# Use of age-at-harvest information to inform wildlife management

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## Abstract

Use of age-at-harvest information to inform wildlife management

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Harvested wildlife must be monitored and managed. Effective assessment of wildlife can be a difficult task because demographic data can be expensive to obtain, especially over large spatial scales. Age-at-harvest and hunter-effort information are routinely collected by managers because hunters can sample populations at very low cost over large geographic areas. However, this information is rarely, if ever, used. Statistical population reconstruction (SPR) provides a flexible model framework which uses age-at-harvest and hunter-effort to simultaneously estimate abundance, survival, harvest probability, and recruitment across large spatial and temporal scales, which has traditionally been a challenge in wildlife management. Here, population reconstruction is shown to accommodate a range of taxa. Furthermore, I show this method can be used with coarsely measured hunter effort or even estimated hunter effort. In addition, I illustrate the application of statistical population

reconstruction with pooled age class information, age classes (0.5, 1.5, 2.5+), which is commonly collected for big game animals. Auxiliary information, beyond age-at-harvest and hunter-effort data, should be an integral part of any population reconstruction process. Auxiliary information stabilizes models, allows for more realistic harvest and survival processes to be modeled, and produces better estimates of precision. Radio-telemetry auxiliary studies can typically be used to estimate both natural survival and harvest probabilities, making them ideal auxiliary studies to augment SPR models. I found population reconstructions based on pooled and unpooled age-class data to be stabilized equally well by auxiliary data. Traditional model evaluation methods such as, chi-square goodness-of-fit, AIC, likelihood ratio test, and residual analysis provide useful information about SPR models. However, these traditional model evaluation methods may not detect model instability. I found point deletion techniques analogous to those used in regression analysis to be very useful in evaluating the stability of population estimates derived from SPR. While SPR is not a panacea for all of the challenges facing wildlife populations and their managers, it is a powerful inventory tool that can be used in conjunction with other demographic analyses to better inform management decisions.

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# Chapter 1: Introduction

Since modern wildlife management began, it has progressed beyond simply preventing overexploitation to three primary tasks: conservation, managing for sustained harvest, and controlling population densities (Strickland 1994). In order to perform these tasks effectively, managers must assess wildlife population status and trends. Estimates of abundance, recruitment, and survival are staples of wildlife assessment and management (Downing 1980, Strickland 1994). Effective assessment of wildlife can be difficult because demographic data can be expensive to obtain, especially over large spatial scales (Downing 1980, Laake 1992). Traditionally, the goal of wildlife managers is to make decisions based on the best information available, within the confines of limited resource availability. Managers often must compromise between management needs, budget restrictions, and staffing resources when making management decisions (Strickland 1994). Since money and labor are often limiting factors, biologists must choose between feasible sampling techniques, which sometimes results in use of inadequate methods for estimating demographic parameters, particularly on large geographic scales (Downing 1980, Laake 1992).

Categories of wildlife population assessment techniques include indices, mark-recapture, sightability, change-in-ratio, and age-at-harvest methods (Strickland 1994, Skalski et. al. 2005). Indices are typically a partial census or an indirect measure of animal abundance such as browse, scat, or nest counts (Anderson 2003). Indices are inexpensive and are commonly used for elusive animals, because they often do not involve counting the actual animal. However, indices can be unreliable, and are routinely unable to produce meaningful demographic information (Seber 1982, Anderson 2003). The Lincoln index, or mark-recapture method, usually requires capturing animals from the population. Those

animals are then marked and re-released into the population. A sample is then taken from the resulting population, and an abundance estimate is derived based on the ratio of marked versus unmarked (Seber 1982). The Lincoln index provides abundance estimates with associated variances, and can be expanded to include multiple mark recaptures. However, this method is impractical to apply on a large scale because of the large number of animals that would need to be marked to produce precise estimates (Laake 1992). In addition, it can be difficult to apply in structurally complex habitats (Novak et al 1991). Change-in-ratio methods are based on estimating a proportion of the population with a given trait (male, female, young etc.), then removing animals from the population with that trait, and then estimating the proportion remaining in the population (Chapman 1954, Seber 1982). Change-in-ratio methods provide abundance and associated variance estimates. They do not, however, estimate survival, capture probability, or recruitment. In addition, change-in-ratio methods assume that the change in the ratio results only from intervention, and it does not work well in the case of a 1:1 ratio (Laake 1992). Sightability and distance methods are based on the probability of sighting an animal from a given distance. With a representative sample of the population, the number of animals seen in a given area is then scaled by the inverse of the detection probability to a larger abundance estimate. These methods are good for large regional surveys and have been used on many species including marine mammals, large game, and small game. Distance methods can be difficult to apply in dense vegetation, are prone to imprecise, positively biased abundance estimates, and do not provide any other population parameter estimates (Seber 1982, Laake 1992). As evidenced above, unrealistic assumptions and data requirements can impose limitations on inventory methods and make abundance estimation difficult and complicated (Novak et al 1991).

Alternatively, hunters can sample populations at very low costs over large geographic areas through collection of age-at-harvest data (Downing 1980). Many states collect age-at-harvest data through hunter check stations, mail-in envelopes, mandatory pelt registration, or other means. A commonly used model that takes advantage of harvest data is the sex-age-kill or SAK model (Skalski and Millspaugh 2002, Millspaugh et. al. 2009). The SAK model is currently used by over 20 state agencies—making it one of the most widely used in big game management today. The SAK model estimates adult male abundance from harvest data and conditional mortality probabilities. The model then estimates adult female and juvenile abundances based on the estimated male abundance and independently estimated sex and juvenile-to-adult ratios. The SAK model is popular because it uses harvest data and is easily understood by wildlife managers (Skalski and Millspaugh 2002). Unfortunately, the assumptions of a stable and stationary population are routinely used to relax data requirements. Violations of the stable–stationary assumption result in wildly inaccurate abundance estimates (Millspaugh et al 2009).

Cohort analysis is another group of wildlife population assessment methods that take advantage of age-at-harvest data. In age-at-harvest data, there is cohort information that can be exploited. This was first done over 60 years ago through virtual population analysis (VPA) (Fry 1949). Fry's VPA provided minimum population estimates by summing harvest across a cohort. The total harvest from a cohort represents the minimum cohort starting size, and would be the true population if there was no natural mortality and 100% harvest (Fry 1949). This analysis could only include complete cohorts, and generally underestimated population abundance. Gulland (1965) used a system of nonlinear equations to improve upon Fry's VPA. In the improved version of VPA, the abundance-to-catch ratio was expressed as a

function of instantaneous natural and harvest mortalities (Gulland 1965, Skalski et al 2005). The major improvement in this analysis was the adjustment for natural mortality. However, major assumptions are required to provide estimates that include incomplete cohorts. In addition, the improved VPA is computationally intensive, requiring iterative solutions (Skalski et al 2005). Pope (1972) offered a simplified version of Gulland's VPA with cohort analysis. Cohort analysis offered closed-form estimators of Gulland's survival parameters, making it easier to compute, but in doing so introduced additional error into the estimates (Pope 1972, Skalski et al 2005). Discreet-time VPA improved upon the concept of cohort analysis once again, by including hunter effort data to model harvest probability (Fryxell et al. 1988). However, discrete-time VPA requires an independent estimate of natural survival. These previous methods of cohort analysis of age-at-harvest data have been unable to estimate incomplete cohort abundances, generally underestimate abundance, and provide no variance estimators.

The most recent advancement in cohort analysis has been statistical population reconstruction (Gove et al 2002, Skalski et al 2005). Statistical population reconstruction has been offered as an alternative to many traditional population evaluation methods to take advantage of age-at-harvest data (Gove et al 2002, Skalski et al 2005). In fisheries management, statistical population reconstruction is commonly referred to as quantitative stock assessment (Hilborn and Walters 1992). In fisheries, a stock recruitment function is often assumed, relating the number of juveniles in a year to the number of adults in the previous year; this is not the case in wildlife statistical population reconstruction. The difference in methods arises because wildlife recruitment is assumed to be extrinsically controlled, by food availability, weather, or other environmental factors, while in fisheries,

recruitment is assumed to be intrinsically controlled. Stock assessment in fisheries has a longer history of use and has widespread application. Statistical population reconstruction is relatively new to wildlife management, and is sparsely used, but gaining in popularity.

Statistical population reconstruction is a flexible model framework based on maximum likelihood estimation, allowing for the inclusion of many data types. This method exploits the cohort relationships found in age-at-harvest and catch-effort data, allowing for the estimation of abundance, survival, harvest probability, and recruitment. Statistical population reconstruction (SPR) allows for parameter estimation across large spatial and temporal scales, which has traditionally been a challenge in wildlife management. It has proved useful in applications with both large and small game (Skalski et al. 2007, Broms et al. 2010).

The purpose of this thesis is to assess the effectiveness and stability of statistical population reconstruction over a range of available data, to provide examples of the application of age-at-harvest data in several unique situations, and provide recommendations for the future use of age-at-harvest data to inform wildlife management decisions. This thesis has five core chapters, each with a unique data source to explore a different facet of age-at-harvest information usage. My objective in this thesis is to evaluate the use of age-at-harvest data with varying levels of information. In doing so, I provide guidance in the use of SPR for future management applications, including recommendations on data requirements and data analysis. The relevance of the individual chapters is as follows.

Chapter 2: This chapter examines how archaeological harvest data can be used in current day game management. The data in this chapter are age-at-harvest information from Native American buffalo (*Bison* spp.) jumps. This chapter illustrates what can be done with a

minimal amount of age-at-harvest data from a single harvest event with no auxiliary information. While not enough information to perform SPR, it can provide useful information for current management through vertical life-table analysis.

Chapter 3: This chapter assesses the loss of information associated with pooling adult age classes. Pooling adult age classes can save a substantial amount of time and money when gathering age-at-harvest data, especially when applied to a statewide monitoring program over several years. The data are 24 years of age-at-harvest and catch-effort information on black-tailed deer (*Odocoileus hemionus*) with both full and pooled age classes, with known effort and 100% aging proportion. Different model structures to pool adult age classes are examined. This method also can be applied to small game species, such as wild turkey (*Meleagris gallopavo*), which are also commonly classified into three age classes.

Chapter 4: This chapter examines the first application of SPR to fur-bearer data. Also this chapter illustrates the incorporation of survey error, associated with estimating effort, into the model structure. Estimating effort is often necessary, especially at larger spatial scales (i.e., statewide management). In addition, not all of the animals harvested are aged so an aging proportion must also be estimated. Aging a sample of the harvest is another common practice to save time and money. The data for this chapter are two data sets, 8 and 12 years of age-at-harvest and catch-effort information for martens (*Martes americana*) and fishers (*Martes pennanti*), respectively. This chapter also assesses the performance of SPR using as few as eight years of data, which may be approaching the lower limit of SPR data requirements.

Chapter 5: This chapter introduces a method to assess the stability of SPR models. In addition, the chapter examines the affect of pooling adult age classes on model stability. This

chapter examines the affect of varying amounts of auxiliary information on model stability, specifically focusing on auxiliary information type, precision, and timing of the data collected. In this chapter I use the same black-tailed deer data used in Chapter 3.

Chapter 6: This chapter illustrates the use of SPR with survival and harvest modeled concurrently. The data set includes eight years of age-at-harvest on Oregon cougar (*Puma concolor*) and catch-effort with full age-class information and known effort. This chapter also provides an example of SPR with radiotelemetry auxiliary data. In addition, this chapter explores the use of the number of hunters, one of the coarsest measures of hunter effort, as the sole measure of hunter effort.

