Abstract

GRIFFITH, EMILY H. Catch Curve and Capture Recapture Models: A Bayesian Combined Approach. (Under the direction of Professors Kenneth H. Pollock and Sujit K. Ghosh.)

When studying animal populations, one demographic parameter of interest is the annual survival rate. Methods for estimating survival rates of animal populations fall into two general categories: methods based on marked and on non-marked animals. Catch curve analysis falls into the latter category, is based on strong assumptions about population dynamics, and is much less expensive than marked animal methods. Capture-recapture methods, on the other hand, use marked animals and require strong assumptions about individual capture and survival probabilities.

Chapman and Robson developed methods to analyze catch curve data in the sixties using geometric and multinomial distributions to obtain an estimate of the survival rate. The assumptions for the Chapman-Robson survival estimate are: a random sample of the age structure of the living population is obtained, that is, equal catchability for all fully vulnerable age classes, and the population has a stable age distribution, meaning that survival and fecundity rates have remained constant for a long period of time. A stable age distribution where the population size also remains constant is called stationary.

Rarely, it is possible to collect ages-at-death data, a random sample from the natural deaths that occur in a population between two time periods. Udevitz and Ballachey augmented catch curve data with ages-at-death data in the late nineties, resulting in the ability to relax either the assumption of a stable age distribution or known population growth rate. Neither type of data involves marking animals.

Marked animal methods include band recovery, telemetry, and capture-recapture data. We focus specifically on capture-recapture data, and the Cormack-Jolly-Seber (CJS) open population model. It is important to note that the CJS model estimate of survival is "apparent survival." In capture-recapture methods, mortality is confounded with emigration. With telemetered animals, the two processes can be separated. Tag-return models where

hunting or fishing occurs over the whole range of the population also allow estimation of survival because emigration is zero.

In Chapter 1, we develop the Bayesian approach to catch curve analysis. We begin with the simple situation of a stable population and a single catch curve. After extending our method to multiple years, we relax the model assumptions to include random effects across years. The proposed model is validated using predictive distributions and compared with the traditional methods using the focused deviance information criterion. We conclude that many benefits can be obtained from the Bayesian approach to the analysis of a single catch curve or multiple catch curves.

In Chapter 2, we augment catch curve data with capture-recapture data by combining the likelihoods in a hierarchical Bayesian framework. We estimate the fidelity rate and the population growth rate, explore using informative priors and auxiliary information, and illustrate these models with a real data set and a small simulation study.

In Chapter 3, we develop a Bayesian method for analyzing catch curve and ages-at-death data, based on the combination of likelihoods developed by Udevitz and Ballachey. We utilize the Bayesian framework, relax both the assumption of a stable age-distribution and the assumption of a known population growth rate, and examine the effects of informative prior distributions.

Future directions for research for us include modeling a capture-recapture design where a known subset of the captured animals is aged at each capture period. Ideally, this would provide a way to link the population estimates across years and ages without the expense of aging the entire sample.

Catch Curve and Capture Recapture Models:
A Bayesian Combined Approach

by

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Dedication

To my husband, Eric Griffith,

and to my parents, Mark and Cay Hohmeister

Biography

Emily Griffith was born on July 11, 1982, in Philadelphia, Pennsylvania. She is the younger child of Mark and Cay Hohmeister. She grew up in Tallahassee, Florida, graduating *cum laude* from Leon High School in 2000. Emily attended Florida State University, earning a B.S. in statistics, with minors in mathematics and Spanish, in 2003. She began graduate studies at North Carolina State University in the fall of 2003, earning a Master of Statistics degree in 2005. She continued her education at North Carolina State University, studying for her doctorate in statistics.

During her graduate studies, Emily taught two semesters of introductory statistics, spent two summers interning with the Applied Ecology and Restoration Research Branch of the National Ocean Service/NOAA in Beaufort, North Carolina, and spent an additional year as a statistical consultant for the College of Agriculture and Life Sciences. She was involved in the departmental Graduate Student Association as both Vice-President for the 2004-2005 academic year and President for the 2005-2006 academic year. She married Eric Griffith in May of 2006. She also took two wonderful trips through Europe with her mother, once in 2004 and again in 2007.

Emily plans to start a post-doctoral position at the Patuxent Wildlife Research Center, Laurel, Maryland in April of 2008. She will study the problem of spatial sampling and design in the context of the North American Breeding Bird Survey.

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CHAPTER 1

Bayesian Catch Curve Analysis

Summary

Catch curves have been used to estimate survival and instantaneous mortality for fish and wildlife populations for many years. We develop a Bayesian approach to catch curve analysis. There are many potential advantages to the Bayesian approach over the traditional methods such as least squares and maximum likelihood, based on large sample theory. Bayesian estimates are valid for finite samples, and efficient numerical methods can be used to obtain estimates of instantaneous mortality. First, the proposed Bayesian approach is illustrated for a single catch curve and then extended to multiple years of catch curves. We also relax the model assumption of a stable age distribution to allow random effects across years. The proposed models are compared with the traditional methods using the focused DIC. We conclude that many benefits can be obtained from the Bayesian approach to a single catch curve and to multiple years of data, such as closed-form variance estimates and the ability to both model and estimate the process variation of survival rates.

Key words: Catch curve; focused DIC; life table methods; Markov chain Monte Carlo methods; standing age distribution; survival estimation.

1.1 Introduction

The first catch curve analysis was developed by Edser (1908), who used a least-squares regression method. Chapman and Robson (1960) and Robson and Chapman (1961) formally developed statistical methods of analyzing catch curve data. They proposed estimating the survival probability, denoted by S, by using a regression model, a geometric model, and a multinomial model. The regression model was based on the idea that $E(n_x) = NS_1S_2S_3\ldots S_x p$ where S_x denotes the survival probability of an individual at age x, N the total number of individuals, p the capture probability, and n_x is the num-

ber of fish captured from age class x. If capture probability (p) and survival (S) are age independent, then it follows that $E(n_x) = NS^x p$ (Seber, 1982, p.426). Next taking logs, $\log E(n_x) = \log(Np) + x \log(S)$. Setting the term $\log(Np) = K$ and assuming that $\log E(n_x) \approx E(\log(n_x))$ we obtain

$$\log(n_x) = K + x \log(S) + \epsilon_x \tag{1.1}$$

where K is an unknown parameter and ϵ_x is the random deviation with $E(\epsilon_x) = 0$ and $\operatorname{var}(\epsilon_x) = \sigma^2$. The assumptions made are: (i) The expected value of $\log(n_x)$ is a linear function of age with slope $\log S$, and (ii) The variance of $\log(n_x)$ is independent of x. They show that the expected value of $\log(n_x)$ can be approximated.

$$E(\log n_x) = \log(p\bar{N}_0) + x \log(\bar{S}) - \frac{1}{p\bar{N}_0 S^x} + o\left(\frac{1}{p\bar{N}_0 S^x}\right) \tag{1.2}$$

where $\bar{N}_0$ is the mean value of the independent random variable N_0, which is the size of the zero age group. (Chapman and Robson (1960) specify that $n_x \sim \operatorname{Binomial}(N_0, pS^x)$.) The departure from the assumption $E(\log(n_x)) = K + x \log(S)$ becomes larger as $p\bar{N}_0 S^x$ decreases and they suggest using the improved regression equation where instead of regressing $\log(n_x)$ on x, one regresses $\log(n_x) - 1/(n_x + 1)$ on x. Both Chapman and Robson (1960) and Seber (1982) recommend truncating the catch curve data at the point where n_x drops below 5 in order to reduce the dependence of σ^2 on x.

Chapman and Robson (1960) also developed methods to use the geometric distribution and the multinomial distribution to obtain a maximum likelihood estimator and then a uniformly minimum variance unbiased estimator (UMVUE) of the survival rate. The assumptions for the Chapman-Robson survival estimate are constant survival for all age classes and all years, a stable age distribution, a stationary population, and equal catchability for all fully vulnerable age classes. A population with a stable age distribution has survival and fecundity rates that have remained constant for a long period of time (Messier 1990; Udevitz and Ballachey 1998). However, a stable age distribution does not necessarily imply that the population size remains constant. A population can increase, decrease, or remain constant in size and still have a stable age distribution (Williams et al. 2002). A stationary population

is one where the populations growth rate, λ, is one. Let N_x be the number of individuals in the sample of age x. Also let $T = \sum_x x N_x$. Notice that there exists a finite x_{max} such that $N_x = 0$ for all $x > x_{max}$ and hence T is finite with probability 1. The N_xs conditional on $\sum N_x = N$ follow a multinomial distribution, given below.

$$L(S|N,T) = P(N_0 = n_o, N_1 = n_1, \ldots |N) = \frac{N!}{\prod_{x=0}^{\infty} n_x!} \prod_{x=0}^{\infty} (S^x)^{n_x} (1-S)^N \propto S^T (1-S)^N.$$

(1.3)

The maximum likelihood estimator of S based on the above likelihood is

$$\hat{S}_{MLE} = \bar{X}/(1 + \bar{X}),$$

(1.4)

where $\bar{X} = T/N$. The MLE is a biased estimator (Chapman and Robson 1960). A uniformly minimum variance unbiased estimator (UMVUE) for S does exist, and is given by the formula

$$\hat{S}_U = \frac{\bar{X}}{1 + \bar{X} - \left(\frac{1}{N}\right)}.$$

(1.5)

The variance for $\hat{S}_U$ cannot be obtained in closed form. The minimum variance unbiased estimator of $\mathrm{var}(\hat{S}_U)$ is

$$\widehat{\mathrm{var}}(\hat{S}_U) = \hat{S}_U \left(\hat{S}_U - \frac{T-1}{N+T-2} \right).$$

(1.6)

Chapman and Robson (1960) also discuss the instantaneous mortality rate, Z, which can be defined by the relationship $Z = -\log S$. For the geometric model, no unbiased estimate of Z exists (Chapman and Robson 1960). Z can be estimated consistently using the fact that $\hat{Z}_{MLE} = \log(\hat{S}_{MLE})$. Z can also be estimated using least-squares estimation using the regression model given in Equation (1.1). However, Chapman and Robson (1960) do not recommend using the regression estimator due to the potential for bias implied by Equation (1.2). Robson and Chapman (1961) conclude that the best estimate for S, and the corresponding standard error, is the UMVUE.

Jensen (1985) compares the UMVUE of S suggested by Chapman and Robson (1960) and Robson and Chapman (1961) to the least-squares estimate from the regression line given in Equation (1.1). Jensen (1985) concludes that the precision of the UMVUE is a function of

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the number of animals in the catch curve. However, the precision of the least-squares estimate of S increases with the number of age classes in the sample. Murphy (1997) also explored the bias in the Chapman-Robson estimator of instantaneous mortality from the UMVUE of S, $\hat{S}_U$, setting $\hat{Z}_U = \log(\hat{S}_U)$ and compared it with the bias for the least-squares regression estimate of the same. Murphy (1997) found that the least-squares regression estimates of Z were biased, underestimating the true instantaneous mortality rate. Small samples and low instantaneous mortality increase this bias (Murphy 1997). We conclude that the UMVUE of S has the most desirable properties out of all these estimators. However, there is not a closed form estimate of the variance of the survival rate parameter under the geometric or multinomial model. Also, the UMVUE does not exist for estimating Z.

In this chapter we develop a Bayesian approach to estimate S and Z and we show that closed form estimates can be obtained based on a finite sample. In Section 1.2, we describe our method for a single catch curve analysis. In Section 1.3, we extend our method to multiple years of catch curves. In Section 1.4, we extend our method further to allow for the survival rate to have a random effect across years. In Sections 1.3 and 1.4, the methods are illustrated with analysis based on real data. In Section 1.5, we report the results of two simulation studies that we performed to test our random effects method. We conclude with some suggestions for future research.

1.2 Bayesian Catch Curve with Conjugate Priors

We now present a Bayesian analysis using conjugate priors. The conjugate prior for the multinomial distribution is the Dirichlet prior (Robert 2001, p. 121). In the specific case of the catch curve's conditional multinomial distribution, because there are only two multinomial probabilities, S and $1-S$, the Dirichlet distribution is equivalent to the Beta(α, β) distribution (Robert 2001, p. 521).

Applying Bayes Theorem to the likelihood of the data given in Equation (1.3) and the Beta(α, β) prior distribution yields

$$\pi(S|T, N, \alpha, \beta) = \frac{S^{T+\alpha-1}(1-S)^{N+\beta-1}}{B(T+\alpha, N+\beta)}, \tag{1.7}$$

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meaning that the posterior distribution of S is a Beta$(T + \alpha, N + \beta)$ distribution.

The Bayes estimator under squared error loss is the posterior expectation of the Beta$(T + \alpha, N + \beta)$ distribution. Thus, the Bayes estimator of S is given by

$$\hat{S}_B = E[S|N, T] = \frac{T + \alpha}{T + \alpha + N + \beta}, \tag{1.8}$$

with corresponding variance

$$\widehat{\text{var}}(\hat{S}_B) = \text{var}[S|N, T] = \frac{(T + \alpha)(N + \beta)}{(T + \alpha + N + \beta)^2 (T + \alpha + N + \beta + 1)}. \tag{1.9}$$

These results hold true for any $\alpha, \beta > 0$. Using specific αs and βs, we can obtain the other estimators of the survival rate using Bayesian inference. Notice that as $\alpha + \beta \to 0$, $\hat{S}_B \to \hat{S}_{MLE}$. Thus the MLE can be obtained as a limiting case of the Bayes estimator using an improper prior $\pi(S) = 1/(S(1 - S))$. This prior has most of its weight at zero and one. Similarly, as $\alpha \to 0$ and $\beta \to -1$, $\hat{S}_B \to \hat{S}_U$ and again we see that the UMVUE is obtained as a limit of the Bayes estimator using an improper prior $\pi(S) = 1/(S(1 - S)^2)$. This prior has most of its weight at one. Alternatively, if we use the weighted squared error loss, $L_w(S, a) = w(S)(S - a)^2$ with $w(S) = 1/(S(1 - S))$ then the Bayes estimator is given by $\hat{S}_{wB} = E(w(S)S|T, N)/E(w(S))|T, N) = \hat{S}_{MLE}$ if $\alpha = \beta = 1$.

Bayesian inference calls for a prior distribution on the parameter S. If we do not have any substantial prior information, we can use a noninformative prior like the Jeffreys prior. Jeffreys prior is $\pi^*(S) \propto I^{\frac{1}{2}}(S)$ where $I(S)$ is Fisher's information matrix (Robert 2001, p. 130). Notice that $I(S) = E\left[-\frac{\partial^2 \log L(S|N,T)}{\partial S^2}\right] = E\left[T/S^2 + N/(1 - S)^2\right] = N/(S(1 - S)^2)$, which leads to Jeffreys prior being $\pi^*(S) \propto I^{\frac{1}{2}}(S) \propto [\sqrt{S}(1 - S)]^{-1}$, which is the limiting kernel of a Beta $(1/2, \beta)$ distribution when $\beta \to 0$. Thus, in this case the posterior distribution, using Jeffreys prior, is a Beta$(T + 1/2, N + 0)$, which is a proper distribution as long as $N > 0$.

