(t)\}$:

Real Function Parameters of {Phi(.) gamma''(.)=gamma'(.). alpha(.) sigma(.) N(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:alpha	2.4536985	0.1478956	2.1805245	2.7610956
2:sigma	0.4376083	0.0655452	0.3268107	0.5859693
3:N	524.49384	28.499239	471.81002	583.68075
4:N	460.04989	24.370049	415.11342	510.78703
5:N	426.24093	23.102678	383.69402	474.39761
6:N	379.16926	20.875980	340.74421	422.70778
7:Phi	0.9858690	0.0178497	0.8499082	0.9988380
8:Gamma''	0.0751540	0.0287552	0.0348592	0.1545672

Here, AIC_c indicates much more support for the simpler model (1012.6 versus 1020.4). Notice that a significant population decline would be inferred from the

latter model (but not the former), one of the advantages of borrowing information across primary intervals that the Poisson-log normal model provides over other previously available mark-resight estimators.

D.3 Suggestions for mark-resight analyses in MARK

1. To start an analysis from scratch (after an input file has been created), select the “Mark-Resight” data type. The option will then be given to select “Logit-Normal” or “Poisson-log normal.” For “Logit-Normal” one doesn’t specify whether or not individual marks were used. This is left to the user to keep track of (by not running any individual heterogeneity models). For “Poisson-log normal” one doesn’t need to specify robust design or not. If there are multiple primary occasions for the group(s), then MARK will automatically set up an analysis that includes the open period parameters (ϕ , γ'' , and γ').
2. Because convergence with these models is sensitive to the starting values (particularly for N), initial values (on the log scale) must always be manually provided in the Run window when using the design matrix. This means that if $N = 100$, then $\log(N) = 4.6$ should be provided as an initial value. MARK provides its own initial values that usually work when running a model from the PIMs, so I suggest that an analysis begin with simple PIM models from which the initial values may then be provided for running more complex models and for when utilizing the design matrix. If convergence issues remain after following this strategy, I suggest trying a series of initial values covering the suspected range of the parameter(s) and possibly other Run window options such as “Do not standardize design matrix.” The “Use Alt. Opt. Method” option is currently not working for the models.
3. The σ parameter must be fixed to zero in the Run window to examine a model

that ignores individual heterogeneity in resighting probabilities.

4. When using the logit-normal model, MARK by default assigns the log link to σ and N , and applies whatever link is specified in the Run window to p .
5. When using the Poisson model, MARK by default assigns the log link to α , σ , and N , and applies whatever link is specified in the Run window to ϕ , γ'' , and γ' (if using the robust design).

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