# Chapter 2: Using Age-at-Harvest Analysis of Archaeological Remains in Managing Current Wildlife Populations

## 2.1 Introduction

The Federal Government mandates that the National Parks System protect animals from wanton destruction and harvest, and retain them in their natural condition (Dennis 1999). The first goal has been easy enough to achieve by allowing little or no harvest of animals, depending on the park, with strict regulations and law enforcement. The second mandate may seem simple on the surface, but it becomes far more convoluted when it is examined more closely. First, "natural condition" must be defined. Shrader-Frechette and McCoy (1995) contend that nothing is natural because everything on earth has been changed by people. This definition of natural may contain truth, but it is not helpful in defining "natural" for the purposes of wildlife management. Bonnicksen and Stone (1985) offer a more useful and widely accepted definition of natural—that which was occurring before European settlement. Whatever faults this definition has, it creates a tangible and adequate benchmark, which is consistent with the spirit of National Park Service policies. The National Parks System must manage animals in their natural condition, but what constitutes "natural" in wildlife populations is rarely known given human effects. In this chapter, I focus on management of bison (*Bison bison*). I define natural as pre-European condition and our focus is on pre-European settlement condition of bison.

The finite population growth rate is a commonly used metric to evaluate the status of a wildlife population. Millspaugh et al. (2008) used a Leslie matrix model populated with demographic data from Wind Cave National Park to estimate the finite population growth rate ($\lambda$) and assess the effects of alternative culling regimes on bison herds in the National

Parks System. I will use the same Leslie matrix model, modified to include annual survival probabilities from vertical life-table analysis of archeological bone assemblages, to estimate the finite population growth rate $\lambda$ of pre-European influence bison herds.

Archeological bone assemblages are almost exclusively the work of Native American hunters. Today these bone assemblages capture the interest of archaeologists because of the vast amount of information they hold about the peoples who used them. The hunting of bison has been a part of Plains Native American culture for many thousands of years. Meriwether Lewis wrote in his journal (Bakeless 1964), ". . . one of the most active and fleet young men is selected and disguised in a robe of buffalo skin . . . . he places himself at a distance between a herd of buffalo and a precipice proper for the purpose; the other Indians now surround the herd on the back and flanks and at a signal agreed on all show themselves at the same time moving forward towards the buffalo; the disguised Indian or decoy has taken care to place himself sufficiently near the buffalo to be noticed by them when they take to flight and running before them they follow him in full speed to the precipice; the Indian (decoy) in the mean time has taken care to secure himself in some cranny in the cliff . . . . the part of the decoy I am informed is extremely dangerous." Going by many names throughout history—buffalo or bison jump, kill, or pound, the practice was perpetrated the same way. Animals were rounded up from the open plains and driven into tighter and tighter corridors, using landforms such as hills or canyons, or using manmade obstacles such as fences. The animals were driven towards the treacherous landform of choice, to their death. Two main landforms were used, arroyos (dry river beds) or other soft steep slopes where animals were driven at a high rate of speed down the slope, where they would lose their footing and trample one another, injuring and eventually killing themselves. In addition to soft embankments, actual

cliffs were used. Animals were driven over rock cliffs, where they would fall to their death. The oldest documented bison jumps are over 10,000 years old (Johnson and Bement 2009). The practice has been documented up until around the introduction of the horse when Native Americans became more selective about which animals were hunted (Reher 1978). The wealth of information available at these sites has resulted in much data collection and publications on the subject of Native American bison jumps.

An exhaustive search of this literature was done to determine the scope and quality of the available data and to obtain age-at-harvest data appropriate for demographic analysis. In the process of this investigation, more than fifty articles were reviewed from more than twenty sources. The sources consulted were published from the 1920s (Gilmore 1924) until 2009 (Johnson and Bement 2009). The works of such prominent authors in the field of North American plains archeology as George C Frison, Charles A Reher, Wilson and Wilson, Niven, and more were reviewed. In addition to peer-reviewed journal articles, original master's theses, doctoral dissertations, book chapters, and governmental agency reports were reviewed in search of usable age-at-harvest data.

The majority of the bison jump sites is concentrated in the Black Hills region of the country, in what is now Wyoming, Montana, and the Dakotas (Niven and Hill 1998; Frison 1973, 1979; Reher and Frison 1980). Bison jumps were also found throughout North America, as far south as Texas and New Mexico, and as far north as Alaska (Hill 2002, Todd et al 1992, Byerly 2005, Skinner 1947). The size and scope of the age-at-harvest data found varied dramatically from several thousand animals to fewer than 10 animals (Reher and Frison 1980, Speer 1978). In the course of the investigation, it was also discovered that Native Americans killed not only the American bison (*Bison bison*)

we know today, but three separate bison species, as well as pronghorn and deer in this catastrophic manner. Interestingly, pronghorn and deer may have been driven into corrals and slaughtered instead of being driven down an embankment. This may be due to the natural agility of these species that may make them more difficult to kill on steep soft embankments. However, the cliff falls may have worked equally well for most species harvested.

Not only did the location, type of site, and species of animal vary, but the sophistication of analyses done on the faunal remains varied as well. Many of the reports commissioned by oil and gas companies simply recorded the number of remains found with no age determination conducted (Darlington et al 1992, 1998; O'Brien et al. 1983; Schrodel 1985). Some archaeologists were interested in estimating the number of animals killed at a site in order to determine how many people the site could have supported; again, no aging was done at these sites (Wheat 1967). Archaeologists were also interested in determining at what time of the year the site was used. To accomplish this task, they aged a few young animals to determine how many months' old they were. By aging the very young, the month of the year when the jump occurred can be determined (Hill 2002, Todd et al 2001). It was a rare occasion when an archaeologist found a substantial bone collection and aged a large proportion of it. The aging process is expensive, time consuming, and typically not of interest to the average archaeologist.

Luckily, there were several sites that yielded large numbers (≥15) of aged individuals. In a few cases, archaeologists attempted to estimate survivorship from the age-at-harvest data (Nimmo 1971, Simpson 1984, Frison 1979). In almost all of these cases, a basic vertical life-table analysis was used. In the best cases, a reliable point estimate was achieved with no

measure of precision. However, it was a common practice to arbitrarily manipulate the data to produce a descending survivorship curve to be analyzed. The process involved adding additional counts to the actual data in order to produce a survivorship curve of the desired amplitude and shape. One frequently used approach was to modify the data to resemble an ideal catastrophic kill profile by adding or removing animals to fit an exponential curve (Voorhies 1969, Deevehy 1947, Kurten 1953). It was also common practice to standardize the actual animal numbers to 1,000 or 10,000 thereby omitting actual sample size. These methods do not produce unbiased or reliable point estimates of survival or standard errors. In this chapter I reanalyzed these data sets using state-of-the-art statistical methods to derive not only point estimates but variance estimates as well.

The derived survival estimates were then combined with fecundity parameters from current bison herds to estimate historic finite growth rates of these populations. The purpose of this chapter is to illustrate the potential usefulness of age-at-harvest analysis of ancient populations in managing current game populations.

## 2.2 Methods

### 2.2.1 Criteria for Data

The criteria for including bone assemblages in the analyses were based on three requirements:

1. The age structure (or a portion of it) is monotonically decreasing (or nearly monotonic).
2. The data are from a time-specific catastrophic kill.
3. The data have a minimum sample size of 10 individuals.

Sample sizes in most of the analyses were based on the concept of Minimum Number of Individuals (MNI). The MNI was the minimum number of individuals that could have produced the bone assemblage found. For example, if 18 mandibles were found, and 10 were left and 8 were right, the MNI is 10. However, some data were only available in numbers of mandibles. Mandible analysis can result in the double count of an animal, because mandibles come in pairs.

### 2.2.2 Statistical Analysis

Animals killed in a catastrophic manner, as in a bison jump, provide a snapshot of the age structure of a population. Native American bison kills provide data uniquely suited to this sort of analysis as long as the event is not age selective. This assumption is often expected to be met given the non-selective nature of Native American harvest before horses were obtained. Assuming a representative sample, a stable age distribution, and a stationary population, vertical life-table analysis can be used to estimate survival in the population (Skalski et al. 2005:160-169).

A multinomial distribution can be used to describe the age-at-harvest data and obtain maximum likelihood estimates of total annual survival. The total abundance ($N_t$) of a population is the sum of the abundances $N_j;\ j = 1, \ldots, A$ in each age class of that population

$$N_t = N_1 + N_2 + \ldots + N_A. \tag{2.1}$$

Assuming a stable age distribution, i.e. every cohort starts as the same size $N_0$, and assuming age-specific survival probabilities, Eq. (2.1) can then be written:

$$N_t = N_0 + N_0 S_1 + N_0 S_1 S_2 + N_0 S_1 S_2 S_3 + \ldots. \tag{2.2}$$

That is, the expected number of animals in each age class is a function of constant recruitment $N_0$ multiplied by age-specific survival probabilities $S_i; i = 1, \ldots, A$ . The probability of an animal being in the first age class is then:

$$\frac{N_0}{N_t} \tag{2.3}$$

or the number of animals in the first age class divided by the total number of animals in the population. This can be rewritten as:

$$\frac{N_0}{N_0 + N_0 S_1 + N_0 S_1 S_2 + N_0 S_1 S_2 S_3 + \ldots} = \frac{1}{1 + S_1 + S_1 S_2 + S_1 S_2 S_3 + \ldots} = \frac{1}{\psi} \tag{2.4}$$

where $\psi = 1 + S_1 + S_1 S_2 + S_1 S_2 S_3 + \ldots$. For the second age class, the probability of occurrence can be expressed as:

$$\frac{N_0 S_1}{N_0 + N_0 S_1 + N_0 S_1 S_2 + N_0 S_1 S_2 S_3 + \cdots} = \frac{S_1}{1 + S_1 + S_1 S_2 + S_1 S_2 S_3 + \ldots} = \frac{S_1}{\psi}. \tag{2.5}$$

For the third age class, the probability of occurrence can be expressed as:

$$\frac{N_0 S_1 S_2}{N_0 + N_0 S_1 + N_0 S_1 S_2 + N_0 S_1 S_2 S_3 + \ldots} = \frac{S_1 S_2}{1 + S_1 + S_1 S_2 + S_1 S_2 S_3 + \ldots} = \frac{S_1 S_2}{\psi}. \tag{2.6}$$

The probabilities for each age class are simply the ratio of the survival probability of surviving to that particular age class over the sum of all the survival probabilities (ψ).

A multinomial likelihood can then be constructed using the above probabilities and the number of animals harvested in each age class. Let $l_x$ be the number of animals harvested in age class $x$, and $l_\bullet$ be the total number of animals harvested. Then the multinomial likelihood is of the form:

$$L \;\; S_a \,|\, l_\bullet, l_x \;\; = \binom{l_\bullet}{l_x} \left(\frac{1}{\psi}\right)^{l_0} \left(\frac{S_1}{\psi}\right)^{l_1} \left(\frac{S_1 S_2}{\psi}\right)^{l_2} \ldots \left(\frac{S_1 S_2 \ldots S_{w-1}}{\psi}\right)^{l_A} \tag{2.7}$$

This model (2.7) derived by Skalski et al. (2005) produces the maximum likelihood estimate:

$$\hat{S}_x = \frac{l_{x+1}}{l_x} \tag{2.8}$$

for $x = 1, \ldots, w-1$.

Equation (2.8) is equivalent to Seber's (1982) equation to estimate age-specific survival probability for a time-specific life table. The variance estimate of $\hat{S}$, calculated by Skalski et. al. (2005) using the delta method, as follows:

$$\text{Var } \hat{S}_x = \left[ \frac{\hat{\psi}\hat{S}_x \; 1 + \hat{S}_x}{l_{\cdot} \prod_{i=0}^{x-1} S_i} \right] \tag{2.9}$$

The assumptions of Eq. (2.8) include the following:

1. Age distribution is stable with age-specific survivals being constant over time.
2. Population is stationary with constant abundance over time (λ = 1).
3. All individuals in the population have the same probability of selection.
4. Fates of all animals are independent.
5. Ages of all animals in the sample are measured without error.