Using Jeffreys prior, the posterior mean and variance of S are

$$\hat{S}_J = \frac{T + \frac{1}{2}}{T + N + \frac{1}{2}} \tag{1.10}$$

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and

$$\widehat{\mathrm{var}}(\hat{S}_J) = \frac{(T + \frac{1}{2})(N)}{(T + N + \frac{1}{2})^2 (T + N + \frac{3}{2})}, \tag{1.11}$$

respectively.

We can calculate instantaneous mortality, $\hat{Z}_B$ using the Bayesian approach by finding the posterior expectation of $-\log S$,

$$E(-\log S | N_x, N, \alpha, \beta) = \int_0^1 -\log S \times B(T + \alpha, N + \beta)^{-1} \times S^{T+\alpha-1}(1 - S)^{N+\beta-1} dS, \tag{1.12}$$

where $B(T + \alpha, N + \beta)$ denotes the beta function. Although this function cannot be integrated analytically, we can integrate it numerically using the `integrate` function in R, as illustrated in Appendix A.1. Alternatively, we may use Monte Carlo methods to approximate $E(-\log S | N_x, N)$.

1.2.1   Illustration: Lake Trout Data

Pollock, et al. (2007) analyzed mark-recapture data on lake trout in Lake Superior. Catch curve data was collected in addition to mark-recapture data. Trout were caught and aged annually from 1986 through 2005. The data are sparse, making annual estimates highly variable. The average sample size for male lake trout is 77.25. However, over the 20 years of catches, the small annual catch curves combine to form a large amount of data, indicating the value of a combined analysis. We are using a subset of the data, from 2000 to 2005. We chose to use this subset because we knew the population had been recovering from lamprey predation. Our goal was to select a subset with a stable age distribution, which is almost certainly not the case in the early years. In our subset, the average sample size of male lake trout is 73.3.

We found the regression estimator and adjusted regression estimator and calculated the corresponding standard errors using the delta method (Seber, 1982). We also analyzed the data using Chapman and Robson's (1960) UMVUE and our Bayesian approach using Jeffreys prior. The results are shown in Figure 1.1.

These results show that our Bayesian estimate, using a Jeffreys prior, is very similar to the UMVUE recommended by Chapman and Robson (1960), Robson and Chapman (1961),
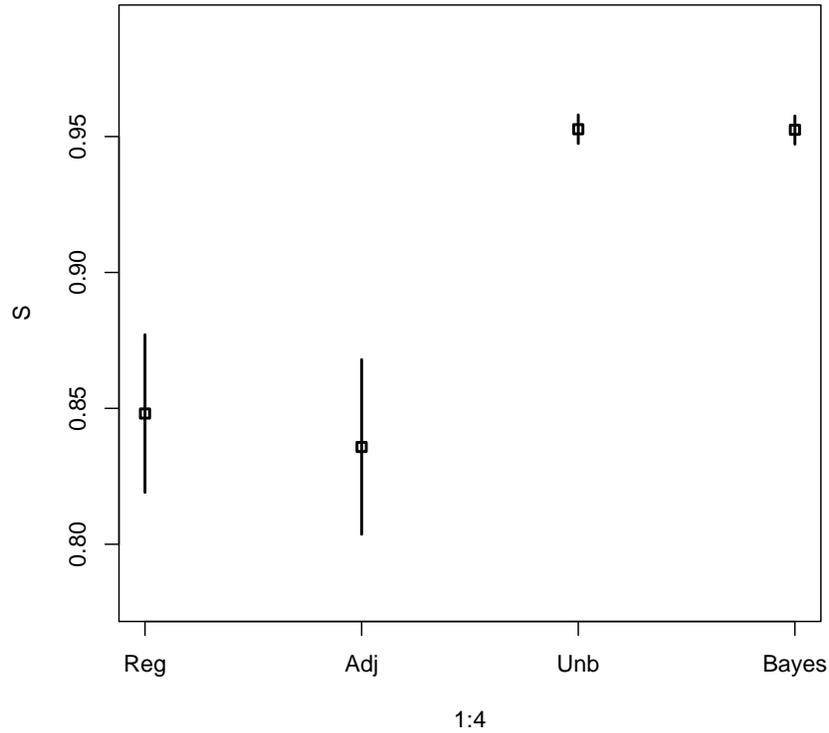
Figure 1.1: Survival rate estimates from each of the four types of estimation. The point estimate is marked by a square. The lines stretch from two standard deviations below the point estimate to two standard deviations above the point estimate. In the Bayesian case, the line stretches to the 95% equal-tailed posterior interval.

Jensen (1985 and 1996) and Murphy (1997). The regression estimate and adjusted regression estimate are close to each other in all the cases, but they do tend to be significantly different from the Bayes estimate and the UMVUE. The bias that we found is the same as the bias found in Jensen (1996).

1.3 Bayesian Catch Curve with Multiple Years of Data

The catch curve estimates by Chapman and Robson (1960) require the assumptions that the age distribution is stable and stationary and survival is constant for all age classes. It is also assumed that the ages are sampled randomly above some minimum age. If we justify these assumptions, combining catch data over multiple years will result in a more precise estimate of the constant survival rate due to the increase in sample size. The likelihood function for k years of catch-curve data, assuming independence, is given by

$$L(S|N_1, N_2, \ldots, N_k, T_1, T_2, \ldots, T_k) \propto S^{T_1+T_2+\cdots+T_k}(1-S)^{N_1+N_2+\cdots+N_k} \tag{1.13}$$

Using the conjugate prior, which remains the Beta(α,β) distribution, the posterior distribution is a Beta(α^*,β^*), where $\alpha^* = T_1+T_2+\cdots+T_k+\alpha$ and $\beta^* = N_1+N_2+\cdots+N_k+\beta$. The Bayesian estimate of survival under Jeffreys prior is

$$\hat{S}_B = \frac{\alpha^*}{\alpha^* + \beta^*} \tag{1.14}$$

with $\alpha = 1/2$ and $\beta = 0$. The corresponding variance is

$$\widehat{\text{var}}(\hat{S}_B) = \frac{\alpha^*\beta^*}{(\alpha^* + \beta^*)^2(\alpha^* + \beta^* + 1)}. \tag{1.15}$$

1.3.1 Illustration: Lake Trout Data

We are using the data collected on male lake trout from 2000 to 2005 in order to illustrate the combination of annual data. The individual year estimates and standard deviations are given in Table 1.1, along with the estimates and standard deviations from combining the data. Combining years involves strict assumptions. The stable age distribution assumption is very important when combining data over many years to form one large sample, as only one parameter will be estimated for all the years of data. Because the underlying assumptions of the catch curve analysis rely on the assumption of constant survival over many years, calculating individual survival rate estimates treating each year as independent is not a consistent method for analyzing this data. By grouping the data together, resolution is lost. Table 1.1 shows that, although the survival estimates vary only slightly between years,

there is some variation that may be lost when data are combined.

Table 1.1: Results of Bayesian estimation of survival using catch curve data from lake trout in Lake Superior from 2000 to 2005. We used Jeffreys prior and WinBUGS to obtain the posterior estimate of the mean and the standard deviation, the DIC and p_D. We used 10,000 MCMC runs and a burn-in time of 1,000 runs for each of two chains.

Year	S	Z
2000	0.901	0.105
	(0.0098)	(0.0109)
2001	0.896	0.110
	(0.0100)	(0.0111)
2002	0.913	0.091
	(0.0120)	(0.0131)
2003	0.911	0.093
	(0.0110)	(0.0121)
2004	0.924	0.079
	(0.0105)	(0.0114)
2005	0.906	0.099
	(0.0093)	(0.0102)
DIC $= 49.2$, $p_D = 6.0$		
Combined	0.900	0.106
	(0.0045)	(0.0050)
DIC $= 43.6$, $p_D = 1.0$		

1.4   Random Effects Model for Multiple Years of Data

Combining across years of data to estimate a constant S yields a good estimate, if the survival rate is constant. If we consider the possibility that the survival rate is a random effect with a constant mean and some variance, we can use multiple years of catch curve data to estimate the mean and variance of the random effect process. We can relax the assumption of constant survival for all age classes and all years, and instead assume survival is constant for all age classes but is a function of a random process with a constant mean and variance for

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all years. Each catch curve will provide a point estimate of survival at that time. Combining years of data will provide estimates of the mean and variance of the random process.

In a Bayesian framework, we can modify the likelihood given in Equation (1.13) to allow for S to vary with year k. The likelihood will then be a product likelihood, given below.

$$L(S_1, \ldots, S_k | N_1, N_2, \ldots, N_k, T_1, T_2, \ldots, T_k) = \prod_{j=1}^{k} L(S_j | N_j, T_j) \propto \prod_{j=1}^{k} S_j^{T_j} (1 - S_j)^{N_j} \quad (1.16)$$

If we assign S_j the random effect distribution Beta($\tau S^*, \tau(1 - S^*)$), each S_j will have population mean S^* and population variance $S^*(1 - S^*)/(\tau + 1)$. Because we do not know S^* or τ, we can use the Bayesian hierarchical framework and assign S^* a Beta(α, β) prior and τ a Gamma(a, b) prior. We set $\alpha = \beta = .5$ and $a = b = 0.001$. Notice that this results in relatively vague priors for S^* and τ, as var(S^*) = 0.125 and var(τ) = 1000.

Our hierarchical framework can be summarized as:

$$
\begin{aligned}
N_j | T_j, S_j &\sim \text{Negative Binomial}(S_j, T_j) \\
S_j | \tau, S^* &\sim \text{Beta}(\tau S^*, \tau(1 - S^*)) \\
\tau | a, b &\sim \text{Gamma}(a.b) \\
S^* | \alpha, \beta &\sim \text{Beta}(\alpha, \beta)
\end{aligned}
$$

We fit this model using the package `R2WinBUGS`, calling WinBUGS from `R`. The data we used are from the male lake trout, between 2000 and 2005. The estimates of survival from our random effect model for each individual year, along with a 95% equal-tailed posterior interval, are given in Table 1.2. We used the equal-tailed posterior interval instead of the highest posterior density (HPD) interval because of the symmetry of the posterior distributions. Recall that $Z^* = -\log S^*$ represents the population level instantaneous mortality rate.

We are using the deviance information criterion (DIC) for model selection. The DIC is based on the deviance, $D(S) = -2\log(f(N, T|S))$, and is DIC $= D(E(S|N, T)) + 2p_D = E(D(S)|N, T) + p_D$ (Spiegelhalter et al. 2002). The p_D represents the number of parameters in the model, is approximately equal to the trace of the product of Fisher's information and

the posterior covariance matrix, and can also be calculated as the mean deviance minus the deviance of the mean. Spiegelhalter et al. (2002) conclude that the DIC is the Bayesian analogue of the AIC. When there is no substantial prior information in the model, the DIC is approximately equal to the AIC. Spiegelhalter et al. (2002) discuss one benefit of the DIC over model selection criteria such as the AIC or BIC, which is that the BIC and AIC involve the number of parameters in the model. The number of parameters is not always easily determined in a Bayesian hierarchical model.

Table 1.2: Results of Bayesian estimation of survival using six years of catch curve data of lake trout in Lake Superior. We fit a random effects model in WinBUGS, using Jeffreys prior. We used 15,000 MCMC runs after a 5,000 run burn-in period.

Parameter	Mean	s.d.
S_{2000}	0.893	0.0089
S_{2001}	0.890	0.0093
S_{2002}	0.902	0.0102
S_{2003}	0.901	0.0096
S_{2004}	0.909	0.0097
S_{2005}	0.904	0.0082
S^*	0.899	0.0082
$\sqrt{\frac{S^*(1-S^*)}{\tau+1}}$	0.015	0.0073
Z^*	0.107	0.0092
DIC $= 46.3$, $p_D = 4$		
fDIC $= 75.3$, $p_D = 2$		

Table 1.2 shows that the random effect standard deviation is relatively small. The deviance information criterion, or DIC, of the random effect model is 46.3, which is larger than the DIC of the constant S model for the same data, which is 43.6. This implies that the random effect model is not an improvement for this subset of the lake trout data. However, the DIC of the random effect model, 46.3, is smaller than that of the individual yearly estimates, which was 49.2. The random effect model is an improvement over estimating each year separately.

The traditional DIC focuses on the posterior distribution, not the level of the hierar-

chy where the difference between the random effects model and the constant survival model lies. The focused DIC (personal communication from Bob O'Hara) looks at the marginal deviance, so it should pick up on the differences between the two models.

The marginal distribution of **N** and **T** for the random effects model is

$$m(N,T|S^*,\tau) = \int_{S_j=0}^{1} \prod_j \binom{N_j+T_j-1}{T_j} S_j^{T_j}(1-S_j)^{N_j} \frac{S_j^{\tau S^*-1}(1-S_j)^{\tau(1-S^*)-1}}{B(\tau S^*,\tau(1-S^*))} dS_j$$

$$= \prod_j \binom{N_j+T_j-1}{T_j} \frac{B(T_j+\tau S^*, N_j+\tau(1-S^*))}{B(\tau S^*,\tau(1-S^*))}. \tag{1.17}$$

The focused DIC, or fDIC, uses the focused deviance. The focused deviance is $D^f(S^*,\tau) = -\log(m(N,T|S^*,\tau))$. The focused DIC, or fDIC, can be defined as

$$fDIC = D^f(\bar{S}^*,\bar{\tau}) + 2p_D^f \tag{1.18}$$

where $p_D^f = E(D^f(S^*,\tau)|N,T) - D^f(\bar{S}^*,\bar{\tau})$ and $\bar{S}^*$ and $\bar{\tau}$ represent the posterior mean of S^* and τ, respectively. The focused DIC, fDIC, is only appropriate to calculate in the presence of a random effect, but it can be compared with the traditional DIC for model selection between models with and without random effects.

The focused DIC for the random effects model is 75.3, with $p_D = 2$. The fixed effects model is clearly selected by the comparison of fDIC to DIC, since the DIC for the fixed model is 43.6, with $p_D = 1$. This makes sense because the variation between years is so small that the extra parameters to account for such a small random effect are not important enough to include. In order to formally explore the use of fDIC as a model selection tool we perform a simulation study.

1.5 Simulation Studies

As it is likely that survival rates will vary between years in real fish as wildlife populations, we were interested in seeing what happens to standard estimates of survival when the survival rate is constant for all ages, but varies randomly from year to year. We

examined survival rates of $S = 0.6$, 0.75 and 0.9 combined with random effects generated from a Normal$(0, \sigma)$ distribution with $\sigma = 0$, 0.05, and 0.25. We added random variation to them using the formula $\text{logit}(S_i) = \text{logit}(S) + \eta_i$, or $S_i = \frac{\left(\frac{S}{1-S}\right)e^{\eta_i}}{1+\left(\frac{S}{1-S}\right)e^{\eta_i}}$, where η_i is generated from a Normal$(0, \sigma)$ distribution. We know that $n_x \sim \text{Binomial}(N_0, \prod_{i=1}^{x} S_i)$, so we generated catch curve data by randomly generating the number of animals caught in each age class using the Binomial distribution. Using $\sigma = 0.25$ means that the range of values within two standard devations is 0.24, 0.19, and 0.09 for survival rates of 0.6, 0.75, and 0.9, respectively.

We generated 10,000 single catch curves with 50 age classes for each combination, setting the number of animals in our sample and in the zero age class, N_0, equal to 100. We estimated the survival rate, S, and the corresponding standard deviation, $\hat{\sigma}_{\hat{S}}$, using the least-squares regression estimator, the UMVUE, and the Bayesian estimator with Jeffreys prior. The results are given in Table 1.3.

The results show that, despite the addition of random variation, the point estimate from a single catch curve remains unbiased. These models appear to be very robust against the random effect in the estimation of the survival rate, S, as long as the age distribution is stable. The variance estimates underestimate the true amount of variability in the population. This can be seen by comparing the mean estimates of the standard deviation of S with the standard deviation of the estimates of S. We think that one reason these results differ from those from the lake trout data in the difference between least-squares and MLEs is because this population was generated with a stable age distribution. That assumption is questionable with the lake trout data.

We also carried out a separate simulation study to judge how well the focused DIC performed at selecting the correct model in the presence of a random effect compared to the traditional DIC.

For this simulation study, we examined two survival rates and four levels of variability. We set $S^* = 0.6$ or 0.8 and $\sqrt{S^*(1 - S^*)/(\tau + 1)} = 0$, 0.05, 0.10, and 0.20. We used a Beta$(\tau S^*, \tau(1 - S^*))$ distribution to generate the survival rates with the random effect. We generated 6 years of catch curve data 1,000 times and fit both the fixed effect and random effect model to each. Those results are given in Table 1.4.

The p_D estimate is good under the fixed effect model. The focused DIC selected the

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Table 1.3: Results from a simulation study in which we generated catch curve data from a population with a randomly varying survival rate. We ran 10,000 MC replications. This table gives the means of the point estimates of the survival rate, S, and its corresponding standard deviation, $\hat{\sigma}(\hat{S})$. The standard deviation of the 10,000 estimates of the survival rate, S, is given in parenthesis after the point estimate of S. The standard errors for all estimated parameters are less than 0.001.

S	σ		Least-Squares Estimates		UMVUE Estimates		Bayesian Estimates with Jeffreys Prior	
0.6	0.00	$\hat{S}$	0.61	(0.051)	0.59	(0.049)	0.59	(0.049)
		$\hat{\sigma}_{\hat{S}}$	0.019		0.026		0.026	
	0.05	$\hat{S}$	0.60	(0.051)	0.59	(0.049)	0.59	(0.049)
		$\hat{\sigma}_{\hat{S}}$	0.020		0.026		0.026	
	0.25	$\hat{S}$	0.60	(0.059)	0.59	(0.055)	0.59	(0.055)
		$\hat{\sigma}_{\hat{S}}$	0.023		0.026		0.026	
0.75	0.00	$\hat{S}$	0.75	(0.033)	0.74	(0.032)	0.74	(0.032)
		$\hat{\sigma}_{\hat{S}}$	0.009		0.013		0.013	
	0.05	$\hat{S}$	0.75	(0.034)	0.74	(0.032)	0.74	(0.033)
		$\hat{\sigma}_{\hat{S}}$	0.009		0.013		0.013	
	0.25	$\hat{S}$	0.75	(0.038)	0.74	(0.036)	0.74	(0.036)
		$\hat{\sigma}_{\hat{S}}$	0.011		0.013		0.013	
0.9	0.00	$\hat{S}$	0.90	(0.014)	0.90	(0.012)	0.90	(0.012)
		$\hat{\sigma}_{\hat{S}}$	0.002		0.003		0.003	
	0.05	$\hat{S}$	0.90	(0.014)	0.90	(0.012)	0.90	(0.012)
		$\hat{\sigma}_{\hat{S}}$	0.002		0.003		0.003	
	0.25	$\hat{S}$	0.90	(0.015)	0.89	(0.013)	0.89	(0.013)
		$\hat{\sigma}_{\hat{S}}$	0.003		0.004		0.004	

fixed effects model correctly much more than the traditional DIC. The focused DIC tended to select the fixed effects model more often than the traditional DIC in all cases, but it did select the random effects model more often as the size of the random effect increased. There was a huge increase in performance between the fDIC and the DIC when the fixed model was the correct model.

The probability of a Type I error, $\Pr[\text{Reject } H_0 | H_0, \sigma = 0]$, when $S = 0.8$ is 0.52

Table 1.4: Results from the simulation study examining the model selection of the focused DIC with and without the presence of a random effect. The mean DIC and fDIC are given with standard errors in parenthesis. Asterisks (**) indicate a significant difference ($p < .0001$) between the fDICs for the random model and the DICs for the fixed model. The standard errors for the estimates of p_D and p_D^f are all less than 0.002. The proportion of times the fixed model is selected by the fDIC is given and compared to the proportion of times the traditional DIC selected the fixed model.

| Survival | | Mean DIC | Mean | Mean fDIC | Mean | Proportion of times fixed model chosen | |
Rate	σ	fixed model	p_D	random model	p_D^f	fDIC	DIC
0.8	0.00	100.4 (0.88)	1.00	93.5 (0.11)	2.3 **	0.48	0.04
0.8	0.05	103.5 (0.96)	1.00	93.6 (0.12)	2.3 **	0.44	0.03
0.8	0.10	111.7 (1.24)	1.00	94.1 (0.15)	2.3 **	0.38	0.03
0.8	0.20	165.8 (3.54)	1.00	95.9 (0.21)	2.3 **	0.21	0.01
0.6	0.00	71.8 (0.39)	1.00	72.2 (0.12)	2.3	0.63	0.18
0.6	0.05	75.1 (0.46)	1.00	72.9 (0.12)	2.3 **	0.54	0.12
0.6	0.10	82.6 (0.68)	1.00	74.1 (0.14)	2.3 **	0.39	0.08
0.6	0.20	124.3 (2.06)	1.00	77.4 (0.20)	2.2 **	0.15	0.03

for the fDIC and 0.96 for the DIC. When $S = 0.6$, the probability of a Type I error is 0.37 for the fDIC and 0.82 for the DIC. Table 1.4 also gives the probabilities of a Type II error, Pr[Fail to reject $H_0|H_A$], for $\sigma = 0.05$, 0.10, and 0.20 and $S = 0.8$ and 0.6. In terms of total error, the sum of Type I and Type II error, for each level of S and σ, it appears that fDIC outperforms DIC. This suggests that when the focused DIC can be calculated, it is a good improvement over the traditional DIC for model selection involving both fixed and random effect models.

1.6 Conclusions

For a single catch curve, the MLE and the least-squares estimators of the survival rate are biased, but for the MLE, the bias reduces to zero as the sample size approaches infinity (Chapman and Robson 1960; Jensen 1985 and 1996; Murphy 1997, Dunn et al. 2002). For the UMVUE, there is no closed form estimate of the variance of the survival rate parameter

under the geometric or multinomial model. Using Bayesian analysis, we can obtain a closed form finite sample estimate of the survival rate(s) as well as a closed form estimate of its variance. It is also straightforward to obtain the Bayesian estimate of Z.

We analyzed catch curve data from lake trout in Lake Superior (Pollock et al. 2007) and found that our closed form Bayesian estimate performed very similar to the UMVUE when Jeffreys prior is used. We also explored analytic relationships between the Bayesian estimator and the UMVUE and MLE and showed that the latter estimates can be obtained as a limiting case of Bayes estimates.

To extend our model, we considered the situation where multiple years of catch data are collected. We first combined the separate years of data which, under the assumptions of the Chapman and Robson (1960) estimator, results in increased precision. However, information about possible assumption violations is lost, because no information about the individual years is part of this model. We relaxed the assumptions of Chapman and Robson (1960) and fit a random effects model to multiple years of catch data. The random effects model is an important advance because real populations are likely to have variation in survival rates between years due to small environmental perturbations. The focused DIC also appears to be a good advance for model selection between fixed and random effects models.

The Bayesian approach to catch curve data analysis provides a broad and flexible method to extract the most information from the data without having to use marked animals. This is a real benefit for studies of animals that are difficult to mark. Bayesian methods are a very useful tool for data analysis. With software like WinBUGS and R widely available and free to use, we think these methods should become more popular in mainstream fisheries journals and in practice.

CHAPTER 2

Augmenting Catch Curve Data with Capture-Recapture Data for Estimation of Demographic Parameters

Summary

The Cormack-Jolly-Seber (CJS) capture-recapture model has been used to estimate survival rates in open populations since its development in the 1960s. The CJS model does not provide estimates of site fidelity or direct estimates of the population growth rate. The catch curve likelihood confounds the population growth rate with the survival rate, while the CJS model confounds fidelity and the survival rate. By combining catch curve data with capture-recapture data, we can obtain an estimate of either fidelity or the population growth rate while assuming a stable age distribution. We illustrate both of these concepts using a data set collected on lake trout in Lake Superior. We also present results from a small simulation study to investigate the presence of bias when combining catch curve and capture-recapture data. We also examine putting an informative prior on the population growth rate in order to estimate both parameters at once. This would correspond to having additional information on population growth rate by having yearly abundance indices. The prior we assigned to the fidelity rate was not a biologically informative prior, and would correspond to expert knowledge about the population of interest. Using both catch curve and capture-recapture data leads to a more realistic model of the population dynamics.

Key words: Capture-recapture; catch curve; CJS model; fidelity; Markov chain Monte Carlo methods; population growth rate; survival rate estimate.

2.1 Introduction

Methods for estimating survival rates of animal populations fall into two general categories: marked animal and non-marked animal methods (Williams et al. 2002). Catch curve data does not involve marked animals, and the subsequent analysis is based on strong assumptions about the population dynamics of the animals under study. Open population capture-recapture methods, on the other hand, use marked animals and require strong assumptions about homogenous survival and capture probabilities as opposed to assumptions about the population dynamics (Cormack 1964; Jolly 1965; Seber 1965; Williams et al. 2002).

Estimation of the population growth rate using capture-recapture data has been studied. Pradel (1996) estimates the population growth rate from capture-recapture data by conditioning on the last capture for each animal in the data set. Nichols and Hines (2002) discuss how the parameterization of the capture-recapture model impacts the identifiability of the demographic parameters of interest. They suggest that direct estimation may improve the estimates of the population growth rate. Nichols and Hines (2002) also suggest several joint analyses that may better estimate demographic parameters such as the population growth rate.

We are interested in the benefits of augmenting multiple years of catch curve data with capture-recapture data also collected over multiple years and analyzed using an open population model. As the assumptions behind a catch curve analysis are so different than the assumptions behind the Cormack-Jolly-Seber (CJS) model, utilizing both types of data in one likelihood could increase precision of estimates, relax some of the stringent but necessary assumptions, add to the ecological information gained, and lead to the estimation of new parameters, specifically site fidelity and the population growth rate.

We use the capture-recapture and catch curve data from a recovering lake trout population (Pollock et al. 2007) collected annually from 1989 through 1994 to illustrate the methods developed. Pollock et al. (2007) analyzed the capture-recapture lake trout data and found that the best model for estimating survival and capture probabilities was additive for sex and year. Therefore, we separated the male lake trout data from the female lake trout data and are only using data from the males for an illustration of our method.

In Sections 2.2 and 2.3, we present the assumptions behind catch curve analysis and

the CJS model, respectively. For each data type we present the structures of the likelihoods and the estimates from our illustrating example. In Section 2.4, we present the joint likelihood and discuss the estimation of parameters. We present a general case which includes fidelity parameters and a population growth rate parameter in addition to survival and capture probabilities, under the assumption of a stable age-distribution. We can use the combination of catch curve data and capture-recapture data to estimate one of these two parameters, under the condition that the other is known. In some cases we may be able to assume that either fidelity or the population growth rate are known, which leads to special cases. We again use the lake trout data as a motivating and illustrating example. We also present a small simulation study to examine bias in the models. In this simulation study, we also explore putting an informative prior on the population growth rate, representing information obtainable from auxiliary data such as abundance indices, and putting an informative prior on the fidelity rate representing expert knowledge. We can then estimate both parameters together. Focusing on both the population growth rate and fidelity leads to a more realistic model, and is an interesting development for future research. We conclude with some discussion of possible research directions.

2.2 Catch-Curve Modeling and Estimation

The assumptions for estimating survival rates using catch curve analysis are:

 (i) the survival rate is constant for all age classes and all years,

 (ii) the age distribution is stable, which means the survival and fecundity rates have remained constant for some time,

(iii) the population growth rate is known, and

(iv) all fully vulnerable age classes have an equal probability of being included in the sample

(Chapman and Robson 1960; Williams et al. 2002; Udevitz and Ballachey 1998). Capture probabilities are not included in the likelihood because of assumption (iv), that the capture probabilities are equal. Let S be the survival rate, λ be the population growth rate, N_x be

the number of individuals in the sample of age x. The N_x's conditional on $\sum_x N_x = N$ follow a multinomial distribution, given by

$$
\begin{aligned}
L(S|N_x, \lambda) &= P(N_0 = n_0, N_1 = n_1, \ldots | S, \lambda) \\
&= \frac{N!}{\prod_{x=0}^{\omega} n_x!} \prod_{x=0}^{\omega} \left(\frac{S^x}{\lambda^x \sum_{x=0}^{\omega} \frac{S^x}{\lambda^x}} \right)^{n_x}
\end{aligned}
\tag{2.1}
$$

An extension of this model is one in which there are k years of data collected, each year is independent, and S is allowed to be a random effect from year to year, with a constant mean and variance. The population growth rate, λ, is assumed to remain constant, which follows from the assumption of a stable age distribution. Let $N_{x,j}$ be the number of animals of age x sampled in year j and $T_j = \sum_x x N_{x,j}$. This likelihood is a product likelihood, given by

$$
\begin{aligned}
L(S_1, \ldots, S_k | N_{x1}, \ldots, N_{xk}, \lambda) &= \prod_{j=1}^{k} L(S_j | N_{xj}, \lambda) \\
&= \prod_{j=1}^{k} \frac{N_k!}{\prod_{x=0}^{\omega} n_{xj}!} \prod_{x=0}^{\omega} \left(\frac{S_j^x}{\lambda^x \sum_{x=0}^{\omega} \frac{S_j^x}{\lambda^x}} \right)^{N_{xj}}
\end{aligned}
\tag{2.2}
$$

One must fix λ to some value in order to estimate the survival rate if catch curve data are the only data available. We set $\lambda = 1$ and obtained posterior estimates of the parameters of this model using WinBUGS (via `openbugs` in R) for the male lake trout data from 1989 to 1994. We used a Beta$(0.5, 0.5)$ prior for each S_j, setting $\lambda = 1$. We used three chains, set a burn-in period of 1,000 runs followed by 10,000 MCMC runs for each chain. The results from our analysis are given in Table 2.1. The posterior medians of the survival rate, again, assuming $\lambda = 1$, are high and the 95% equal-tailed posterior intervals are fairly narrow. Ecologically, this means that lake trout are a long-lived species. Because the probability of survival to age x is S^x, survival rates over 0.90 indicate that we expect half the population to survive for at least 6 years after full vulnerability to the catch equipment. Also the survival rate seems to increase from year 1989 to 1993 followed by a drop at year 1994. However the 95% credible intervals of the S_j's indicate that such increase in the yearly rate is not statistically significant after the first year (as the 95% posterior intervals intersect with each

other except for year 1989).