Skalski et al. (2005) also point out that bias can exist if these assumptions are violated, especially if animals are not aged correctly. Aging animals correctly may be difficult in the case of multiple thousand-year-old bison jumps. Also, if the population is not stable and stationary, results could be biased. However, since it is difficult to test for these biases, we must simply acknowledge the potential exists for these biases.

### 2.2.3 Bison Population Modeling

I used a deterministic age- and sex-specific Leslie matrix model (Leslie 1945) to estimate the finite population growth rate, commonly referred to as lambda (λ). The model is

based on a projection matrix containing age-specific survival and fecundity rates (Figure 2.1). The projection matrix was populated by annual survival estimates from the archaeological data and fecundity rates from the National Park Service (Millspaugh et al. 2008). The population can be projected ahead one year by multiplying the initial age- and sex-specific vector of abundance by the demographic, or projection matrix. Using this method, the population was projected until a stable age distribution was reached. The current year's population abundance ($N_t$) was then compared to the next year's population abundance ($N_{t+1}$) resulting in an estimate of the finite population growth rate $\left(\text{i.e., } \lambda = \frac{N_{t+1}}{N_t}\right)$.

## 2.3 Results

### 2.3.1 Survival Analysis

#### 2.3.1.1 Overall Results

Data from nine sites from the Great Plains were analyzed, seven of which were from Wyoming, and the others were from Oklahoma and Nebraska. Remains of *Bison* spp. were found at six of nine sites, while the remaining three sites yielded remains from pronghorn (*Antilocapra americana*) or mule deer (*Odocoileus hemionus*). A model assuming a common survival probability was the best model for five of the six bison sites, and two of the three non-bison sites. Annual survival probability estimates for bison ranged from 0.6110 to 0.9085 (SE = 0.0593) and non-bison from 0.2513(SE = 0.0812) to 0.8402 (SE = 0.1071) (Table 2.1).

Table 2.1. Approximate year, species, maximum likelihood estimates, and standard errors from nine Great Plains archaeological sites. Either a common annual survival probability across age classes was estimated (S) or age class specific survival probabilities were estimated ($S_{i-j}$).

| Site | Year (Approximate) | Species | Parameter | Estimate | SE |
|---|---|---|---|---|---|
| Eden-Farson | Unknown | *A. americana* | $S$ | 0.6080 | 0.0446 |
| Rieser Canyon | 1991 A.D. | *A. americana* | $S_0$ | 0.7609 | 0.1707 |
| | | | $S_1$ | 0.2513 | 0.0812 |
| | | | $S_{2-5}$ | 0.8402 | 0.1071 |
| Dead Indian Creek | 3,000 B.C. | *O. hemionus* | $S$ | 0.7440 | 0.0430 |
| Cooper | 10,200 B.C. | *B. antiquus* | $S$ | 0.6143 | 0.1617 |
| Casper | 10,000 B.C. | *B. antiquus* | $S$ | 0.6110 | 0.0945 |
| Hudson-Meng | 7,500 B.C. | *B. occidentalis* | $S$ | 0.7723 | 0.0586 |
| Hawken | 4,500 B.C. | *B. occidentalis* | $S$ | 0.7000 | 0.0718 |
| Scoggin | 2,500 B.C. | *B. bison* | $S$ | 0.6763 | 0.0786 |
| Wardell | 300 A.D. | *B. bison* | $S_{0-2}$ | 0.9085 | 0.0593 |
| | | | $S_{3-7}$ | 0.8027 | 0.0342 |
| | | | $S_{8-12}$ | 0.6233 | 0.0954 |

#### 2.3.1.3 Eden-Farson Site

The Eden-Farson site is located in Sweetwater County, Wyoming. The species killed there was the pronghorn. Nimmo (1971) offered no background on the archaeological context from which these bones were recovered. All animals were aged based on tooth eruption and wear. Nimmo (1971) attempted a vertical life-table analysis, assuming a starting cohort of 1,000 to simplify calculations.

Excavation of the Eden-Farson site yielded mandibles from at least 79 individuals (Figure 2.1). All mandibles found at this site were used in the analysis. Four models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_{y/o}$: Assumed a constant survival rate across the first three age classes and a distinct constant survival rate across the remainder of the age classes.

Model $MS_{y/c}$: Assumed age-specific survival rates for the first three age classes and a constant survival rate across the remainder of the age classes.

Model $MS_a$: Assumed age-specific survival rates.

The inclusion of all of the age classes allowed for a wider breadth of model definition. The likelihood ratio test revealed that no model was significantly different from the most simple model (*MS*) $P\ \chi_1^2 = 0.5352 = 0.4644$ , $P\ \chi_3^2 = 4.909 = 0.1786$ , $P\ \chi_5^2 = 9.3409 = 0.09621$ (Table 2.2). The Akaike information criterion (AIC) values supported this conclusion (Table 2.2). The alternative model ($MS_a$) produced one estimate of annual survival greater than one (Table 2.2). The residuals did not indicate a lack of fit for the *MS* model (Figure 2.1). All of the Anscombe residuals were within +/-2 and were

randomly dispersed (Figure 2.2). Based on all available evidence, a survivorship model for pronghorn from the Eden-Farson site fit best, assuming a common survival probability across all age classes. The common annual survival probability was estimated to be $\hat{S}$ = 0.6080 ( SE = 0.0446).

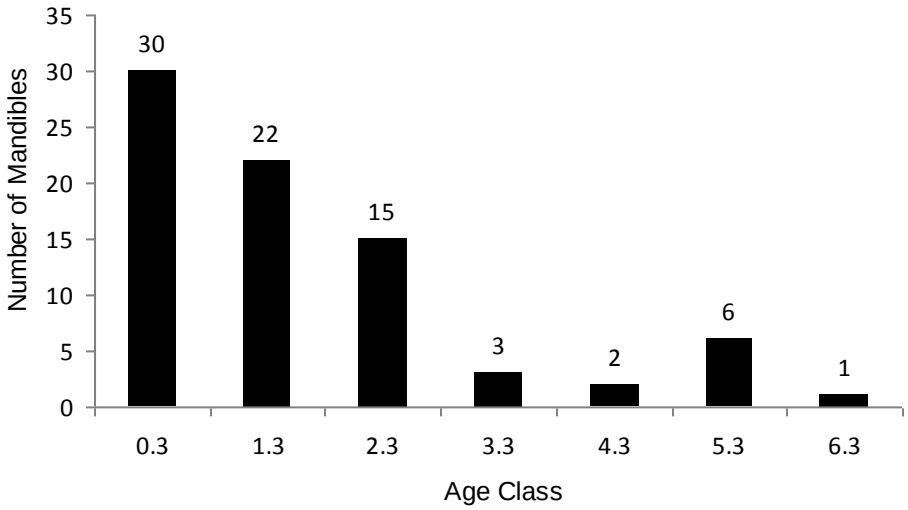



Figure 2.1. Age-class abundances of pronghorn from mandibles at the Eden-Farson, Wyoming.

Table 2.2. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS*, $MS_{y/o}$, $MS_{y/c}$, and $MS_a$ models for pronghorn at the Eden-Farson, Wyoming (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -14.5663 | 1 | 31.1326 |
| $MS_{y/o}$ | -14.2987 | 2 | 32.5974 |
| $MS_{y/c}$ | -12.1118 | 4 | 32.2236 |
| $MS_a$ | -9.89583 | 6 | 31.7917 |

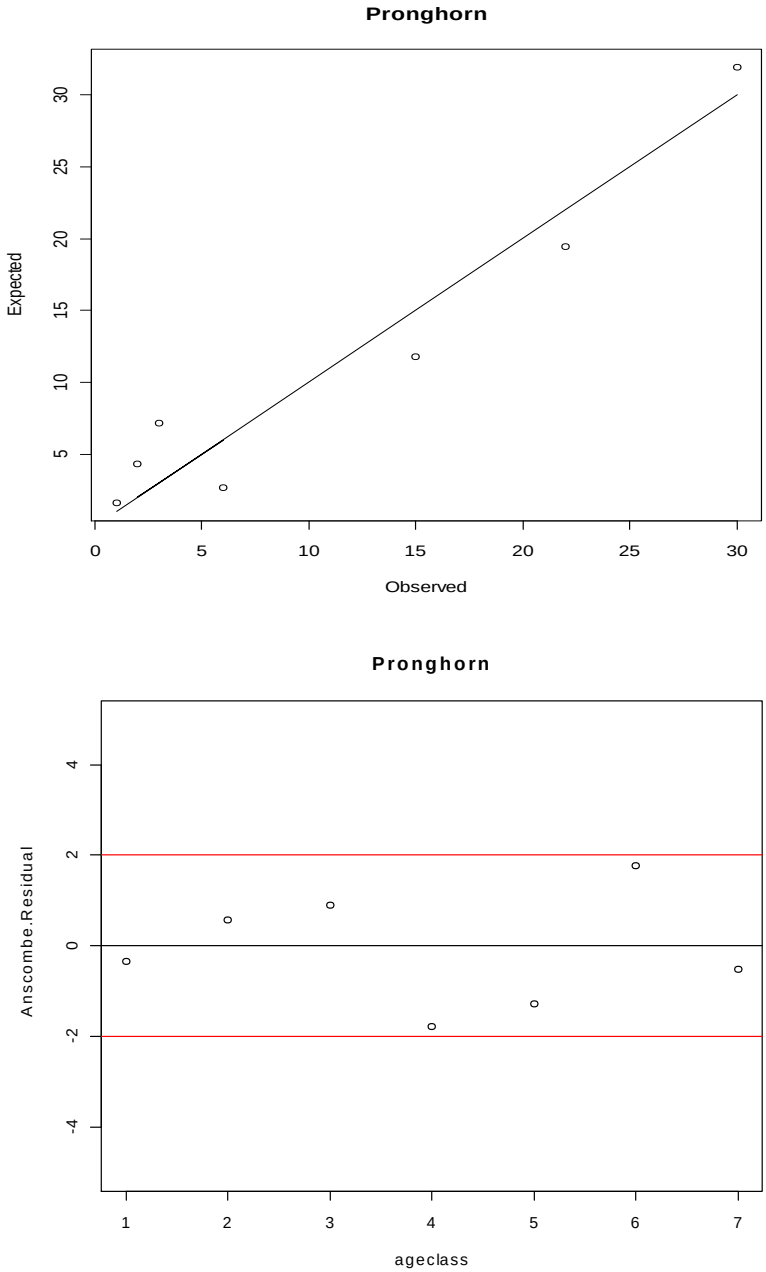



Figure 2.2. Observed vs. expected numbers of animals by age class and Anscombe residuals for model *MS*, for the pronghorn data at the Eden-Farson site, Wyoming.

Table 2.3. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS*, $MS_{y/o}$, $MS_{y/c}$, and $MS_a$ for pronghorn at the Eden-Farson site, Wyoming (*indicates best-fit model).

| *MS** | | | $MS_{y/o}$ | | | $MS_{y/c}$ | | | $MS_a$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE |
| $S$ | 0.6080 | 0.0446 | $S_y$ | 0.5698 | 0.0660 | $S_0$ | 0.7333 | 0.2058 | $S_0$ | 0.7333 | 0.2058 |
| | | | $S_o$ | 0.7053 | 0.1477 | $S_1$ | 0.6818 | 0.2283 | $S_1$ | 0.6818 | 0.2283 |
| | | | | | | $S_2$ | 0.2204 | 0.1175 | $S_2$ | 0.2000 | 0.1265 |
| | | | | | | $S_c$ | 0.9354 | 0.2420 | $S_3$ | 0.6667 | 0.6084 |
| | | | | | | | | | $S_4$ | 3.0000 | 2.4490 |
| | | | | | | | | | $S_5$ | 0.1667 | 0.1800 |

#### 2.3.1.4 Rieser-Canyon Site

The Rieser-Canyon site is located near Green River in Sweetwater County, Wyoming. The species killed here was the pronghorn. This site was not an ancient Native American hunting site. Rieser Canyon was the site of the natural catastrophic death of a herd of pronghorns in 1991. According to the Wyoming Bureau of Land Management, the herd ran off a cliff during a heavy fog. The site was preserved for study purposes by Wyoming Game and Fish and archeologists from Western Wyoming College. The pronghorns were aged to estimate seasonality of the site. All animals were aged based on tooth eruption and wear (Lubinski and O'Brien 2001).