Table 2.1: Posterior estimates for the survival rate for male lake trout from 1989 to 1994, assuming $\lambda = 1$. We ran 10,000 MCMC runs for each of three chains in WinBUGS, using a Beta(0.5,0.5) prior for each S. The burn-in period was 1,000 runs.

	Posterior Estimates for S		
Year	Median	Std. Dev.	95% Equal-Tailed Interval
1989	0.83	0.017	(0.79, 0.86)
1990	0.89	0.011	(0.87, 0.91)
1991	0.90	0.019	(0.87, 0.94)
1992	0.91	0.020	(0.87, 0.95)
1993	0.95	0.019	(0.91, 0.99)
1994	0.92	0.013	(0.89, 0.95)
DIC $= 852.2$, $p_D = 6.2$			

2.3   Capture-Recapture Modeling and Estimation

The Cormack-Jolly-Seber (CJS) open capture-recapture model assumes

(i) that the capture and recapture probabilities (p_i) are the same for all animals in the population at a particular time,

(ii) the conditional probability (ϕ_i) of surviving from one sampling period to the next is the same for all animals,

(iii) tags are not lost, overlooked, or recorded incorrectly,

(iv) there is no temporary emigration,

(v) there is no correlation between capture and survival probabilities of different animals, and

(vi) each capture period is treated as instantaneous with animals being returned to the population immediately

(Williams, et al. 2002; Pollock 1991). It is important to note that the survival rate estimated by the CJS model is apparent survival. When using capture-recapture methods, the emigration of a marked animal or failure to return to the same spawning ground is synonymous with the death of the animal (Jolly 1965).

We use the formulation of the CJS model given in Williams et al. (2000, Chapter 17). Let

ϕ_i denote the probability that an animal who is present and alive in capture period i survives to capture period $i+1$ and *does not emigrate permanently*,

p_j denote the probability an animal is captured in period j,

$m_{i,j}$ be the number of animals released at time i and recaptured at time j,

ν_i be the number of animals released at time i and never recaptured, and

R_i be the total number of animals released at time i.

The structure of the likelihood is based on conditioning the number of recaptures on the number of marked animals released in each capture period. This structure is given in Table 2.2 (Table 17A from Williams et al. 2002). Table 2.2 clearly shows that $\phi_3 p_4$ is identified as a product only. The last ϕ, ϕ_J, is estimable if the last two capture probabilities are set to be equal (i.e. $p_J = p_{J-1}$).

Table 2.2: Expected numbers of recaptures $E(m_{ij}|R_i)$ for the CJS model with four sample periods. This is Table 17A in Williams et al. (2002).

Releases in period i	Recapture period j		
	2	3	4
R_1	$R_1\phi_1 p_2$	$R_1\phi_1(1-p_2)\phi_2 p_3$	$R_1\phi_1(1-p_2)\phi_2(1-p_3)\phi_3 p_4$
R_2		$R_2\phi_2 p_3$	$R_2\phi_2(1-p_3)\phi_3 p_4$
R_3			$R_3\phi_3 p_4$

The formal likelihood is given by

$$L(\phi, p|R, m) \propto \prod_{i=1}^{I} \chi_i^{\nu_i} \prod_{j=i+1}^{J} \left(\phi_i p_j \prod_{k=i+1}^{j-1} \phi_k(1-p_k) \right)^{m_{ij}}. \tag{2.3}$$

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We modeled χ_i using the recursive relationship $\chi_i = 1 - \phi_i + \phi_i (1 - p_{i+1}) \chi_{i+1}$.

The assumption of no tag loss can be relaxed by allowing tag retention rates to be in the model. If we let θ be the tag retention rate, the likelihood of the CJS model will be

$$L(\phi, p, \theta; R, m) \propto \prod_{i=1}^{I} \chi_i^{\nu_i} \prod_{i=1}^{I} \prod_{j=i+1}^{J} \left(\left(\frac{\phi_i}{\theta} \right) p_j \prod_{k=i+1}^{j-1} \left(\frac{\phi_k}{\theta} \right) (1 - p_k) \right)^{m_{ij}} \qquad (2.4)$$

If the tag retention rate is lower than the survival rate, there will be problems with model convergence. A double-tagging study done during the capture-recapture study we are using for our example shows that the mean tag retention rate is 0.9259, so we are not too concerned about our tag retention rate being lower than the survival rate.

We programmed the CJS model with tag loss given in Equation (2.4) into WinBUGS using the male lake trout data from 1989 through 1994. Like Brooks et al. (2000), we assigned Beta$(1, 1)$ priors to the capture probabilities and the survival probabilities. Based on maximum likelihood estimates in Pollock et al. (2007), and because $\theta \in [0, 1]$ with probability one, we assigned an informative Beta prior, Beta$(\tau \theta^*, \tau(1 - \theta^*))$, with mean $\theta^* = 0.9259$ and standard deviation 0.0356 to θ (ie., $\tau = 53.14$) , the tag retention rate. We also assumed $p_6 = p_7$. The results of this analysis are given in Table 2.3. The chains mixed well and the Gelman Rubin diagnostic (Brooks and Gelman 1998) given in WinBUGS did not indicate a lack of convergence.

By comparing Table 2.1 and Table 2.3 it is obvious that the posterior medians from the capture-recapture data do not match up at all with the posterior medians from the catch curve data. The posterior medians from the catch curve data tend to be higher than those from the capture-recapture data. Four out of the six 95% equal-tailed posterior intervals do not overlap, indicating large differences in the survival rate estimates. There are two possible reasons for this.

First, the catch curve survival rate, S, is not the same quantity as the capture-recapture apparent survival rate ϕ. The capture-recapture data provide estimates of apparent survival, which confounds death and emigration. If we let F be the probability of site fidelity for the population of interest, we know that $\phi = S \times F$, meaning that ϕ equals S only when $F = 1$. In tag-return data there is no emigration and we could reasonably assume that the

Table 2.3: Posterior estimates for the survival rate for male lake trout from 1989 to 1994. We ran 3 chains with 10,000 MCMC runs in WinBUGS, using a Beta(1,1) prior for each S and a Beta prior with mean 0.9259 and standard deviation 0.0356 for the tag loss parameter θ. We used a burn-in time of 1,000 runs.

	Posterior Estimates for ϕ		
Year	Median	Std. Dev.	95% Equal-Tailed Interval
1989	0.57	0.0586	(0.46, 0.69)
1990	0.81	0.0901	(0.64, 0.99)
1991	0.67	0.0870	(0.58, 0.86)
1992	0.45	0.0591	(0.34, 0.57)
1993	0.81	0.1199	(0.58, 1.00)
1994	0.53	0.0644	(0.41, 0.66)
	DIC $= 148.8$, $p_D = 10.3$		

fidelity rate is one. However, these lake trout data were collected at a spawning ground in Lake Superior, and we could reasonably assume that fidelity is less than one.

Second, the catch curve's likelihood depends on both S and λ, the population growth rate. The estimate of S is correct only if λ is known or equal to one. We do not know λ for this population and we are assuming that it is equal to one. If we do not know λ, we cannot be sure that the catch curve's survival estimate is correct.

If we can assume that fidelity, F, is either one or known, we can use that value of F in the likelihood and estimate the survival rate, S, and the population growth rate, λ. Similarly, we can assume that the population growth rate is either one or known and use that value of λ in the likelihood. This will allow us to estimate both the survival rate and site fidelity.

These two cases motivate us to combine the likelihoods of catch curve and capture-recapture data, in order to estimate either site fidelity or the population growth rate.

2.4   Combining Catch Curve and Capture Recapture Data

We combined the catch curve and capture-recapture analyses with the goal of possibly increasing precision of estimates and in addition estimating either fidelity, F, or the

population growth rate, λ.

The catch curve likelihood is given in Equation (2.2). The capture-recapture likelihood is given in Equation (2.4). Making use of the fact that $\phi_i = S_i \times F_i$, we can reparameterize Equation (2.4) to:

$$L(S, F, p, \theta | R, m) \propto \prod_{i=1}^{I} \chi_i^{\nu_i} \prod_{j=i+1}^{J} \left(\left(\frac{S_i F_i}{\theta} \right) p_j \prod_{k=i+1}^{j-1} \left(\frac{S_k F_k}{\theta} \right) (1 - p_k) \right)^{m_{ij}} \qquad (2.5)$$

where χ_i is modeled using the recursive relationship $\chi_i = 1 - S_i F_i / \theta + (S_i F_i / \theta)(1 - p_{i+1}) \chi_{i+1}$.

We will denote the catch curve likelihood from Equation (2.2) as $L_1(\mathbf{S}, \lambda | \mathbf{N_x})$ and the capture-recapture likelihood from (2.5) as $L_2(\mathbf{S}, \mathbf{F}, \mathbf{p} | \mathbf{R}, \mathbf{m})$. The combined likelihood for the general case is $L(\mathbf{S}, \mathbf{F}, \mathbf{p}, \lambda | \mathbf{N_x}, \mathbf{R}, \mathbf{m}) = L_1(\mathbf{S}, \lambda | \mathbf{N_x}) \times L_2(\mathbf{S}, \mathbf{F}, \mathbf{P} | \mathbf{R}, \mathbf{m})$, which is

$$
\begin{aligned}
L(\mathbf{S}, \mathbf{F}, \mathbf{p}, \lambda | \mathbf{N_x}, \mathbf{R}, \mathbf{m}) \quad \propto \quad & \prod_{j=1}^{J} \frac{N_k!}{\prod_{x=0}^{\omega} n_{xj}!} \prod_{x=0}^{\omega} \left(\frac{S_j^x}{\lambda^x \sum_{x=0}^{\omega} \frac{S_j^x}{\lambda^x}} \right)^{n_{xj}} \\
& \times \prod_{i=1}^{I} \chi_i^{\nu_i} \prod_{j=i+1}^{J} \left(\frac{S_i F_i}{\theta} p_j \prod_{k=i+1}^{j-1} \frac{S_k F_k}{\theta} (1 - p_k) \right)^{m_{ij}}
\end{aligned}
$$

$$(2.6)$$

If we do not know either F or λ, we are faced with an identifiability problem and cannot estimate S. However, if we know either F or λ, we can estimate the other. We can also extend this to the case where we have independent information on λ. We can use that estimate, $\hat{\lambda}$, and corresponding standard error to create an informative prior distribution for λ.

2.4.1 Population Growth Rate Known

If we assume that we know the population growth rate, λ, we can estimate the survival rate S and fidelity F. Here, we assumed that the population growth rate is 1, although we have no real reason for this choice. We are doing this for illustration of the methodology. We programmed this model in WinBUGS, using Beta$(1, 1)$ priors for S and p. We used a Gamma(5,4) prior, bounded above by 1, for F. Notice that the truncated Gamma(5,4) prior

on F allows $P[F = 1] = \int_{u=1}^{\infty} \frac{4^5 u^4 e^{-4u}}{4!} du = 0.63$. We also used a Beta$(\tau\theta^*, \tau(1 - \theta^*))$ prior for θ, where θ^* and τ are set such that the mean is 0.9259 and standard deviation is 0.0356. The results are given in Table 2.4.

Table 2.4: Posterior estimates for the fidelity rate for male lake trout from 1989 to 1994, assuming $\lambda = 1$. We used three chains with 10,000 MCMC runs each in WinBUGS, and Beta$(1, 1)$ for S and p, Gamma$(5, 4)$ priors bounded above by 1 for F, and a Beta prior for θ with mean 0.9259 and standard deviation 0.0356. The burn-in time was 1,000 runs.

	Posterior Estimates for S		
Year	Median	Std. Dev.	95% Equal-Tailed Interval
1989	0.83	0.0171	(0.79, 0.86)
1990	0.89	0.0111	(0.87, 0.91)
1991	0.90	0.0189	(0.86, 0.94)
1992	0.90	0.0200	(0.86, 0.94)
1993	0.95	0.0178	(0.91, 0.98)
1994	0.92	0.0131	(0.89, 0.95)
	Posterior Estimates for F		
Year	Median	Std. Dev.	95% Equal-Tailed Interval
1989	0.71	0.0679	(0.59, 0.85)
1990	1.00	0.0702	(0.77, 1.00)
1991	0.75	0.1056	(0.59, 1.00)
1992	0.51	0.0646	(0.40, 0.65)
1993	1.00	0.1037	(0.67, 1.00)
1994	0.61	0.0670	(0.49, 0.75)
	DIC $= 987.4$, $p_D = 3.1$		

WinBUGS provides a Brooks-Gelman-Rubin (BGR) diagram, plotting the Gelman-Rubin convergence statistic, R, which is a variance ratio comparing pooled and within-chain inferences (Brooks and Gelman 1998). We checked the Gelman-Rubin diagnostic for lack of convergence and found no apparent problems. The trace plots indicated no lack of convergence. The chains mixed well and the posterior distributions were empirically found to be nearly symmetric.

2.4.2 Fidelity Known

If we assume that we know the fidelity rate, F, we can estimate the survival rate S and the population growth rate λ. Here, we assumed that fidelity is $F = 1$, purely as an illustration of the methodology. We programmed this model in WinBUGS, using Beta$(1,1)$ priors for S and p, a Gamma$(1,.01)$ prior for λ, and a the same Beta prior for θ as mentioned in the previous section, with mean 0.9259 and standard deviation 0.0356. The results are given in Table 2.5.

Table 2.5: Posterior estimates for the population growth rate and survival rates for male lake trout from 1989 to 1994, assuming $F = 1$. We used three chains with 10,000 MCMC runs each in WinBUGS, and Beta$(1,1)$ priors for S and p, a Gamma$(2,3)$ prior for λ and a Beta$(\tau\theta^*, \tau(1-\theta^*))$ prior for θ with mean $\theta^* = 0.9259$ and standard deviation 0.0356. The burn-in time was 1,000 runs.

		Posterior Estimates for S	
Year	Median	Std. Dev.	95% Equal-Tailed Interval
1989	0.60	0.0400	(0.51, 0.66)
1990	0.64	0.0422	(0.55, 0.71)
1991	0.65	0.0433	(0.55, 0.72)
1992	0.64	0.0434	(0.54, 0.71)
1993	0.68	0.0459	(0.58, 0.76)
1994	0.66	0.0438	(0.56, 0.73)
	Posterior Estimate for λ		
	Median	Std. Dev.	95% Equal-Tailed Interval
	0.72	0.0468	(0.60, 0.79)
	DIC $= 1012.2$, $p_D = 11.9$		

Again, we used the Gelman Rubin diagnostic to check for lack of convergence, and none was indicated. The trace plots indicated good mixing based on the initial values which were suitably chosen to be well dispersed.

The posterior median for the population growth rate is $\hat{\lambda} = .72$, which is very low and is probably not a realistic estimate. The estimates for the survival rate S are also much lower when $F = 1$ than when $\lambda = 1$. This problem underscores the need to be able to take into account both fidelity and the population growth rate when analyzing a population.

If it is reasonable to assume that both fidelity and the population growth rate are equal to one, we can set $S = \phi$ without having to use that relationship to estimate λ. Doing this would increase the precision of our estimate of the survival rate by utilizing more data to estimate the same number of parameters. It does not seem reasonable to assume that fidelity is one using our example, especially for the earlier years as the 95% posterior credible intervals do not contain 1.

Looking at the DICs, we can see that the model using a combination of catch curve and capture-recapture data with the population growth rate, λ, assumed to be one is the best fitting model. The DIC for that model is 987.4, which is less than the sum of the DICs for the catch curve model and capture-recapture model. The DIC of the model with fidelity, F, set equal to one is 1012.2, which is much higher than that of the model with the known population growth rate. This is further indication that site fidelity for this population is less than one.

2.4.3 Additional Information on Population Growth Rate

In order to estimate fidelity, F, and the population growth rate, λ, together, we need independent information on one of the parameters. If we had information on λ from another study on the same population, we could use that information to create an informative prior for λ. For example, in fisheries it is common for agencies to carry out fisheries independent surveys where catch per unit effort is measured on a population over a series of years. From this information estimates of population growth rates could be obtained. We could then use expert knowledge and perhaps prior studies to create a relatively informative prior for fidelity, F. Utilizing a highly informative prior for the population growth rate and an informative prior on F leads to the ability to estimate F and λ in addition to the survival rate, S, and capture probabilities, p.

2.4.4 Simulation Study

In order to test our method of combining catch curve data with capture-recapture data, we performed a small simulation study. We generated 4 years of data from a population with a starting size of 3,000 and a population growth rate of 1.1 each year. The other

parameters were set to be: $p_j = 0.15$, $F_j = 0.9$, and $S_j = 0.9$ for all j.

We ran this simulation study again with a higher capture probability of $\mathbf{p} = 0.3$. We let all of the other parameters remain the same. We analyzed the data in the same three ways as we did with the lower capture probability. The results of this simulation study are given in Table 2.7.

First, we analyzed the generated data assuming that λ is known to be 1.1. Then we analyzed the same generated data assuming that $\mathbf{F}$ is known to be 0.9. Finally, we analyzed the generated data with an informative prior for λ and $\mathbf{F}$. The prior that we used for λ was a Gamma distribution with mean 1.1 and standard deviation 0.05. This kind of information could be obtained about λ via an independent estimate based on a series of catch per unit effort indices as described earlier. The prior we used for each F was a Beta prior with mean 0.9 and standard error 0.10. Although this is not a noninformative prior, it is fairly noninformative in a biological sense. The results from each analysis are given in Table 2.6. We have reported the bias and standard deviations of the posterior medians for each parameter. As we set all the parameters equal over time, we also have reported the bias and standard error for the combined estimate across years.

For the model with the population growth rate, λ, known, none of the parameters are significantly biased. The same holds for the model with fidelity, F, known. The model with informative priors for both λ and F results in significantly biased posterior medians for the survival rate and the population growth rate. These estimates all tend to be too high.

For the model with the population growth rate, λ, known, none of the parameters are significantly biased. The standard deviations for fidelity, F, are smaller with the higher capture probability of $p = 0.3$ than with the lower capture probability of 0.15.

For the model with fidelity, F, known, again none of the parameters are significantly biased. The standard deviation of λ is smaller with the higher capture probability of $p = 0.3$ than with the lower one of $p = 0.15$.

The higher capture probability also helps the model with informative priors for both the population growth rate, λ, and fidelity, F. Only the population growth rate is significantly biased. It is biased high, as it was in estimates from the data with a lower capture probability.

Table 2.6: Bias of posterior means for individual parameter estimates and combined parameter estimates from the simulation study. We used the posterior medians for these calculations. The MCMC sample size is 100. The true parameters are capture probabilities of 0.15, survival rates of 0.9, fidelity rates of 0.9, and a population growth rate of 1.1. We fixed $\lambda = 1.1$ for the first model and $F = 0.9$ for the second. For the third model, we assigned a Gamma prior to λ with a mean of 1.1 and standard deviation of 0.05. We assigned a Beta prior to F with a mean of 0.9 and a standard deviation of 0.1. Each sample was run using `openbugs`, with 20,000 runs for each of three chains and a burn-in period of 1,000 runs.

Parameter	λ Known		F Known		λ and F Unknown	
	Bias	Std. Dev.	Bias	Std. Dev.	Bias	Std. Dev.
S_1	-0.01	0.027	-0.02	0.020	0.05	0.044
S_2	-0.00	0.026	-0.02	0.020	0.05	0.045
S_3	-0.00	0.025	-0.02	0.020	0.05	0.045
S_4	-0.00	0.025	-0.02	0.021	0.04	0.046
$\bar{S}$	-0.00	0.026	-0.02	0.020	0.05	0.045
F_1	0.02	0.062	-	-	-0.00	0.070
F_2	-0.00	0.046	-	-	-0.02	0.076
F_3	0.03	0.024	-	-	-0.03	0.078
F_4	0.01	0.018	-	-	-0.03	0.084
$\bar{F}$	0.01	0.041	-	-	-0.02	0.077
λ	-	-	-0.02	0.093	0.06	0.070
p_2	0.00	0.095	0.01	0.029	0.01	0.027
p_3	0.01	0.030	0.01	0.029	-0.00	0.027
p_4	0.01	0.019	0.01	0.032	0.01	0.025
p_5	0.01	0.015	0.01	0.032	0.01	0.025
$\bar{p}$	0.01	0.051	0.01	0.031	0.00	0.026

Both the lower capture probability and the higher capture probability studies show that with prior information on λ, we can relax the assumption of a known fidelity rate. We found that a noninformative prior for fidelity when the population growth rate was informed, but not known, led to convergence and estimation problems. Although we cannot use a noninformative prior for the fidelity rate, we can use a biologically noninformative prior and obtain posterior estimates with nice properties.

Table 2.7: Bias of posterior means for individual parameter estimates and combined parameter estimates from the simulation study. We used the posterior medians for these calculations. The MCMC sample size is 100. The true parameters are capture probabilities of 0.3, survival rates of 0.9, fidelity rates of 0.9, and a population growth rate of 1.1. We fixed $\lambda = 1.1$ for the first model and $F = 0.9$ for the second. For the third model, we assigned a Gamma prior to λ with a mean of 1.1 and standard deviation of 0.05. We assigned a Beta prior to F with a mean of 0.9 and a standard deviation of 0.1. Each sample was run using `openbugs`, with 20,000 runs for each of three chains and a burn-in period of 1,000 runs.

Parameter	λ Known Bias	λ Known Std. Dev.	F Known Bias	F Known Std. Dev.	λ and F Unknown Bias	λ and F Unknown Std. Dev.
S_1	-0.01	0.021	-0.01	0.040	0.04	0.039
S_2	-0.00	0.021	-0.01	0.039	0.03	0.039
S_3	-0.01	0.021	-0.01	0.043	0.03	0.040
S_4	-0.00	0.021	-0.01	0.044	0.03	0.040
$\bar{S}$	-0.01	0.021	-0.01	0.041	0.03	0.039
F_1	0.04	0.055	-	-	-0.02	0.049
F_2	0.00	0.062	-	-	-0.03	0.052
F_3	0.06	0.069	-	-	-0.00	0.054
F_4	0.03	0.070	-	-	-0.00	0.057
$\bar{F}$	0.03	0.064	-	-	-0.01	0.053
λ	-	-	-0.00	0.044	0.04	0.049
p_2	-0.01	0.026	0.00	0.024	-0.00	0.025
p_3	-0.00	0.024	0.00	0.029	-0.00	0.023
p_4	-0.01	0.027	0.00	0.034	-0.01	0.026
p_5	-0.01	0.027	0.00	0.034	-0.01	0.026
$\bar{p}$	-0.01	0.026	0.00	0.030	-0.00	0.025

2.5   Conclusions

Combining catch curve data with capture-recapture data can provide increased precision if the combined assumptions hold. As long as the age structure is stable, we can estimate either fidelity or the population growth rate. This is a nice advance, as these are both important demographic parameters of interest.

One important issue to keep in mind is that catch curve data assume that the population of interest has a stable age-distribution. If the survival rates estimated by the combined likelihood vary wildly from year-to-year, these methods are probably not appropriate. A small amount of variation can be attributed to process variation, which is acceptable. A random effects model can handle this type of variation. Developing a random effects model which involves catch curve data with capture-recapture data would be a good direction for future research.

In fisheries applications, tag-return data may be collected instead of capture-recapture data. In tag return data, the survival estimate obtained is of S, true survival, instead of the capture-recapture model's estimate of ϕ, apparent survival (Brownie et al. 1985, Pollock 1991). The issue of site fidelity is not as important when tags are returned from the entire lake, for example, instead of only from fish returning to a specific spawning ground. If we had tag-return data and catch curve data from a population, we would be able to estimate the population growth rate in addition to the survival rate and the band recovery rate. We would not require any additional information in this case.

There is not enough information in the combined likelihoods of catch curve data and capture-recapture data to estimate both the population growth rate, λ, and the fidelity rates, $\mathbf{F}$ without prior information from another data source. Further augmenting capture-recapture and catch curve data with ages-at-death data may provide estimates for both the population growth rate and fidelity. This would be an interesting subject for future research. Eliminating the assumption of known fidelity or known population growth rate results in drawing stronger inferences from models that better describe the population of interest.

Chapter 3

Augmenting Catch Curve Data with Ages-at-Death Data for Estimation of Demographic Parameters

Summary

Augmenting catch curve data with ages-at-death data can provide estimates of the population growth rate under the assumption of a stable age-distribution. We develop a Bayesian approach to the joint analysis of standing age-structure data and ages-at-death data. First, we review the approaches to the combined data analysis that are already used in practice. We compare our Bayesian approach to the existing maximum likelihood approach. We also discuss the identifiability of the population growth rate under the relaxed assumption of an unstable age-distribution. We conclude that the Bayesian approach to this combined data analysis has benefits such as the ability to relax assumptions about population dynamics without losing the ability to estimate certain parameters.

Key words: Catch curve; ages-at-death data; Markov chain Monte Carlo methods; population growth rate estimation; survival estimation.

3.1 Introduction

There are two main classes of methods for estimating survival rates for animal populations. The first approach involves marking animals ie., capture-recapture methods (Williams et al. 2002, Chapter 17). The second approach does not involve marking animals and instead is based on taking a sample of the standing age distribution or the ages at death (Williams et al. 2002, Chapter 15).

Capture-recapture methods require no assumptions about population dynamics, but they do require strong assumptions about homogeneity of individual capture and survival probabilities (Cormack 1964; Jolly 1965; Seber 1965; Williams et al. 2002, Chapter 17).

They are expensive to implement and may not work for the species of interest (Udevitz and Ballachey 1998). Each animal needs to be marked uniquely so that its capture history can be obtained without error, which is not always possible for all species (Jolly 1965).

In Chapter 1, we looked at methods of analyzing "catch curve" data, that is a sample of the age distribution of the living population (Chapman and Robson 1960). Catch curve data is inexpensive to collect as it does not involve marking animals. One problem with using standard catch curve methods is that they assume a stable age distribution which requires that annual survival rates and population growth rates are constant over time. A population with a stable age distribution has reached a state of equilibrium (Udevitz and Ballachey 1998). In addition, another crucial assumption is that capture probability is equal for all fully vulnerable age classes (Chapman and Robson 1960), that is the sampling is random.

Udevitz and Ballachey (1998) augmented catch curve data, that is standing age-structure data from a random sample of live animals, with ages-at-death data. They state that the data augmentation results in the ability to relax either the assumption of a stable age distribution or the assumption of a known population growth rate. However, neither type of data involves marking animals, which lets the estimators remain in the class of unmarked studies and hence often be much less costly to collect.

Udevitz and Ballachey (1998) look at three different scenarios when combining standing age-structure data and ages-at-death data. These are: stability assumed and population growth rate known and equal to 1; stability unknown and population growth rate known and equal to 1; and stability assumed and population growth rate unknown. We will review these in the order they are discussed in Udevitz and Ballachey (1998), develop a Bayesian approach for Udevitz and Ballachey's models, and conclude with a proposed extension to a more general case.

3.2 General Likelihood (Udevitz and Ballachey 1998)

Udevitz and Ballachey (1998) introduce a general likelihood for the standing age structure data. The assumptions for the general standing age structure data are that the age distribution is not necessarily stable and the demographic parameters are allowed to vary over time. The population growth rate is also allowed to vary over time. The sample needs

to be a random sample with each age correctly determined. We are also assuming that there is an oldest age class, ω, such that the survival rate, $S_{\omega t}$, is zero for all times t. The notation is defined as follows (Udevitz and Ballachey 1998):

$N_t =$ the total number of individuals in the population at time t,

$c_{it} =$ the proportion of the individuals in the population at time t that are in age class i, $i = 1, \ldots, \omega$,

$S_{it} =$ the probability of surviving to be in age class $i+1$ at time $t+1$ for individuals in age class i at time t, $i = 1, \ldots, \omega$.

$\lambda_t =$ the population growth rate at time t, defined as $\lambda_t = \frac{N_t}{N_{t-1}}$

Suppose we have determined the age of each individual in a random sample from the population at time t. Let x_{it} be the number of age class i individuals in the sample at time t. The x_{it}, $i = 0, \ldots, \omega$ are the standing age-structure data. The distribution of the age frequencies, conditioned on total sample size, $\sum_{i=0}^{\omega} x_{it}$, is given by the multinomial likelihood

$$\frac{(\sum_{i=0}^{\omega} x_{it})!}{\prod_{i=0}^{\omega}(x_{it}!)} \left(\frac{\lambda_t - \sum_{i=1}^{\omega} c_{i-1,t-1} S_{i-1,t-1}}{\lambda_t} \right)^{x_{0t}} \times \prod_{i=1}^{\omega} \left(\frac{c_{i-1,t-1} S_{i-1,t-1}}{\lambda_t} \right)^{x_{it}}. \qquad (3.1)$$

The general likelihood of the ages-at-death data (y_{it}, $i = 0, \ldots, \omega$), conditioned on total sample size, $\sum_{i=0}^{\omega} y_{it}$, is multinomial with likelihood

$$\frac{(\sum_{i=0}^{\omega} y_{it})!}{\prod_{i=0}^{\omega}(y_{it}!)} \prod_{i=0}^{\omega} \left(\frac{c_{i,t-1}(1 - S_{i,t-1})}{\sum_{i=0}^{\omega} c_{i,t-1}(1 - S_{i,t-1})} \right)^{y_{it}}. \qquad (3.2)$$

The joint likelihood is the product of the two individual likelihoods (Udevitz and Ballachey 1998). Equations (3.1) and (3.2) involve a subscript t as a time index, but estimates are obtained separately for each time period. We will be examining data from only one time period, and therefore we will no longer include the time subscript in the general likelihoods.