The Rieser-Canyon site yielded mandibles from at least 113 individuals (Figure 2.3). All mandibles found at this site were used in the analysis. Four models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_{y/o}$: Assumed a constant survival rate across the first two age classes and a distinct constant survival rate across the remainder of the age classes.

Model $MS_{y/c}$: Assumed age-specific survival rates for the first two age classes and a constant survival rate across the remainder of the age classes.

Model $MS_a$: Assumed age-specific survival rates.

The inclusion of all of the age classes allowed for a wider breadth of model definition.

The likelihood ratio test revealed that the $MS_{y/c}$ model was significantly different from the most simple model (*MS*) $P\ \chi^2_2 = 9.2756\ = 0.0097$ and that no other model was significantly different from the $MS_{y/c}$ $P\ \chi^2_1 = 5.6482\ = 0.0231$ $P\ \chi^2_3 = 5.6868\ = 0.1270$ (Table 2.4). The AIC values supported this conclusion (Table 2.4). The alternative model

($MS_a$) gave at least one estimate of annual survival greater than one (Table 2.5). The residuals did not indicate a lack of fit for the $MS_{y/c}$ model (Figure 2.4). All of the Anscombe residuals were within +/-2 and were randomly dispersed (Figure 2.4). Based on all available evidence, a survivorship model for pronghorn from the Rieser-Canyon site fit best, assuming age-specific survival rates for the first two age classes and a constant survival rate across the remainder of the age classes. The age-specific survival rates for the first two age classes and common annual survival probability for older animals were estimated to be $\hat{S}_0$ = 0.7609 (SE = 0.1707), $\hat{S}_1$ = 0.2513 (SE = 0.0812), $\hat{S}_{2-5}$ =0.8402 (SE = 0.1071).

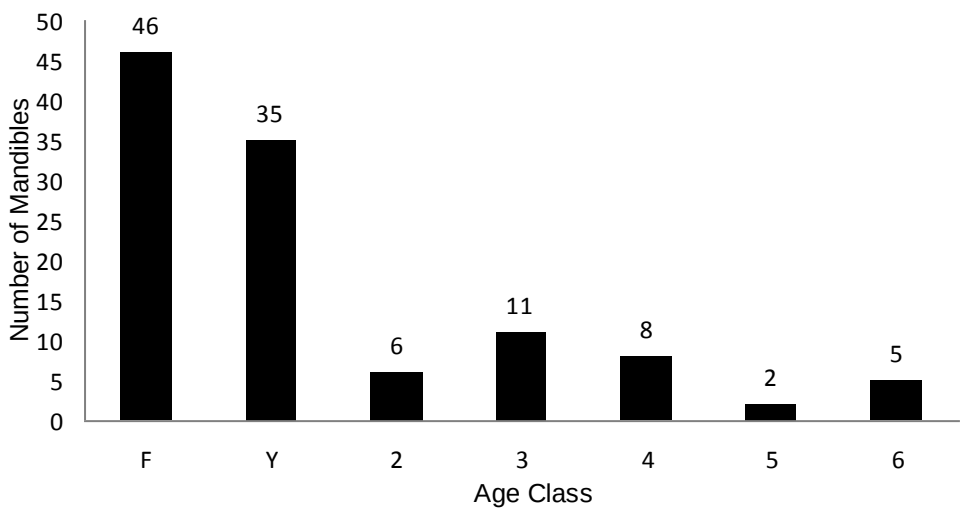


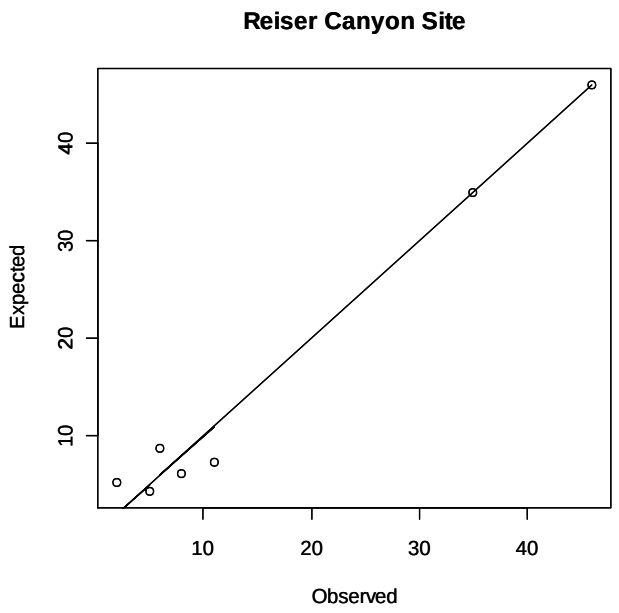

Figure 2.3. Age-class abundances of pronghorn from mandibles at the Rieser Canyon site, Wyoming.

Table 2.4. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS*, $MS_{y/o}$, $MS_{y/c}$ and $MS_a$ models for pronghorn at the Rieser Canyon site, Wyoming (* indicates best fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS* | -18.7023 | 1 | 39.4046 |
| $MS_{y/o}$ | -16.8886 | 2 | 37.7773 |
| $MS_{y/c}$* | -14.0645 | 3 | 34.1290 |
| $MS_a$ | -11.2211 | 6 | 34.4421 |

Table 2.5. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS*, $MS_{y/o}$, $MS_{y/c}$, and $MS_a$ for pronghorn at the Rieser Canyon site, Wyoming (* indicates best-fit model).

| *MS* | | | $MS_{y/o}$ | | | $MS_{y/c}$* | | | $MS_a$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE |
| $S$ | 0.6121 | 0.0373 | $S_0$ | 0.4900 | 0.0655 | $S_0$ | 0.7609 | 0.1707 | $S_0$ | 0.7600 | 0.7609 |
| | | | $S_{1\text{-}5}$ | 0.7450 | 0.0853 | $S_1$ | 0.2513 | 0.0812 | $S_1$ | 0.1700 | 0.1714 |
| | | | | | | $S_{2\text{-}5}$ | 0.8402 | 0.1071 | $S_2$ | 1.8330 | 0.9304 |
| | | | | | | | | | $S_3$ | 0.7273 | 0.3379 |
| | | | | | | | | | $S_4$ | 0.2500 | 0.1976 |
| | | | | | | | | | $S_5$ | 2.5000 | 2.0915 |



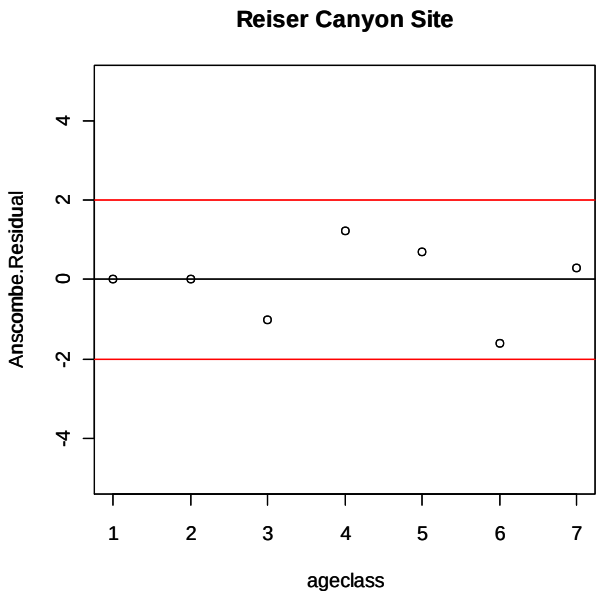




Figure 2.4. Observed vs. expected numbers of animals by age class and Anscombe residuals for model $MS_{y/c}$ for the pronghorn data at the Rieser Canyon site, Wyoming.

#### 2.3.1.5 Dead Indian Creek Site

The Dead Indian Creek site, named for the valley in which it is found, is located near the city of Cody in Park County, Wyoming. This site was a campsite used in the early Archaic Period, around 3,000 B.C. The species killed at this site was mule deer. Animals were aged based on tooth eruption and wear. Simpson (1984) attempted a vertical life-table analysis. In that analysis, the data set was standardized to 100 animals, because it was "common practice for ease in calculations," and an unexplained smoothing technique was used to create a survivorship curve, because it was "common practice in population modeling" (Simpson 1984).

Excavation of the Dead Indian Creek site yielded a total of 60 mandibles; an MNI measurement was not available at this site (Figure 2.5). All mandibles were included in this analysis. Two models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_a$: Assumed age-specific survival rates.

These were the only models explored because the animal's life history and the data suggested no other probable model structures.

The likelihood ratio test revealed that the full model ($MS_a$) was not significantly different from the reduced model $P\ \chi^2_6 = 3.9496\ = 0.6848$ (Table 2.6). The AIC values supported this conclusion (Table 2.6). The full model ($MS_a$) gave several survival estimates over 1, suggesting it was not a realistic model for this data set (Table 2.7). The residuals did not indicate a lack-of-fit for the *MS* model (Figure 2.6). All of the Anscombe residuals were within +/-2 and were randomly dispersed (Figure 2.6). Based on all available evidence, a

survivorship model for mule deer from the Dead Indian Creek site fit best, assuming a common survival probability across all age classes. The common annual survival probability was estimated to be $\hat{S}$ = 0.7440 (SE = 0.0430).

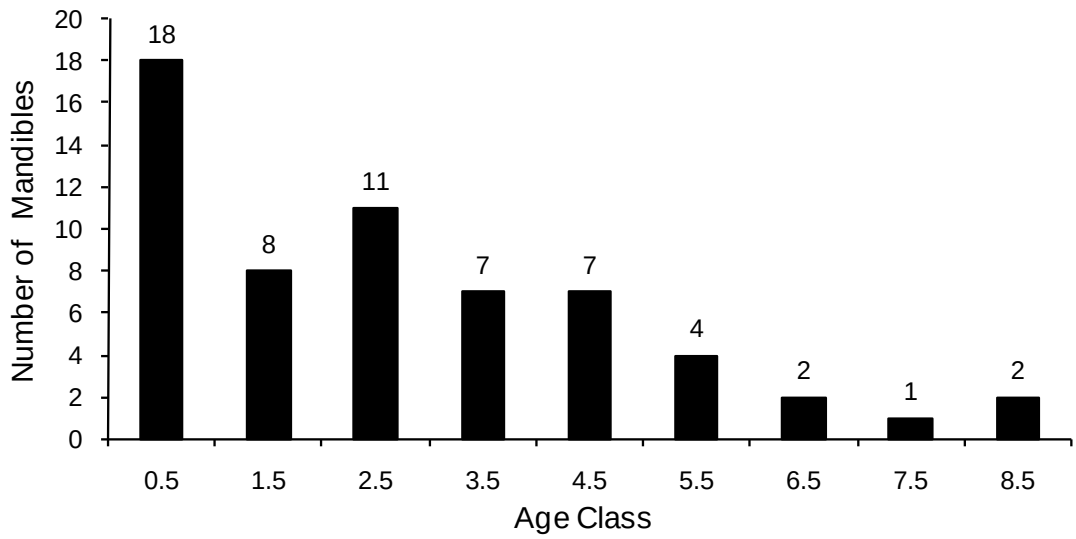



Figure 2.5. Age-class abundances from mandibles of mule deer at the Dead Indian Creek site, Wyoming.