3.3 Stable Age Distribution, Population Growth Rate Known or Unknown

If we assume that the age distribution is stable, we require that the age-class proportions at time $t - 1$ are the same as the age class proportions at time t, meaning that $\lambda_t = \lambda$, $c_{it} = c_i$ and $S_{it} = S_i$ for all t. This means $c_i = l_i / (\lambda^i \sum_{i=0}^{\omega} \frac{l_i}{\lambda^i})$ for $i = 0, \ldots, \omega$, where $l_0 = 1$, and $l_i = \prod_{k=0}^{i-1} S_k$ for $i = 1, \ldots, \omega$. The assumption of stability simplifies the likelihood for the standing age-structure to

$$\frac{(\sum_{i=0}^{\omega} x_i)!}{\prod_{i=0}^{\omega} (x_i!)} \prod_{i=0}^{\omega} \left(\frac{l_i}{\lambda^i \sum_{i=0}^{\omega} \frac{l_i}{\lambda^i}} \right)^{x_i} \tag{3.3}$$

and the likelihood for the ages-at-death data, assuming stability, to

$$\frac{(\sum_{i=0}^{\omega} y_i)!}{\prod_{i=0}^{\omega} (y_i!)} \prod_{i=0}^{\omega} \left(\frac{l_i(1 - S_i)}{\lambda^i \sum_{i=0}^{\omega} \frac{l_i(1-S_i)}{\lambda^i}} \right)^{y_i} \tag{3.4}$$

(Udevitz and Ballachey 1998). Maximum likelihood estimates can be obtained separately from each of these likelihoods if λ is known. The standing age-structure likelihood gives the estimate $\hat{S}_i = x_{i+1} \lambda / x_i$. Notice that the MLE is not well defined when $x_i = 0$ for some i. This not only affects the expectation of S_i, but the variance calculations using the delta method as well. The Bayesian estimates would not suffer from such problems as all estimates are based on medians and quantiles which are always finite. Bayes estimates are well defined as long as we use proper priors. The ages at death likelihood produces the estimator $\hat{S}_i = 1 - y_i \lambda^i / \sum_{k=1}^{\omega} y_k \lambda^k$. The case where $\lambda = 1$ gives the standard estimators $\hat{S}_i = x_{i+1}/x_i$ and $\hat{S}_i = 1 - y_i / \sum_{k=1}^{\omega} y_k$.

In order to obtain one overall estimator, the likelihoods can be combined by multiplying the individual likelihoods given in Equations (3.3) and (3.4). When these likelihoods are combined, λ can also be estimated as long as we continue to assume stability.

Udevitz and Ballachey's (1998) model can be fitted within a full hierarchical Bayes model using WinBUGS. Concerns about sensitivity to priors were raised by Udevitz (personal communication, April 2007). We addressed these concerns by studying the sensitivity of

Beta(α, β) priors for the age-specific survival rates, S_i. We are assuming that $\lambda = 1$. Within the family of Beta priors, we set $\alpha = \beta = 0.5$, which corresponds to a noninformative prior (Jeffreys 1946), and $\alpha = \beta = 1$, which corresponds to a Uniform$(0, 1)$ prior.
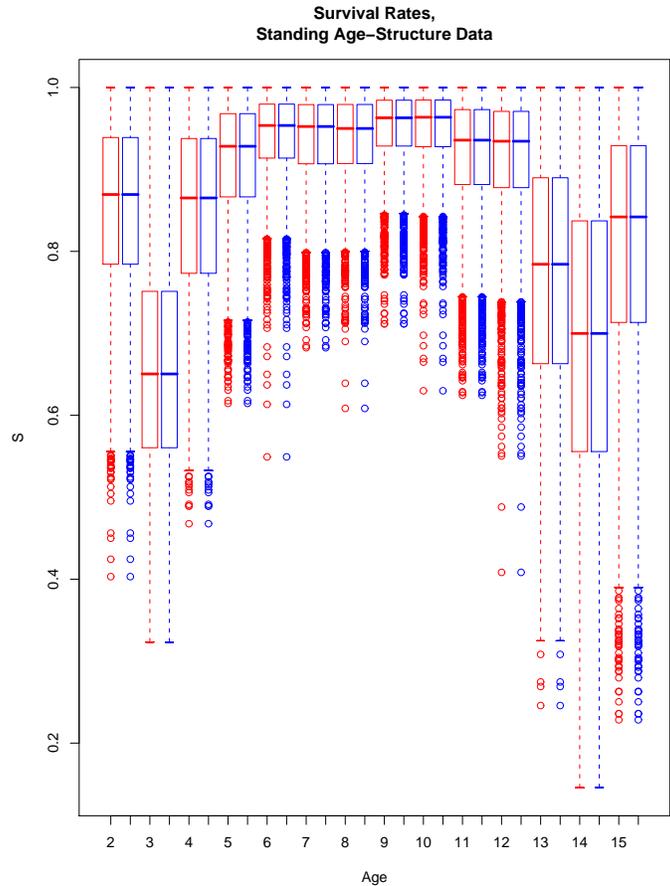
Figure 3.1: Survival rate estimates from WinBUGS and the standing age-structure data alone. The red boxplots are the survival rate estimates from the model with a Beta(0.5,0.5) prior for each S_i, and the blue boxplots are the survival rate estimates from the model with a Beta(1,1) prior for each S_i. This model assumes a stable age distribution and a known population growth rate, which we set equal to one. We deleted the last 5 years of data due to the fact that there were no animals in those categories. We used Beta(α, β) priors in each case, with three chains, 15,000 MCMC runs and a burn-in time of 5,000 runs. The DIC is 79.8 (p_D=3.6) for the model with $\alpha = \beta = 0.5$ and 83.9 (p_D=3.7) for the model with $\alpha = \beta = 1$.

There is no standing age-structure data for ages 16-20. Udevitz and Ballachey
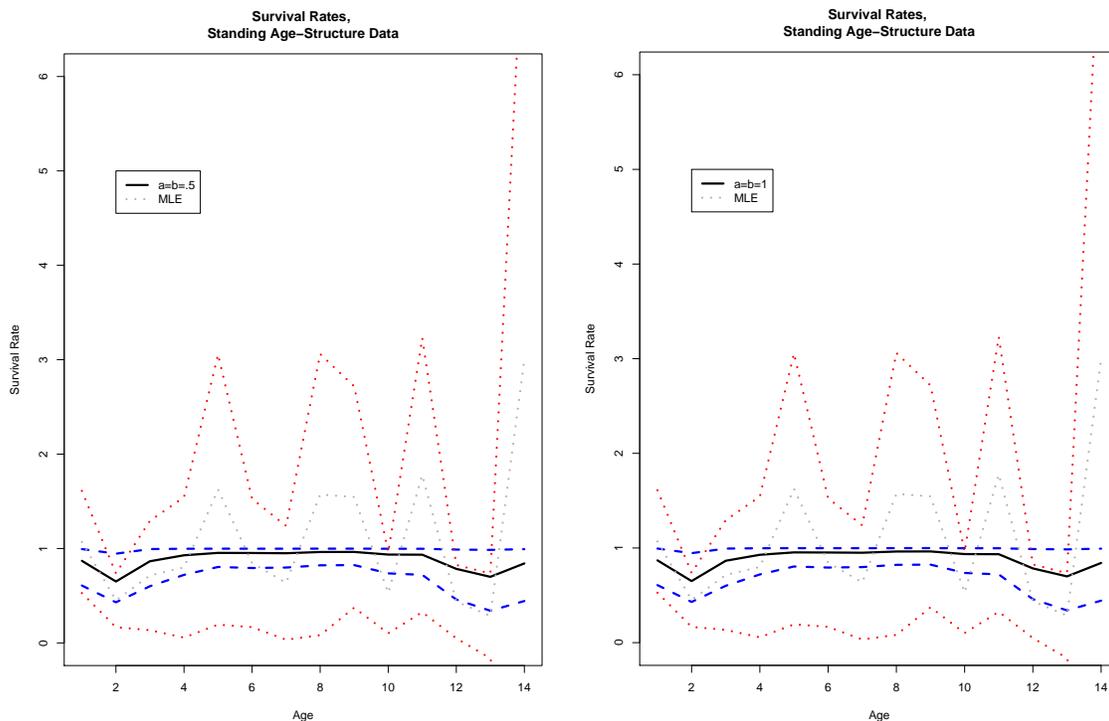
Figure 3.2: Survival rate estimates from the standing age-structure data alone, comparing MLEs with posterior medians using Beta priors with $\alpha = \beta = 0.5$ and $\alpha = \beta = 1$. The black line is the posterior medians from the Beta(.5,.5) and Beta(1,1) prior, from left to right, respectively. The blue lines are the 95% equal-tailed posterior intervals (which are bounded above by one). The grey line is the MLEs (not bounded above), and the red lines are the 95% confidence intervals for the MLEs. This model assumes a stable age distribution and a known population growth rate, which we set equal to one. For the Bayesian estimation, we used three chains, 15,000 MCMC runs and a burn-in time of 5,000 runs. The confidence intervals cover the Bayesian estimates. The posterior intervals are much narrower.

(1998) set ages 5-8 equal and ages 16-20 equal. We choose to delete years 16-20 and keep years 5-8 for our illustration. We ran the model in WinBUGS, using `openbugs` in R, without years 16-20, in order to check the two prior distributions for sensitivity. Figure 3.1 shows boxplots of the posterior distributions for the two sets of estimates. There does not appear to be much prior sensitivity as long as there is data in each category. Figure 3.2 compares MLEs from Udevitz and Ballachey's (1998) results with out Bayesian approach with two different priors. However, for consistency, we will use $\alpha = \beta = 0.5$, which resulted in a slightly lower value of DIC indicating relatively better fit. The MLEs of the S_i's are very different from the posterior medians and also lie outside the range of $[0, 1]$.

The estimates for the ages-at-death data alone were also obtained in WinBUGS. The ages-at-death survival rate estimates are shown in Figure 3.3. We assumed that $\lambda = 1$ for all years. We also used Beta(α, β) priors for the age-specific survival probabilities, S_i. We programmed this model into WinBUGS, and obtained the survival estimates in Figure 3.3.
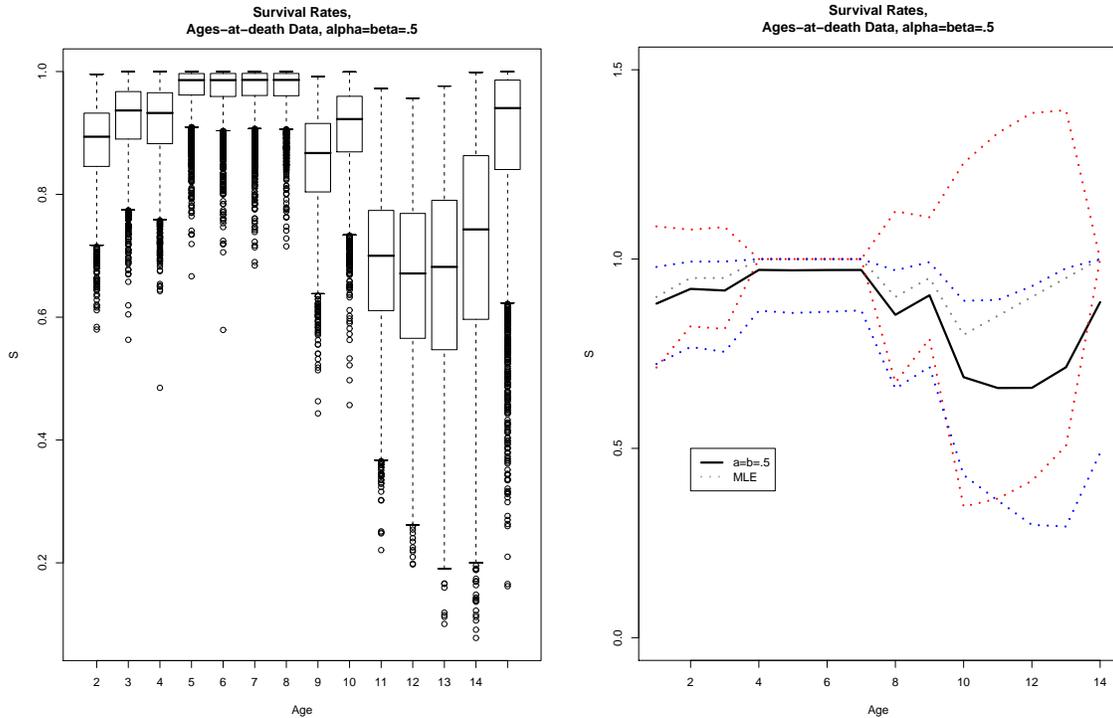
Figure 3.3: Survival rate estimates from WinBUGS using the ages-at-death data alone. The plot on the left displays the boxplots for the posterior distributions for each age-specific survival rate. The plot on the right compares the posterior medians and 95% equal-tailed posterior credible intervals from our Bayesian estimates (the solid black line surrounded by the dotted blue lines) with the MLEs and corresponding 95% confidence intervals (the dotted gray line surrounded by the dotted red lines). This model assumes a stable age distribution and a known population growth rate. We set the population growth rate equal to one and calculated these results using a Bayesian approach similar to Udevitz and Ballachey's (1998) model. We used Beta(0.5,0.5) priors for each of the $\omega + 1$ age-specific survival rates, with three chains, 15,000 MCMC runs and a burn-in time of 5,000 runs. The DIC is 41.6 (p_D=8.0). The MLEs and Bayesian estimates are not significantly different when well-defined.

These results match well with Udevitz and Ballachey's (1998) results, as is shown in Figure 3.3. This means that our Bayesian approach should work well. Also, where the MLEs are well defined, the point estimates do not differ significantly from the posterior medians

from our Bayesian estimates.

3.4 Unstable Age Distribution, Population Growth Rate Known

Udevitz and Ballachey (1998) also discuss the more general situation where stability is unknown but λ is known. These estimates can be calculated from the product of likelihoods (3.1) and (3.2), below.

$$\frac{(\sum_{i=0}^{\omega} x_i)!}{\prod_{i=0}^{\omega}(x_i!)} \left(\frac{\lambda - \sum_{i=1}^{\omega} c_{i-1}S_{i-1}}{\lambda}\right)^{x_0} \times \prod_{i=1}^{\omega} \left(\frac{c_{i-1}S_{i-1}}{\lambda}\right)^{x_i}$$
$$\times \frac{(\sum_{i=0}^{\omega} y_i)!}{\prod_{i=0}^{\omega}(y_i!)} \prod_{i=0}^{\omega} \left(\frac{c_i(1 - S_i)}{\sum_{i=0}^{\omega} c_i(1 - S_i)}\right)^{y_i}$$

$$(3.5)$$

This likelihood yields an explicit maximum likelihood estimator for the age-specific survival, which is $\hat{S}_i = (\hat{c}_{i+1}\lambda)/(\hat{c}_{i+1}\lambda + \hat{d}_i(1 - \lambda(1 - \hat{c}_0)))$ for $i = 0, \ldots, \omega - 1$ where $\hat{c}_i = x_i/\sum_{i=0}^{\omega} x_i$ and $\hat{d}_i = y_i/\sum_{i=0}^{\omega} y_i$.