Table 2.6. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS* and $MS_a$ models for mule deer at the Dead Indian Creek site, Wyoming (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -14.5247 | 1 | 31.0494 |
| $MS_a$ | -12.5499 | 8 | 41.0999 |

Table 2.7. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS* and $MS_a$ for mule deer at the Dead Indian Creek site, Wyoming (* indicates best-fit model).

| *MS** | | | $MS_a$ | | |
|---|---|---|---|---|---|
| Parameter | Estimate | SE | Parameter | Estimate | SE |
| $S$ | 0.7444 | 0.0438 | $S_0$ | 0.4440 | 0.1888 |
| | | | $S_1$ | 1.3750 | 0.6389 |
| | | | $S_2$ | 0.6364 | 0.3077 |
| | | | $S_3$ | 1.0000 | 0.5345 |
| | | | $S_4$ | 0.5714 | 0.3581 |
| | | | $S_5$ | 0.5000 | 0.4329 |
| | | | $S_6$ | 0.5000 | 0.6121 |
| | | | $S_7$ | 2.0000 | 2.4485 |

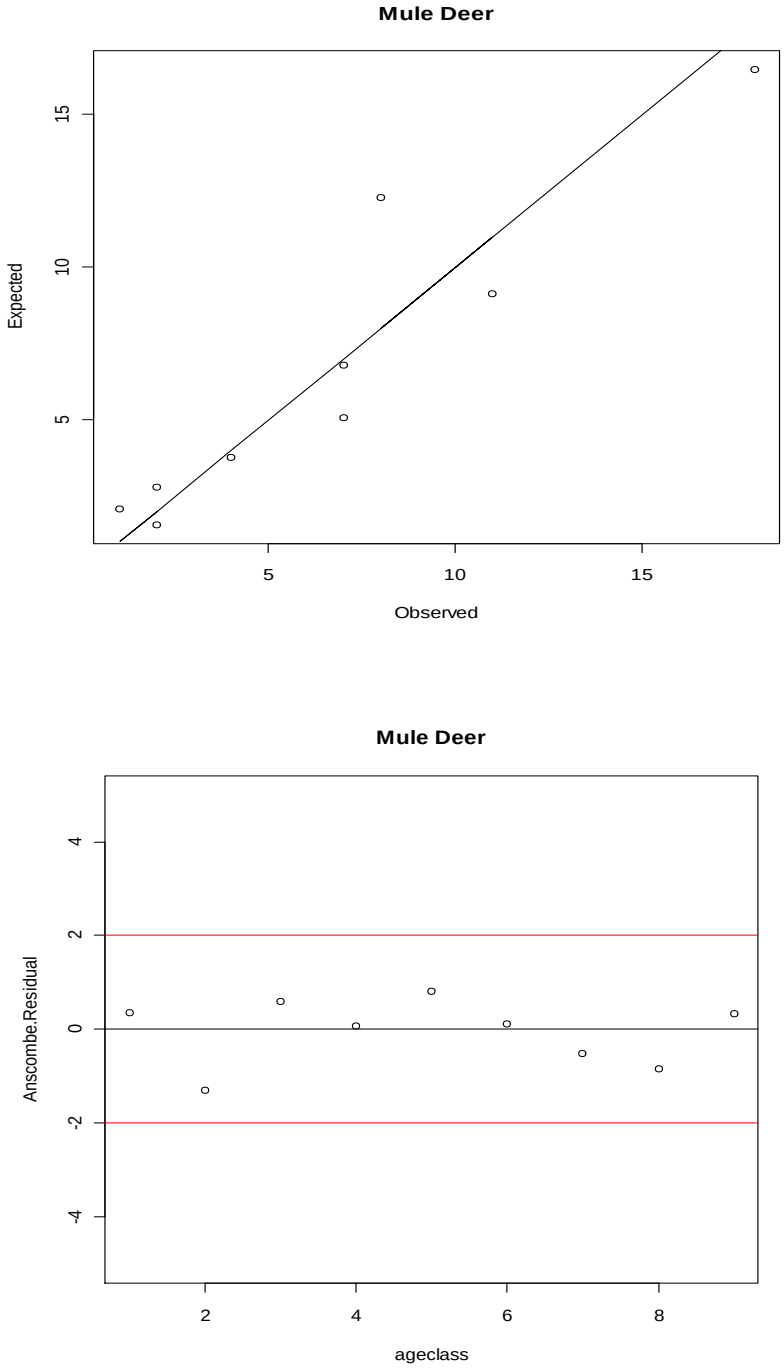



Figure 2.6. Observed vs. expected numbers of animals by age class and Anscombe residuals for model *MS* for the mule deer data at the Dead Indian Creek site, Wyoming.

#### 2.3.1.6 Cooper Site

The Cooper site is located on the bank of the Beaver River in Harper County, Oklahoma. The species killed at this site was *B. antiquus*, the oldest bison species harvested by the Plains Native Americans. The Cooper site was used around 10,200 B.C., making it the oldest site analyzed in this chapter. All animals were aged using tooth eruption and wear. There was no attempt made by the original authors to estimate survivorship, or any other population parameters (Johnson and Bement 2009).

Excavation of the Cooper site revealed three distinct kills over time. The middle kill was the only one that yielded enough information for analysis. A total of 17 mandibles were found in the middle kill at the Cooper site (Figure 2.7). The first two age classes were not used in this analysis because each only had one or two individuals. A total of 14 mandibles, in four age classes were included in this analysis, making it the smallest sample analyzed in this chapter. Two models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_a$: Assumed age-specific survival rates.

These were the only models explored because of the extremely small sample size.

The likelihood ratio test revealed that the full model ($MS_a$) was not significantly different from the reduced model P $\chi^2_2 = 0.3327$ $= 0.8467$ (Table 2.8). The AIC values supported this conclusion (Table 2.8). The full model ($MS_a$) gave fairly similar results (Table 2.9). The residuals did not indicate a lack-of-fit for the *MS* model (Figure 2.8). All of the Anscombe residuals were within +/-2 and were randomly dispersed (Figure 2.8). Based on all available evidence, a survivorship model for bison from the Cooper site fit best, assuming

a common survival probability across all age classes. The common annual survival probability was estimated to be $\hat{S}$ = 0.6143 (SE = 0.1617).

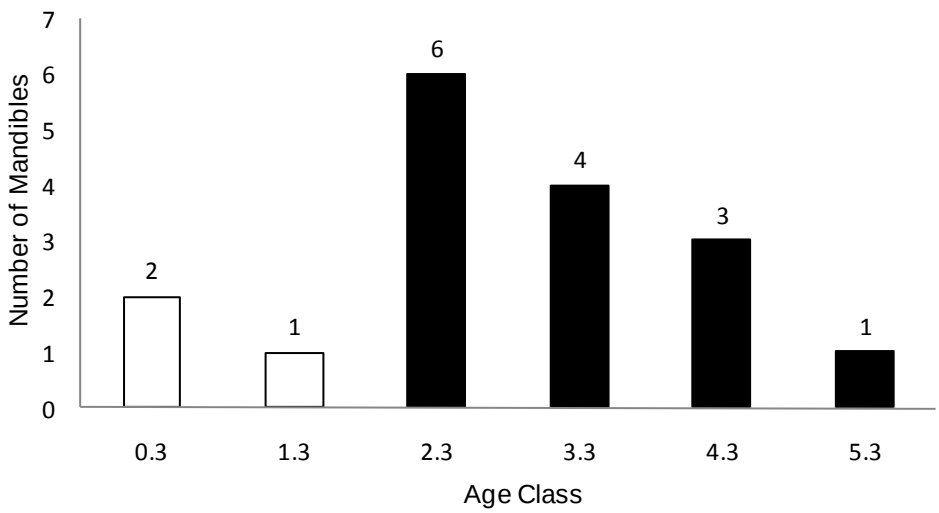



Figure 2.7 Age-class abundances from mandibles of *B. antiquus* at the Cooper site, Oklahoma. Age classes 2.3–5.3 used in the analysis (shaded bars).

Table 2.8. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS* and $MS_a$ models for the bison (*B. antiquus*) at the Cooper site, Oklahoma (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -3.8794 | 1 | 9.7588 |
| $MS_a$ | -3.7131 | 3 | 13.4261 |

Table 2.9. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS* and $MS_a$ for the bison (*B. antiquus*) at the Cooper site, Oklahoma (* indicates best-fit model).

| *MS** | | | $MS_a$ | | |
|---|---|---|---|---|---|
| Parameter | Estimate | SE | Parameter | Estimate | SE |
| $S$ | 0.6143 | 0.1617 | $S_0$ | 0.6667 | 0.4303 |
| | | | $S_1$ | 0.7500 | 0.5728 |
| | | | $S_2$ | 0.3333 | 0.3849 |

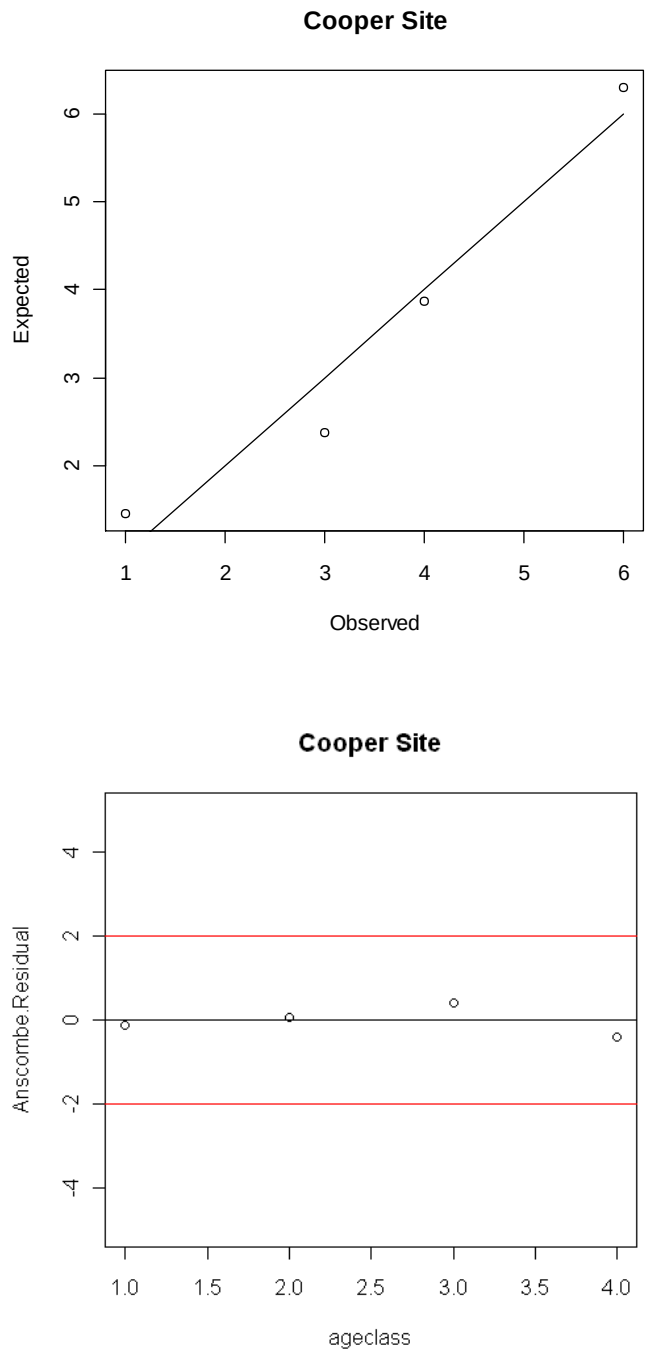



Figure 2.8. Observed vs. expected numbers of animals by age class and Anscombe residuals for model *MS* for the bison (*B. antiquus*) data (age classes 3–6) at the Cooper site, Oklahoma.

#### 2.3.1.7 Casper Site

The Casper site, named for its proximity to the city of Casper, Wyoming, in what is now Natrona County, Wyoming, was a steep sandy dune. The animals killed at the site were *B. antiquus*, the oldest bison species found to have been hunted by the Native Americans of the Great Plains. The Casper site was used around 8,000 B.C., making it the second oldest site analyzed in this chapter. The kill at this site occurred in what is commonly referred to as "pre-history," pre-dating the invention of the wheel. All animals were aged based on tooth eruption and wear. Frison (1979) attempted a vertical life-table analysis. The initial cohort size was set to 1,000 to simplify calculations, and the data were adjusted with "additions needed to approximate normal populations" (Frison 1979).

Excavation of the Casper site yielded mandibles from at least 74 animals. However, because of the need for monotonicity in the data, only age classes 7.6 through 11.6 were used (28 mandibles) (Figure 2.9). Two models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_a$: Assumed age-specific survival rates.

These were the only models explored because of the mature age classes used.

The likelihood ratio test revealed that the full model ($MS_a$) was not significantly $x$ different from the reduced model $P\ \chi^2_3 = 1.8169\ = 0.6102$ (Table 2.10). The AIC values supported this conclusion (Table 2.10). The full model ($MS_a$) gave fairly disparate results (Table 2.11), and estimated one survival probability over one, indicating it was an unrealistic option for these data. The residuals did not indicate a lack-of-fit for the *MS* model (Figure 2.10). All of the Anscombe residuals were within +/-2 and were randomly dispersed (Figure

2.10). Based on all available evidence, a survivorship model for bison from the Casper site fit best, assuming a common survival probability across all age classes. The common annual survival probability was estimated to be $\hat{S} = 0.6110$ (SE = 0.0945).

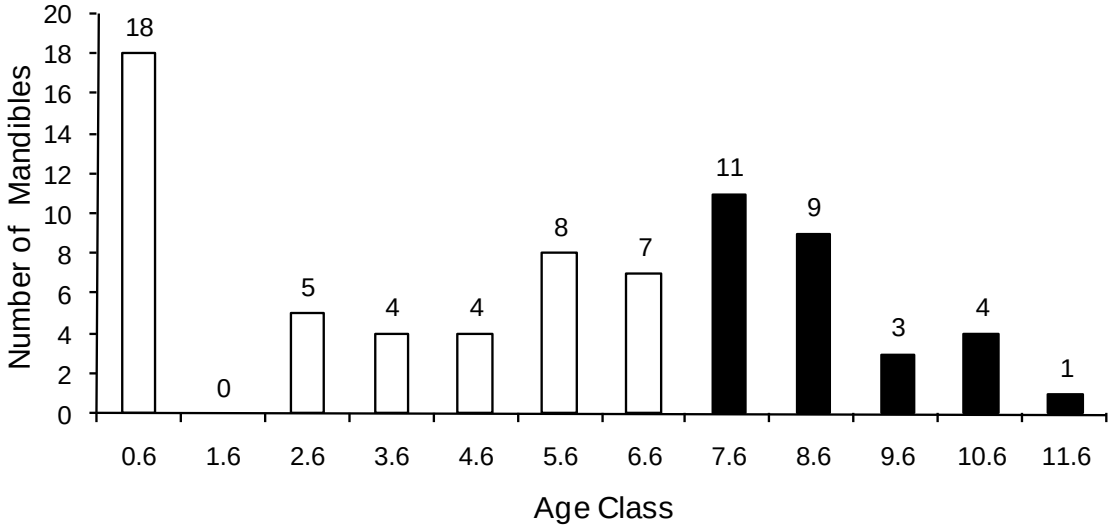


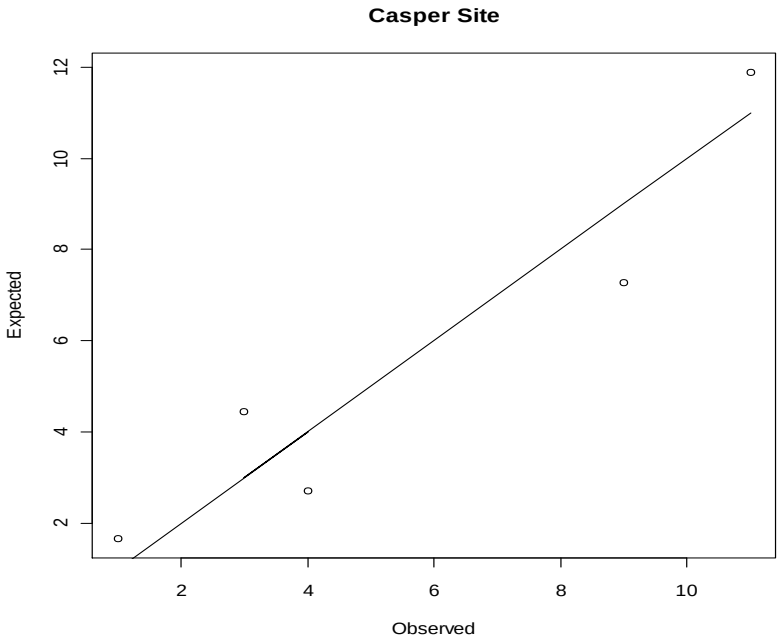

Figure 2.9. Age-class abundances from mandibles of *B. antiquus* at the Casper site, Wyoming. Age classes 7.6–11.6 used in the analysis (shaded bars).

Table 2.10. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS* and $MS_a$ models for the bison (*B. antiquus*) at the Casper site, Wyoming (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -6.6015 | 1 | 15.2030 |
| $MS_a$ | -5.6931 | 4 | 19.3861 |

Table 2.11. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS* and $MS_a$ for the bison (*B. antiquus*) at the Casper site, Wyoming (* indicates best-fit model).

| *MS** | | | $MS_a$ | | |
|---|---|---|---|---|---|
| Parameter | Estimate | SE | Parameter | Estimate | SE |
| $S$ | 0.6110 | 0.0945 | $S_0$ | 0.8181 | 0.3677 |
| | | | $S_1$ | 0.3333 | 0.2222 |
| | | | $S_2$ | 1.3333 | 1.0184 |
| | | | $S_3$ | 0.2500 | 0.2795 |



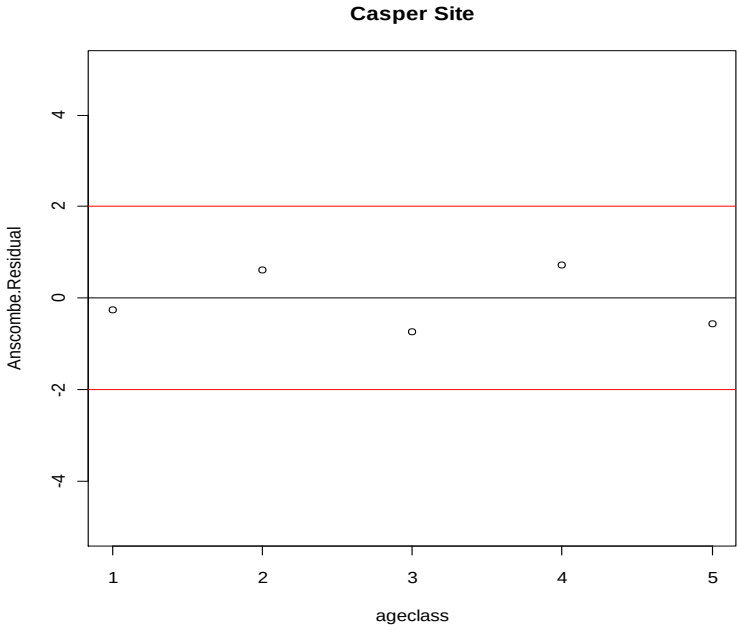




Figure 2.10. Observed vs. expected numbers of animals by age class and Anscombe residuals for model *MS* for the bison (*B. antiquus*) data (age classes 7–11) at the Casper site, Wyoming.

#### 2.3.1.8 Hudson-Meng Site

The Hudson-Meng site, named for the ranchers who discovered it in the early 1950s, Albert Meng and Bill Hudson, is located in northwestern Sioux County, Nebraska. The animals killed at this site were *B. occidentalis*. The artifacts found at the site were from the ancient Alberta culture and place the site at around 7,500 B.C. Larry Agenbroad and his team excavated the site in the early 1970s. All animals were aged based on tooth eruption and wear. There was no attempt made by the original authors to estimate survivorship or any other population parameters (Agenbroad 1978).

Excavation of the Hudson-Meng site yielded 217 mandibles (Figure 2.11). The first three age classes were not included in this analysis because of the need for some monotonicity. Age classes 3.5 through 9.5 were used in the analysis (51 mandibles). Two models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_a$: Assumed age-specific survival rates.

These models were chosen because of the mature age classes used and the structure of the data.

The likelihood ratio test revealed that the full ($MS_a$) model was not significantly different from the reduced model $P\ \chi^2_5 = 8.9110\ = 0.1126$ (Figure 2.12). The AIC values supported this conclusion (Figure 2.12). The full model, $MS_a$, estimated several survival probabilities over 1, indicating it was an unrealistic model for this data set (Table 2.13). The residuals showed a repeating trend, suggesting the best-fit model (*MS*) failed to capture all of the trends within the data (Figure 2.12). All of the Anscombe residuals fell within +/-2 (Figure 2.12). Based on all available evidence, a survivorship model for bison from the

Hudson-Meng site fit best, assuming a constant survival rate across all age classes. The common annual survival probability was estimated to be $\hat{S} = 0.7723$ (SE = 0.0585).