We applied a Bayesian approach to obtain posterior estimates of the S_i's and c_i's, as well. We continued using Beta$(0.5, 0.5)$ priors for the age-specific survival rates. In order to satisfy the constraint that the c_i's must sum to one, we created a set of variables, g_i, each with a Gamma$(1,0.5)$ distribution. We then set $c_i = g_i/\sum_{i=0}^{\omega} g_i$. These results are given in Table 3.1.

3.5 Unstable Age Distribution, Unknown Population Growth Rate

Udevitz and Ballachey (1998) present two estimable cases: a known population growth rate combined with an unstable age-distribution, and an unknown population growth rate combined with a stable age-distribution. There would be real benefit to being able to relax both the assumption of a stable age-distribution and the assumption of a known population growth rate.

40

Table 3.1: Results from the model assuming that λ is known and equal to one and the age-distribution is unstable. This model was run in R using openbugs. We used three chains, 15,000 MCMC runs and a burn-in time of 5,000 runs.

Parameter	Median	Std. Dev.	95% Equal-tailed posterior interval
S_1	0.92	0.0532	(0.78, 0.98)
S_2	0.90	0.0839	(0.68, 0.99)
S_3	0.87	0.1026	(0.60, 0.99)
S_4	0.96	0.0868	(0.68, 1.00)
S_5	0.98	0.0586	(0.80, 1.00)
S_6	0.97	0.0655	(0.76, 1.00)
S_7	0.96	0.0948	(0.65, 1.00)
S_8	0.81	0.1105	(0.54, 0.96)
S_9	0.92	0.0726	(0.72, 0.99)
S_{10}	0.63	0.1278	(0.37, 0.86)
S_{11}	0.80	0.0954	(0.57, 0.94)
S_{12}	0.72	0.1443	(0.39, 0.94)
S_{13}	0.60	0.2187	(0.16, 0.95)
S_{14}	0.96	0.1062	(0.63, 1.00)
S_{15}	0.23	0.2515	(0.00, 0.84)
	DIC $= 123.6$, $p_D = 21.1$		

If we put the maximum likelihood estimators back into the likelihood given in Equation (3.5), we can reduce the likelihood to the form, below.

$$\frac{(\sum_{i=0}^{\omega} x_i)!}{\prod_{i=0}^{\omega}(x_i!)} \left(1 - \sum_{i=1}^{\omega} \frac{\hat{c}_{i-1}\hat{c}_i}{\hat{c}_i + \hat{d}_{i-1} - \lambda\hat{d}_{i-1}(1-\hat{c}_0)} \right)^{x_0} \times \prod_{i=1}^{\omega} \left(\frac{\hat{c}_{i-1}\hat{c}_i}{\hat{c}_i + \hat{d}_{i-1} - \lambda\hat{d}_{i-1}(1-\hat{c}_0)} \right)^{x_i} \quad (3.6)$$

$$\times \frac{(\sum_{i=0}^{\omega} y_i)!}{\prod_{i=0}^{\omega}(y_i!)} \prod_{i=0}^{\omega} \left(\frac{\hat{c}_i\hat{d}_i - \lambda\hat{c}_i\hat{d}_i(1-\hat{c}_0)}{\hat{c}_{i+1} + \hat{d}_i - \lambda\hat{d}_i(1-\hat{c}_0)} \right)^{y_i}$$

Equation (3.6) is still a function of λ, which means that we can profile λ using the MLEs for $\hat{S}$.
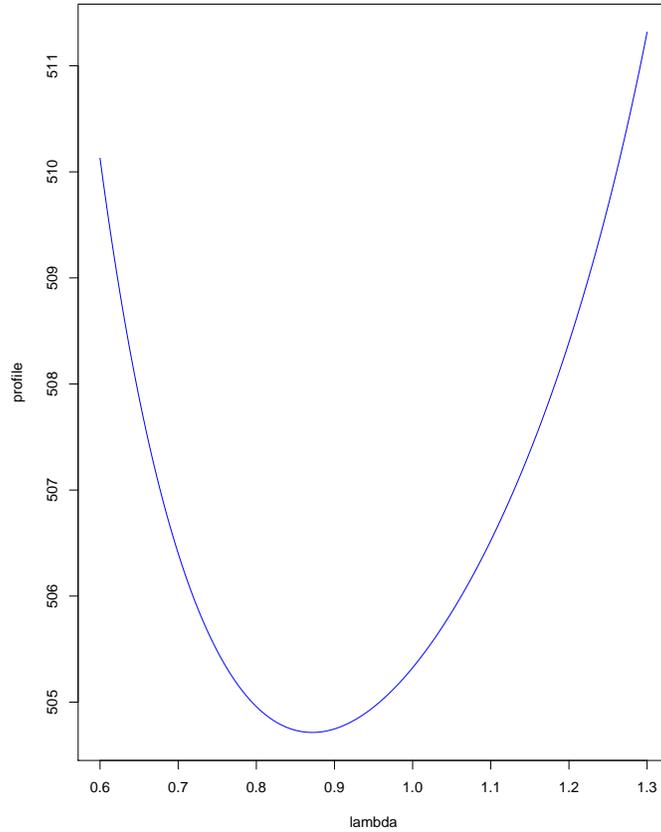
Figure 3.4: The profile negative log likelihood of λ for the unstable age-distribution model of the standing age structure data. This plot suggests that there is information on λ contained in the likelihood function.

Figure 3.4 shows the profile negative log likelihood of λ for the standing age structure data. Because the MLEs are not well-defined at zero, we used the truncated standing age-structure data in this figure to better show how the value of the likelihood changes with λ. The minimum of the negative log-likelihood is achieved at $\hat{\lambda} = 0.87$. We obtained this estimate using the function `optimize` in `R`. This corresponds with the estimates that we obtained via Bayesian methods, as well as to the estimates of λ in Udevitz and Ballachey (1998).

We also implemented a Bayesian approach for the model given in Equation (3.5). We used proper priors for λ: a Gamma(1,1) prior and a Gamma(10,10) prior. We used a Gamma prior because it has the same range as the parameter λ, from 0 to ∞. The Gamma(10,10) prior is very informative, so we would expect the posterior distribution to be close to the prior distribution if there is no information about λ coming from the likelihood.

The plots in Figure 3.5 suggest that there is information on λ contained in the likelihoods. In other words, the likelihood still dominates the prior even when a highly informative prior (e.g. Gamma(10,10)) is used. This confirms, numerically, our findings from Equation (3.6).
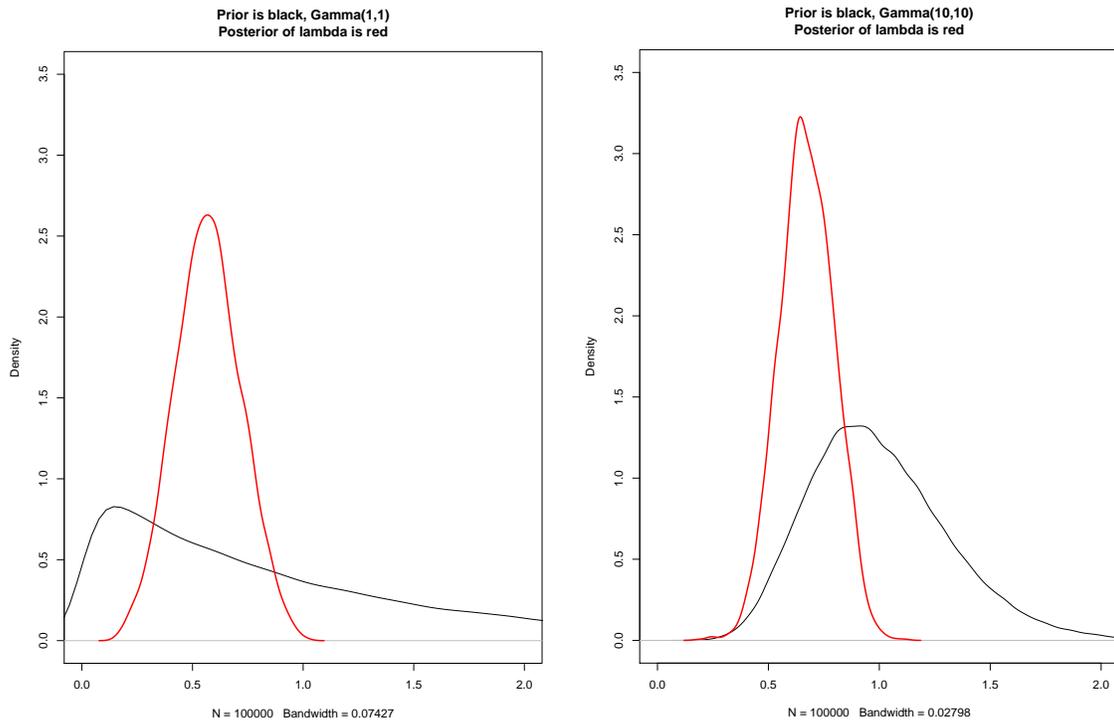
Figure 3.5: Estimates of the population growth rate, λ, compared to its prior distribution. The plot of the left compares the posterior of λ (in red) to its Gamma(1,1) prior (in black). The plot of the right compares the posterior of λ (in red) to its Gamma(10,10) prior (in black). These plots suggest that there is information about λ coming from the data and informing the prior distribution to become the posterior. We ran these models using `openbugs` in `R`, with three chains, 15,000 MCMC runs and a burn-in time of 5,000 runs.

The results from the posterior distributions of S and λ do not change a lot with the

prior for λ. Table 3.2 compares the 95% equal-tailed posterior intervals for the parameters estimated with the priors $\lambda \sim \text{Gamma}(1, 1)$ and $\lambda \sim \text{Gamma}(10, 10)$ under the assumptions of a stable age-distribution and an unstable age-distribution.

Our model converged in WinBUGS for all of those variances, according to the facts that our chains mixed well, our estimates were consistent, and the BGR diagnostic (Brooks and Gelman 1998) indicated no lack of convergence. The 95% equal-tailed posterior intervals for S_i and λ when $\lambda \sim \text{Gamma}(1, 1)$ and $\sim \text{Gamma}(10, 10)$ are given in Table 3.2. These intervals are very similar within each model, regardless of the choice of prior for λ. The intervals are much wider in the model that assumes stability. The DICs for the stability assumed models are much higher than those for the models that do not assume stability. Both of these results indicate that the stability assumed model may not be valid for this data.

The estimates of the population growth rate, λ, are quite different between the stable age distribution and the unstable age distribution models, although they do not change with the prior distribution. The population growth rate estimates are low for the model that does not assume stability. If these estimates are correct, the population is declining very rapidly. However, the population growth estimates correspond with the estimates obtained by Udevitz and Ballachey (1998), as well as the estimate indicated by the profile negative log likelihood of the population growth rate for the standing age structure data.

3.6   Conclusions

Bayesian inference is a useful tool for drawing inferences from combined standing age-structure data and ages-at-death data. Our results suggest that the maximum likelihood estimates for S can be used to calculate a profile likelihood for λ. The benefits of Bayesian estimation include the fact that the Bayesian estimates are well-defined even when the data contain zeros, unlike the maximum likelihood estimates. Also, using the Bayesian approach yields estimates of all the parameters of interest in one step. Even though we had a very small sample from the ages-at-death data ($N = 20$), using that data to augment the standing age-structure data lead to great improvement with both the number and type of assumptions needed for inference.

Table 3.2: Results from both the model that does assume a stable age distribution and the model that does not assume a stable age distribution, neither model assumes a known population growth rate. These are the 95% equal-tailed posterior intervals for each of the age-specific survival rates as well as λ, the population growth rate under a Gamma(1,1) prior for λ and a Gamma(10,10) prior for λ. The posterior intervals under the more informative prior are narrower than those from the relatively vague prior.

	95% Equal-tailed Posterior Interval			
	Stable Age Distribution		Unstable Age Distribution	
Parameter	Gamma(1,1) Prior	Gamma(10,10) Prior	Gamma(1,1) Prior	Gamma(10,10) Prior
S_1	(0.48, 0.92)	(0.47, 0.92)	(0.33, 0.94)	(0.45, 0.95)
S_2	(0.01, 0.98)	(0.01, 0.97)	(0.24, 0.96)	(0.33, 0.97)
S_3	(0.01, 0.97)	(0.01, 0.97)	(0.17, 0.95)	(0.25, 0.96)
S_4	(0.14, 1.00)	(0.14, 1.00)	(0.27, 1.00)	(0.36, 1.00)
S_5	(0.09, 1.00)	(0.11, 1.00)	(0.37, 1.00)	(0.48, 1.00)
S_6	(0.07, 1.00)	(0.08, 1.00)	(0.33, 1.00)	(0.43, 1.00)
S_7	(0.06, 1.00)	(0.07, 1.00)	(0.24, 1.00)	(0.30, 1.00)
S_8	(0.00, 0.85)	(0.00, 0.85)	(0.14, 0.85)	(0.21, 0.88)
S_9	(0.00, 0.96)	(0.00, 0.95)	(0.28, 0.97)	(0.39, 0.98)
S_{10}	(0.00, 0.59)	(0.00, 0.59)	(0.08, 0.62)	(0.11, 0.69)
S_{11}	(0.00, 0.69)	(0.00, 0.70)	(0.15, 0.80)	(0.23, 0.85)
S_{12}	(0.00, 0.82)	(0.00, 0.82)	(0.09, 0.79)	(0.14, 0.84)
S_{13}	(0.00, 0.94)	(0.00, 0.94)	(0.03, 0.81)	(0.04, 0.86)
S_{14}	(0.01, 1.00)	(0.01, 1.00)	(0.21, 1.00)	(0.29, 1.00)
S_{15}	(0.00, 0.65)	(0.00, 0.65)	(0.00, 0.81)	(0.00, 0.83)
λ	(1.04, 1.12)	(1.04, 1.12)	(0.28, 0.86)	(0.44, 0.90)
	DIC = 127.9, p_D = 5.0	DIC = 127.9, p_D = 5.0	DIC = 117.8, p_D = 16.3	DIC = 121.3, p_D = 19.7

Chapter 4

Future Directions for Research

Augmenting capture-recapture data with catch curve data provides the ability to estimate either the population growth rate or the fidelity rate of the population of interest under the assumption of a stable age-distribution. Further augmenting this combination with ages-at-death data could provide a way to relax the assumption of a stable age-distribution while preserving the ability to estimate both the population growth rate and the fidelity rate. We could combine the likelihoods from Udevitz and Ballachey's (1998) paper with the CJS likelihood. This would be a useful development for situations where all three types of data are available.

Augmenting catch curve data with tag-return data would provide a way to estimate the survival rate and the population growth rate without requiring additional information on site fidelity. In tag-return data, the models estimate true survival. There is not the same problem with fidelity with tag-return data as in capture-recapture data.

An additional direction for future research that we are interested in involves following a cohort of animals through time. One negative aspect of using catch curve data is that the researcher cannot follow a cohort of animals through time, since the likelihood for each sample is conditional on its capture probability (Chapman and Robson 1960). Using catch curve data collected over time to follow a cohort would require estimates of those capture probabilities, which are unattainable. In capture-recapture analysis, you can follow animals through time, but age-specific capture recapture methods are expensive and may not work for every population, especially populations where aging animals requires sacrificing them.

By combining catch-curves with age-specific capture-recapture methods, the researcher could obtain estimates of site fidelity or the population growth rate. It might be a little much to age both the capture-recapture sample and the catch curve sample, especially in populations where aging the animals is expensive or time consuming.

To address those problems, while still providing estimates of site fidelity or the

population growth rate, we would like to examine the benefits of aging a known subset of a capture-recapture sample.

For example, if we captured 100 animals and aged 25 of them, we would have catch curve type data but with a known capture probability. The same thing would not be true if we had two independent samples: one capture-recapture sample and one catch curve sample.

The issue with modeling two data sets like this is that they would not be independent. In Chapter 2, we could multiply the CJS likelihood with the catch curve likelihood to create a joint likelihood because we assumed the two samples were independent. We would have to consider what kind of structure the combined likelihoods have when the samples are correlated.

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Appendices

APPENDIX A

Supplement to Chapter 1

A.1 R Code for Estimating Instantaneous Mortality

```
alpha.star=T+.5
beta.star=N
func=function(S){-log(S)*dbeta(S,alpha.star,beta.star)}
Z=integrate(func.n,0.00001,0.99999)
func2=function(S){(-log(S))^2*dbeta(S,alpha.star,beta.star)}
Z.sqd=integrate(func.n2,0.00001,0.99999)
var.Z=Z.sqd$value-Z$value^2
sd.Z=sqrt(var.Z)
```

A.2 WinBUGS Code for Fixed Effects Model

The code for the model to estimate S for each individual year is given below:

```
model{
    for(j in 1:n.years){
    N[j]~dnegbin(S[j],T[j])
    S[j]~dbeta(alpha,beta)
    Z[j]<- -log(S[j])
}
}


### Define the Data ###
```

```
list(n.years=6, N=c(93, 99, 48, 60, 48, 92), T=c(1587, 1640, 888,
1093, 967, 1624), a=.001, b=.001, alpha=.5, beta=.001)
```

The code for the model to estimate constant S over six years is given below:

```
model{
    for(j in 1:n.years){
    N[j]~dnegbin(S,T[j])
}
S~dbeta(alpha,beta)
Z<- -log(S)
}
```

Define the Data

```
list(n.years=6, N=c(93, 99, 48, 60, 48, 92), T=c(1587, 1640, 888,
1093, 967, 1624), a=.001, b=.001, alpha=.5, beta=.001)
```

A.3 WinBUGS Code for Random Effects Model

```
model{

for(j in 1:n.years){

N[j]~dnegbin(S[j],T[j])
S[j]~dbeta(first, second)
mu[j]<-T[j]*(1-S[j])/S[j]
}
```

```
first<- S.star*tau

second <- (1-S.star)*tau tau~dgamma(a, b)


S.star~dbeta(alpha, beta)

variance<- S.star*(1-S.star)/(tau+1)


Z<- -log(S.star)
}


### Define the Data ###


list(n.years=6, N=c(93, 99, 48, 60, 48, 92), T=c(1587, 1640, 888,
1093, 967, 1624), a=.001, b=.001, alpha=.5, beta=.5)
```

Appendix B

Supplement to Chapter 2

B.1 WinBUGS Code for Combined Likelihoods with Fidelity Variable

```
model{

for(i in 1:n.years){
n.x[i,1:omega]~dmulti(cc.cell.prob[i,1:omega],N[i])
N[i]<-sum(n.x[i,1:omega])
for(j in 1:omega){
cell.prob.numerator[i,j]<-pow(S[i],j-1)/pow(lambda, j-1)
}
cell.prob.denominator[i]<-sum(cell.prob.numerator[i,1:omega]) }
for(i in 1:n.years){
for(j in 1:omega){
cc.cell.prob[i,j]<-cell.prob.numerator[i,j]/cell.prob.denominator[i]
}}
 ### define the CJS likelihood ###
for(i in 1:ni){
m.omega[i,1:(nj+1)]~dmulti(cell.prob[i,],R[i])
R[i]<-sum(m.omega[i,])
}
 ### define the recursive relationship of the Chi's ###
Chi[7]<-1
for(i in 1:ni){
```

```
Chi[i]<-(1-phi[i]/theta)+phi[i]/theta*(p.tilde[i])*Chi[i+1] }


 ### define p.tilde=1-p ###
for(i in 1:ni){
p.tilde[i]<-1-p[i]
}
for(i in 1:ni){
for(j in (i+2):nj){
for(k in (i+1):(j-1)){
wp[i,j,k]<-log(phi[k]/theta*p.tilde[k-1])}
cell.prob[i, j]<-phi[i]/theta*p[j-1]*exp(sum(wp[i,j,(i+1):(j-1)])) }
cell.prob[i,i+1]<-phi[i]/theta*p[i] }
 ### define unused cell probabilities as zero ###
for(i in 1:ni){
cell.prob[i,(nj+1)]<-Chi[i] }
for(i in 1:ni){
for(j in 1:i){
cell.prob[i, j]<-0
} }
 ### define prior distributions ###
for(i in 1:ni){
phi[i]<-S[i]*F[i]/theta
S[i]~dbeta(1,1)
F[i]<-min(G[i],1)
G[i]~dgamma(5,4)
}
for(i in 1:(ni-1)){
p[i]~dbeta(1,1)
}
p[ni]<-p[ni-1]
```

```
S.star<-.9259
tau<-S.star*(1-S.star)/pow(.0356,2)-1
beta<-tau*(1-S.star)
alpha<-tau*S.star
theta~dbeta(alpha,beta)
lambda<-1
}


### define the data ###

list(ni=6,nj=7,list(n.x=structure(.Data=c( 1, 6, 15, 21, 14, 16, 10,
9, 6, 3, 3, 0, 0, 0, 2, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 4, 2, 11,
28, 34, 34, 12, 14, 10, 6, 3, 8, 0, 5, 4, 0, 1, 1, 1, 0, 0, 0, 0, 0,
0, 0, 4, 7, 12, 6, 3, 3, 5, 10, 1, 0, 1, 4, 0, 2, 1, 0, 0, 0, 0, 2,
0, 0, 0, 0, 1, 7, 8, 4, 2, 5, 5, 2, 7, 0, 2, 2, 4, 1, 1, 1, 1, 0, 0,
0, 0, 0, 0, 1, 0, 0, 0, 4, 3, 5, 5, 7, 7, 5, 1, 8, 2, 4, 4, 1, 0, 1,
0, 0, 2, 0, 0, 0, 1, 0, 0, 1, 10, 18, 12, 14, 10, 8, 7, 8, 5, 4, 4,
6, 2, 2, 2, 1, 3, 0, 0, 0, 0, 0 ),.Dim=c(6,25)), omega=25,n.years=6,
m.omega=structure(.Data=c(0,101,72,39,33,15,5,1813,
    0,0,116,95,60,35,17,2113,
    0,0,0,76,56,31,12,1630,
    0,0,0,0,74,48,22,1740,
    0,0,0,0,0,91,65,1935,
    0,0,0,0,0,0,64,1909),.Dim=c(6,8)))
```

B.2 WinBUGS Code for Combined Likelihoods with Population Growth Rate Variable

```
model{

for(i in 1:n.years){
n.x[i,1:omega]~dmulti(cc.cell.prob[i,1:omega],N[i])
N[i]<-sum(n.x[i,1:omega])
for(j in 1:omega){
cell.prob.numerator[i,j]<-pow(S[i],j-1)/pow(lambda, j-1) }
cell.prob.denominator[i]<-sum(cell.prob.numerator[i,1:omega]) }
for(i in 1:n.years){
for(j in 1:omega){
cc.cell.prob[i,j]<-cell.prob.numerator[i,j]/cell.prob.denominator[i]
}}
 ### define the CJS likelihood ###
for(i in 1:ni){
m.omega[i,1:(nj+1)]~dmulti(cell.prob[i,],R[i])
R[i]<-sum(m.omega[i,]) }
 ### define the recursive relationship of the Chi's ###
Chi[7]<-1 for(i in 1:ni){
Chi[i]<-(1-phi[i]/theta)+phi[i]/theta*(p.tilde[i])*Chi[i+1] }


 ### define p.tilde=1-p ###
for(i in 1:ni){ p.tilde[i]<-1-p[i] }
for(i in 1:ni){
for(j in (i+2):nj){
for(k in (i+1):(j-1)){
wp[i,j,k]<-log(phi[k]/theta*p.tilde[k-1])}
cell.prob[i,j]<-phi[i]/theta*p[j-1]*exp(sum(wp[i,j,(i+1):(j-1)])) }
```

```
cell.prob[i,i+1]<-phi[i]/theta*p[i] }
 ### define unused cell probabilities as zero ###
for(i in 1:ni){ cell.prob[i,(nj+1)]<-Chi[i] }
for(i in 1:ni){
for(j in 1:i){ cell.prob[i, j]<-0 } }
 ### define prior distributions ###
for(i in 1:ni){
phi[i]<-S[i]*F[i]/theta
S[i]~dbeta(1,1)
F[i]<-1 }
for(i in 1:(ni-1)){
p[i]~dbeta(1,1) }
p[ni]<-p[ni-1]
S.star<-.9259
tau<-S.star*(1-S.star)/pow(.0356,2)-1
beta<-tau*(1-S.star)
alpha<-tau*S.star
theta~dbeta(alpha,beta)
lambda~dgamma(1,0.01) }


###  define the data ###

list(ni=6,nj=7,list(n.x=structure(.Data=c( 1, 6, 15, 21, 14, 16, 10,
9, 6, 3, 3, 0, 0, 0, 2, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 4, 2, 11,
28, 34, 34, 12, 14, 10, 6, 3, 8, 0, 5, 4, 0, 1, 1, 1, 0, 0, 0, 0, 0,
0, 0, 4, 7, 12, 6, 3, 3, 5, 10, 1, 0, 1, 4, 0, 2, 1, 0, 0, 0, 0, 2,
0, 0, 0, 0, 1, 7, 8, 4, 2, 5, 5, 2, 7, 0, 2, 2, 4, 1, 1, 1, 1, 0, 0,
0, 0, 0, 0, 1, 0, 0, 0, 4, 3, 5, 5, 7, 7, 5, 1, 8, 2, 4, 4, 1, 0, 1,
0, 0, 2, 0, 0, 0, 1, 0, 0, 1, 10, 18, 12, 14, 10, 8, 7, 8, 5, 4, 4,
6, 2, 2, 2, 1, 3, 0, 0, 0, 0, 0 ),.Dim=c(6,25)), omega=25,n.years=6,
```

```
m.omega=structure(.Data=c(0,101,72,39,33,15,5,1813,
    0,0,116,95,60,35,17,2113,
    0,0,0,76,56,31,12,1630,
    0,0,0,0,74,48,22,1740,
    0,0,0,0,0,91,65,1935,
    0,0,0,0,0,0,64,1909),.Dim=c(6,8)))
```

Appendix C

Supplement to Chapter 3

C.1 WinBUGS Code for Standing Age-Structure Data

```
model{
x[1:(omega+1)]~ dmulti(cell.prob.as[1:(omega+1)],N.as)
for(i in 1:(omega+1)){ to.prod[i]<-log(S[i]) }
L[1]<-1
for(i in 2:(omega+1)){ L[i]<-exp(sum(to.prod[1:(i-1)]))}
for(i in 1:(omega+1)){
lambda.i[i]<-pow(lambda,(i-1))
fraction[i]<-L[i]/lambda.i[i]   }
denom.part<-sum(fraction[1:(omega+1)])
for(i in 1:(omega+1)){
cell.prob.as[i]<-L[i]/(lambda.i[i]*denom.part)}
 ### Define Priors ###
for(i in 1:(omega+1)){ S[i]~dbeta(1,1) }
lambda<-1
}


### Define the Data ###
list(omega=14,x=c(29,31,14,10,8,13,11,7,11,17,9,16,7,2,6), N.as=191)
```

C.2 WinBUGS Code for Ages-at-Death Data

```
model{

y[1:(omega+1)]~dmulti(cell.prob.ad[1:(omega+1)],N.ad)
for(i in 1:(omega+1)){ to.prod[i]<-log(S[i]) }
L[1]<-1
for(i in 2:(omega+1)){ L[i]<-exp(sum(to.prod[1:(i-1)]))}
for(i in 1:(omega+1)){
lambda.i[i]<-pow(lambda,(i-1))
fraction[i]<-L[i]*(1-S[i])/lambda.i[i] }
denom.part<-sum(fraction[1:(omega+1)])
for(i in 1:(omega+1)){
cell.prob.ad[i]<-L[i]*(1-S[i])/(lambda.i[i]*denom.part)}

### Define Priors ###

for(i in 1:(omega+1)){ S[i]~dbeta(.5,.5) }
lambda<-1
}

### Define Data ###

list(omega=14, y=c(2,1,1,0,0,0,0,2,1,4,3,2,1,0,3), N.ad=20)
```

C.3 WinBUGS Code for Both Lambda and Stability Unknown Data

```
model{

x[1:(omega+1)]~dmulti(cell.prob.as[1:(omega+1)],N.as)

for(i in 2:(omega+1)){
cell.prob.as[i]<-cprob[i-1]*S[i-1]/lambda }
cell.prob.as[1]<-1-sum(cell.prob.as[2:(omega+1)])
y[1:(omega+1)]~dmulti(cell.prob.ad[1:(omega+1)],N.ad)
for(i in 1:(omega+1)){ denom.part.to.sum.ad[i]<- cprob[i]*(1-S[i]) }
denom.ad<-sum(denom.part.to.sum.ad[1:(omega+1)])

for(i in 1:(omega+1)){
cell.prob.ad[i]<-cprob[i]*(1-S[i])/denom.ad }

 ### Define Priors ###

lambda~dgamma(10,10)
for(i in 1:(omega+1)){
S[i]~dbeta(1,1)
g[i]~dgamma(1,.5)
cprob[i]<-g[i]/sum(g[]) }
}

### Define Data ###

list(omega=14, y=c(2,1,1,0,0,0,0,2,1,4,3,2,1,0,3), N.ad=20,
    x=c(29,31,14,10,8,13,11,7,11,17,9,16,7,2,6), N.as=191))
```