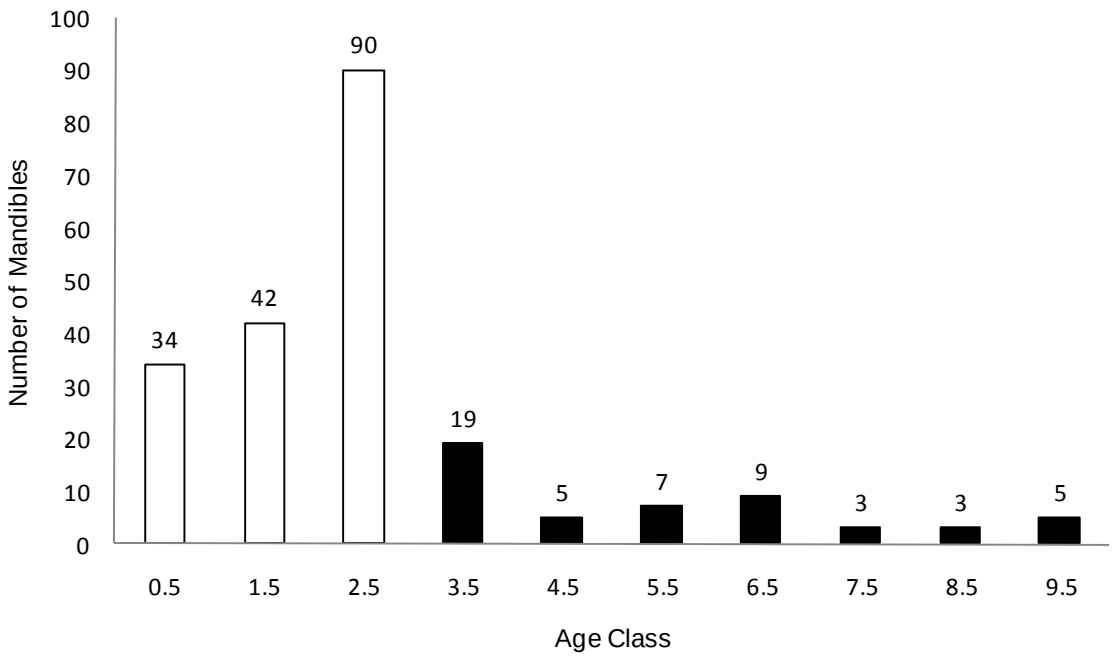


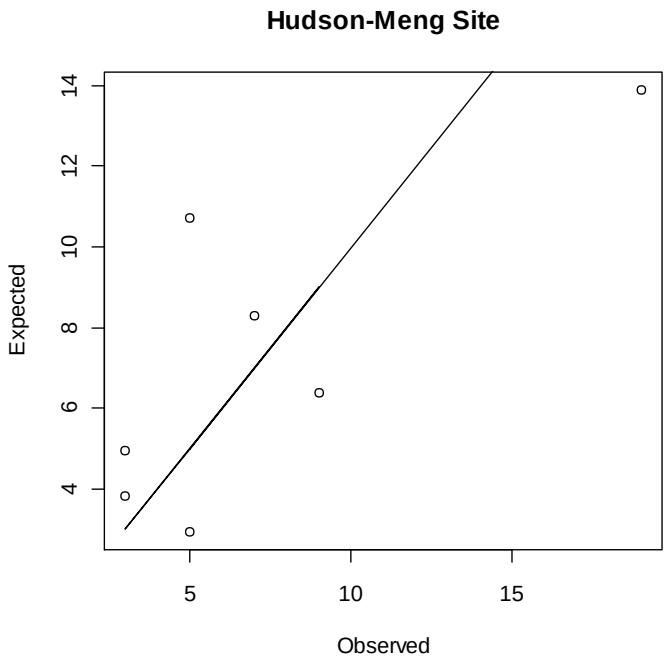

Figure 2.11. Age-class abundances from bison (*B. occidentalis*) mandibles at the Hudson-Meng site, Nebraska. Age classes 3.5–9.5 were used in the analysis (shaded bars).

Table 2.12. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS* and $MS_a$ models for the bison (*B. occidentalis*) at the Hudson-Meng site, Nebraska (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -14.3676 | 1 | 30.7352 |
| $MS_a$ | -9.9121 | 6 | 31.8242 |

Table 2.13. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS* and $MS_a$ for the bison (*B. occidentalis*) at the Hudson-Meng site, Nebraska (* indicates best-fit model).

| *MS** | | | $MS_a$ | | |
|---|---|---|---|---|---|
| Model | Parameters | Estimate | Model | Parameters | Estimate |
| $S$ | 0.7723 | 0.0586 | $S_0$ | 0.2630 | 0.1323 |
| | | | $S_1$ | 1.4000 | 0.8198 |
| | | | $S_2$ | 1.2857 | 0.6479 |
| | | | $S_3$ | 0.3330 | 0.2222 |
| | | | $S_4$ | 1.0000 | 0.8167 |
| | | | $S_5$ | 1.6667 | 1.2172 |



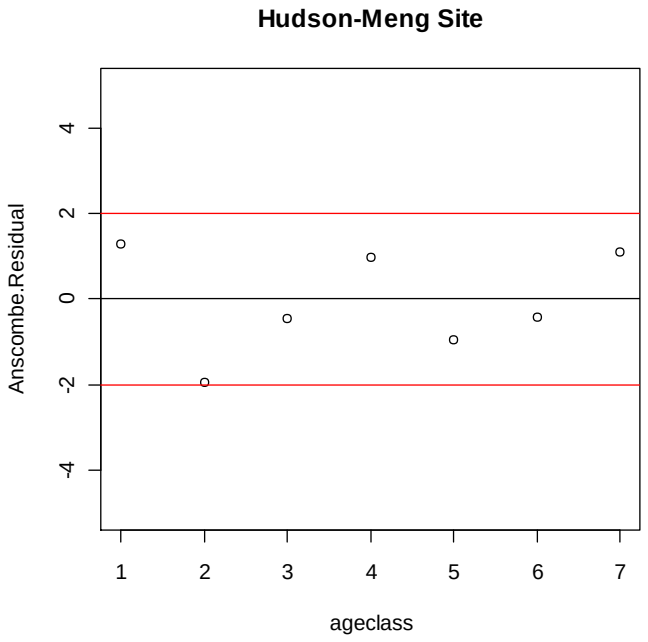




Figure 2.12. Observed vs. expected number of animals by age class and Anscombe residuals for model *MS* for the bison (*B. occidentalis*) data (age classes 3–9) at the Hudson-Meng site, Nebraska.

#### 2.3.1.9 Hawken Site

The Hawken site, named for the family that owns the land, is located in the Black Hills of northeastern Crook County, Wyoming. This site is a steep, dry creek bed around 35-feet deep. The animals killed at this site were *B. occidentalis*, an intermediate species believed to be the link between the ancient and massive *B. antiquus*, which were found at the Casper and Cooper sites, and *B. bison*, which were found at the Wardell and Scoggin sites and are found alive today. Based on the artifacts found at the site, the Hawken site was used during the late altithermal period, which is consistent with the two carbon dates taken from the site of 4520 and 4320 B.C. All animals were aged based on tooth eruption and wear. The mandibles from this study were aged in order to determine seasonality of the site. There was no attempt made by the original authors to estimate survivorship or any other population parameters (Frison et al. 1976).

Excavation of the Hawken site yielded mandibles from at least 95 animals (Figure 2.13). However, because of the need for monotonicity in the data, only age classes 6.7 through 11.7 were used (41 mandibles). Two models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_a$: Assumed age-specific survival rates.

These two models were chosen because of the mature age classes used.

The likelihood ratio test revealed that the full model ($MS_a$) was not significantly different from the reduced model P $\chi^2_4 = 1.6916$ $= 0.7896$ (Table 2.14). The AIC values supported this conclusion (Table 2.14). The full model, $MS_a$, gave similar results for most age classes (Table 2.15). The residuals show the *MS* model fit better than the $MS_a$ model. All of the

Anscombe residuals fell within +/-2, and there were no discernable trends in the observed vs. expected plot or the Anscombe residuals (Figure 2.14). Based on all available evidence, a survivorship model for bison from the Hawken site fit best, assuming a constant survival rate across all age classes. The common annual survival probability was estimated to be $\hat{S}$ = 0.7083 (SE = 0.0719).

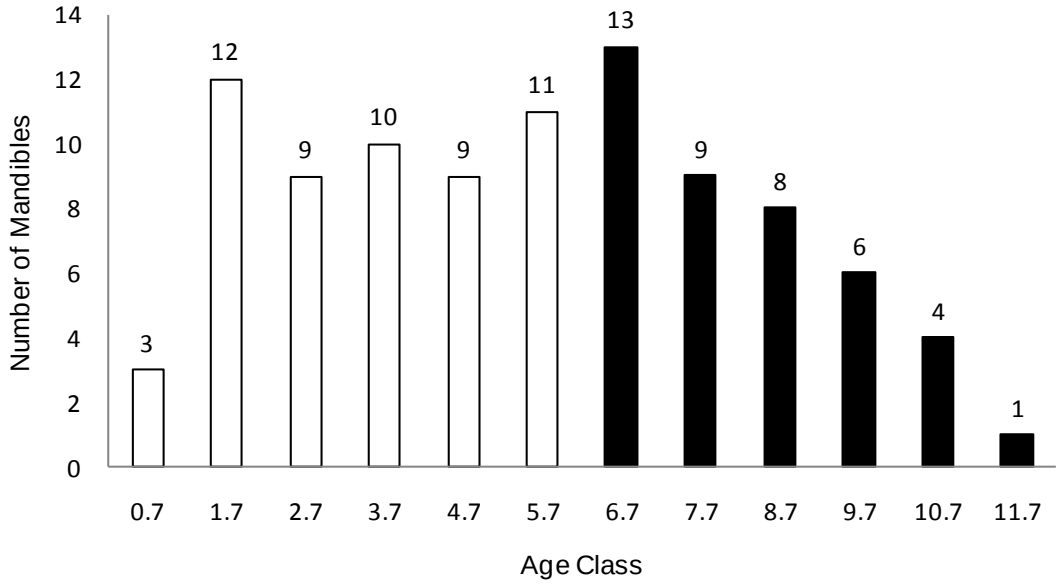



Figure 2.13. Age-class abundances from mandibles of *B. occidentalis* at the Hawken site. Age classes 6.7–11.7 used in the analysis (shaded bars). Notice the monotonic trend.

Table 2.14. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS* and $MS_a$ models for the bison (*B. occidentalis*) at the Hawken site, Wyoming (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -8.7333 | 1 | 19.4666 |
| $MS_a$ | -7.8875 | 5 | 25.7750 |

Table 2.15. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS* and $MS_a$ for the bison (*B. occidentalis*) at the Hawken site, Wyoming (* indicates best-fit model).

| *MS** | | | $MS_a$ | | |
|---|---|---|---|---|---|
| Parameter | Estimate | SE | Parameter | Estimate | SE |
| $S$ | 0.7083 | 0.0719 | $S_0$ | 0.6923 | 0.3002 |
| | | | $S_1$ | 0.8889 | 0.4319 |
| | | | $S_2$ | 0.7500 | 0.4051 |
| | | | $S_3$ | 0.6666 | 0.4304 |
| | | | $S_4$ | 0.2500 | 0.2795 |

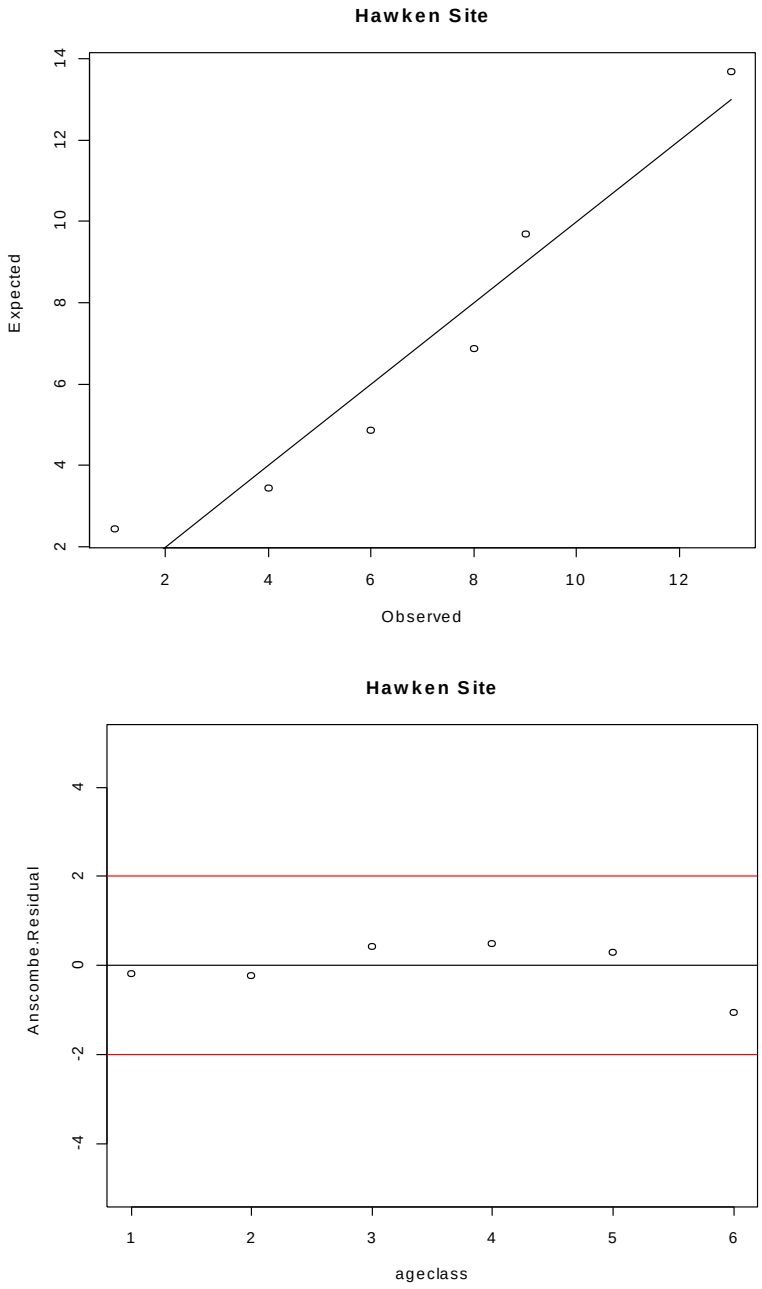



Figure 2.14. Observed vs. expected number of animals by age class and Anscombe residuals for model *MS* for the bison (*B. occidentalis*) data (age classes 7–12) at the Hawken site, Wyoming.

#### 2.3.1.10 Scoggin Site

The Scoggin site is located near the coal creek river in Carbon County, Wyoming. The site was a corral of wood and stone built on the edge of an arroyo. The species killed here was *B. bison*. The Scoggin site was used around 2,500 B.C. This site has been analyzed several times (Lobdell 1973, Miller 1976, Frison 1991, Niven and Hill 1998) because of its historical significance; it represents some of the earliest evidence of the use of corrals to hunt bison. All animals were aged based on tooth eruption and wear. In this analysis, all age classes are two-year increments, because some of the data were only available in two-year age classes. The mandibles from this study were aged in order to determine seasonal use of the site. There was no attempt made by the original authors to estimate survivorship or any other population parameters (Niven and Hill 1998).

Excavation of the Scoggin site yielded mandibles from at least 36 animals. However, because of the need for monotonicity in the data, all but the first age classes were used (33 mandibles) (Figure 2.15). Three models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_{y/o}$: Assumed a constant survival rate for the first three age classes and a different constant survival rate for the last three age classes.

Model $MS_a$: Assumed age-specific survival rates.

These three models were chosen because: the *MS* model was the simplest and most parsimonious model. The $MS_{y/o}$ model was included because the look of the data seemed to suggest a bimodal survivorship pattern, and the $MS_a$ model was the most complex and robust model. The likelihood ratio test revealed that the more complex models were not

significantly different from the reduced model $P\ \chi_1^2 = 0.0093\ = 0.9232$,

$P\ \chi_4^2 = 2.7748\ = 0.5962$ (Table 2.16). The AIC values supported this conclusion (Table 2.16). The $MS_{y/o}$ model gave similar results to model MS for most age classes (Table 2.17). The $MS_a$ model gave fairly disparate results (Table 2.17), and it estimated multiple survival probabilities over 1, indicating it was an unrealistic option for these data. All of the Anscombe residuals for model *MS* fell within +/−2 and there were no alarming trends in the observed vs. expected plot or the Anscombe residuals (Figure 2.16). Based on all available evidence, a survivorship model for bison from the Scoggin site fit best, assuming a constant survival rate across all age classes. The common survival probability was estimated to be $\hat{S}$ = 0.6763 ( SE = 0.0786). However, since age classes for this site were represented in two-year increments, the annual survival probability was $\hat{S}$ = ( SE = 0.0612).

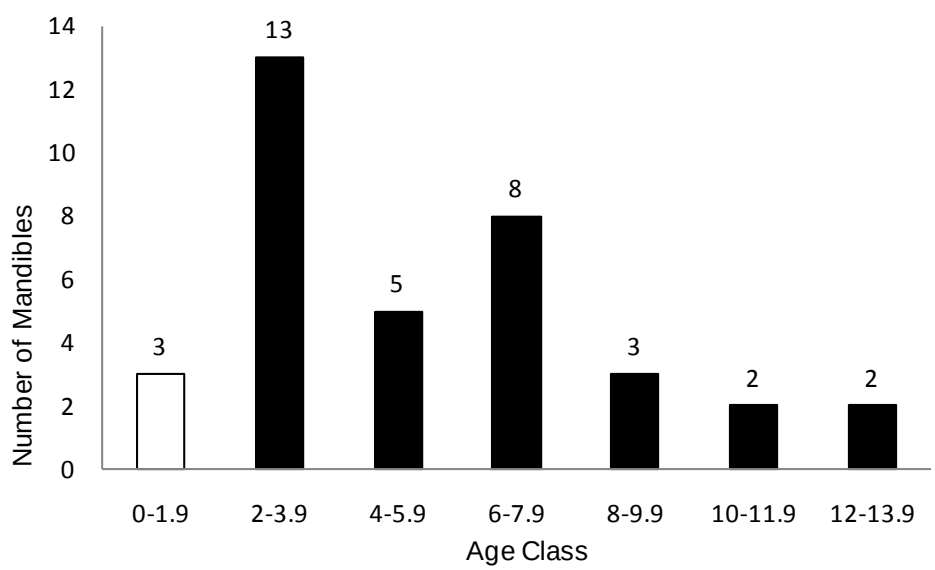


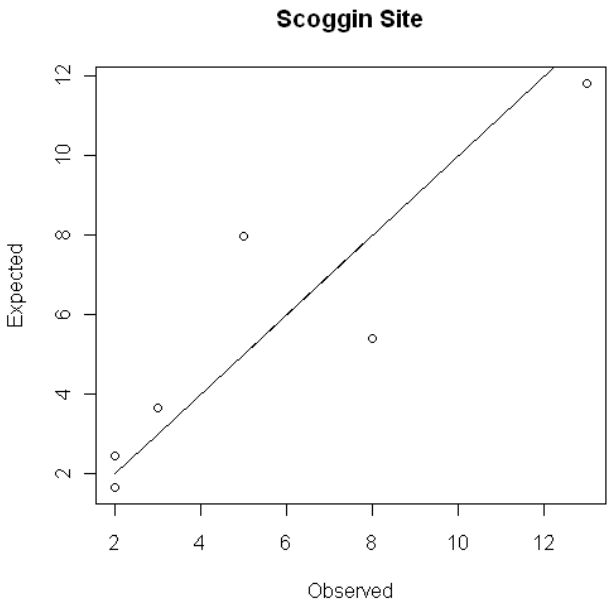

Figure 2.15. Age-class abundances from mandibles of *B. bison* at the Scoggin site, Wyoming. Age classes 2–13.9 used in the analysis (shaded bars).

Table 2.16. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS* $MS_{y/o}$, and $MS_a$ models for bison (*B. bison*) at the Scoggin site, Wyoming (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS** | -8.7445 | 1 | 19.4890 |
| $MS_{y/o}$ | -8.7398 | 2 | 21.4797 |
| $MS_a$ | 7.3571 | 5 | 24.7142 |

Table 2.17. Maximum likelihood estimates of biannual survival and standard errors estimated by the models *MS*, $MS_{y/o}$, and $MS_a$ for bison (*B. bison*) at the Scoggin site, Wyoming (* indicates best-fit model).

| *MS** | | | $MS_{y/o}$ | | | $MS_a$ | | |
|---|---|---|---|---|---|---|---|---|
| Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE |
| $S$ | 0.6763 | 0.0786 | $S_y$ | 0.6680 | 0.1159 | $S_0$ | 0.3846 | 0.2024 |
| | | | $S_o$ | 0.7023 | 0.2849 | $S_1$ | 1.6000 | 0.9122 |
| | | | | | | $S_2$ | 0.3750 | 0.2539 |
| | | | | | | $S_3$ | 0.6667 | 0.6086 |
| | | | | | | $S_4$ | 1.0000 | 1.0001 |



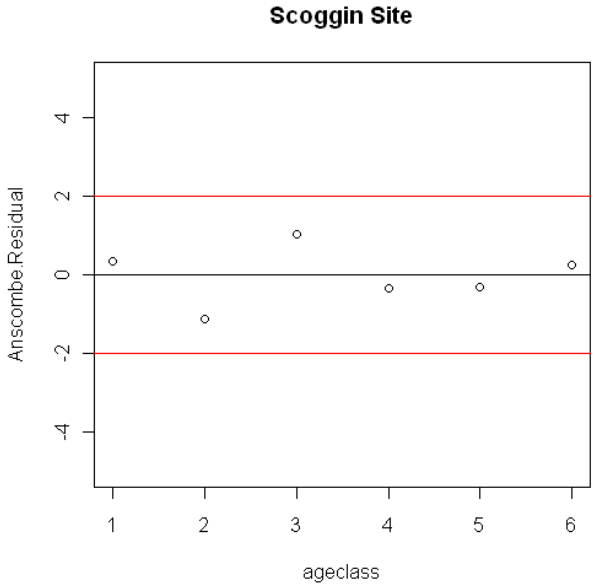




Figure 2.16. Observed vs. expected numbers of animals by age class and Anscombe residuals for model *MS* for the bison (*B. bison*) data (age classes 2–7) at the Scoggin site, Wyoming.

#### 2.3.1.11 Wardell Site

The Wardell site is located in Sublette County, western Wyoming. This site is a long box canyon in the Green River Basin. The animals killed at this site were *B. bison*, which is the extant bison in the US. The site is estimated to have been used between 370 and 960 A.D., making it the most recent site analyzed in this chapter. All animals were aged based on tooth eruption and wear. The mandibles from this study were aged in order to determine seasonality of the site. There was no attempt made by the original authors to estimate survivorship or any other population parameters (Frison 1973).

Excavation of the Wardell site yielded mandibles from at least 274 animals. However, because of the need for monotonicity in the data, the first two age classes were not used, resulting in the use of 252 mandibles, still making it by far the largest bison data set analyzed (Figure 2.17). Five models were investigated for the analysis of the jump data. The models were as follows:

Model *MS*: Assumed a constant survival rate across all age classes.

Model $MS_{y/c}$: Assumed a distinct survival rate for the first age class and a constant survival rate across all remaining age classes.

Model $MS_r$: Assumed three survival rates, the first for age classes 2.4–5.4, the second for age classes 6.4–11.4 and the third for age classes 12.4+.

Model $MS_{a/o}$: Assumed age-specific survival rates for the first 10 age classes, and a common survival rate for age classes 12.4+.

Model $MS_a$: Assumed age-specific survival rates.

The $MS_r$ model was formed based on the residual analysis of the *MS* model which showed a cyclic pattern (Figure 2.18). The biological significance of the three annual survival estimates

may be the first set of age classes were young adults, the second were mature adults, and the third were exhibiting senescence.

The likelihood ratio test revealed that the only model that was significantly different from the reduced model (*MS*) was the $MS_r$ model $P\ \chi^2_1 = 2.4294\ = 0.1191$ ,

$P\ \chi^2_{10} = 10.9698\ = 0.4457$ , $P\ \chi^2_{12} = 11.0512\ = 0.5245$ , $P\ \chi^2_2 = 7.7456\ = 0.0208$

(Table 2.18). The AIC values supported this conclusion (Table 2.18). These statistical criteria indicate the $MS_r$ model was the best model. The alternative models (*MS*, $MS_{y/c}$, $MS_{a/o}$, and $MS_a$) gave fairly similar results for most age classes (Table 2.19). The residuals show the $MS_r$ model fit better than the other models.

All of the Anscombe residuals fell within +/-2, although there was a slight trend remaining, suggesting the best fit model ($MS_r$) failed to capture all of the trends in the data (Figure 2.18). Based on all available evidence, a survivorship model for bison from the Wardell site fit best, assuming constant survival for three age categories, the first for age classes 2.4–5.4, the second for age classes 6.4–11.4 and the third for age classes 12.4+. The annual survival probabilities for these three age categories, respectively were estimated to be $\hat{S}_{0-2}$ = 0.9085 (SE = 0.0593), $\hat{S}_{3-7}$ = 0.8027 (SE = 0.0342), $\hat{S}_{8-12}$ = 0.6233 (SE = 0.0954).

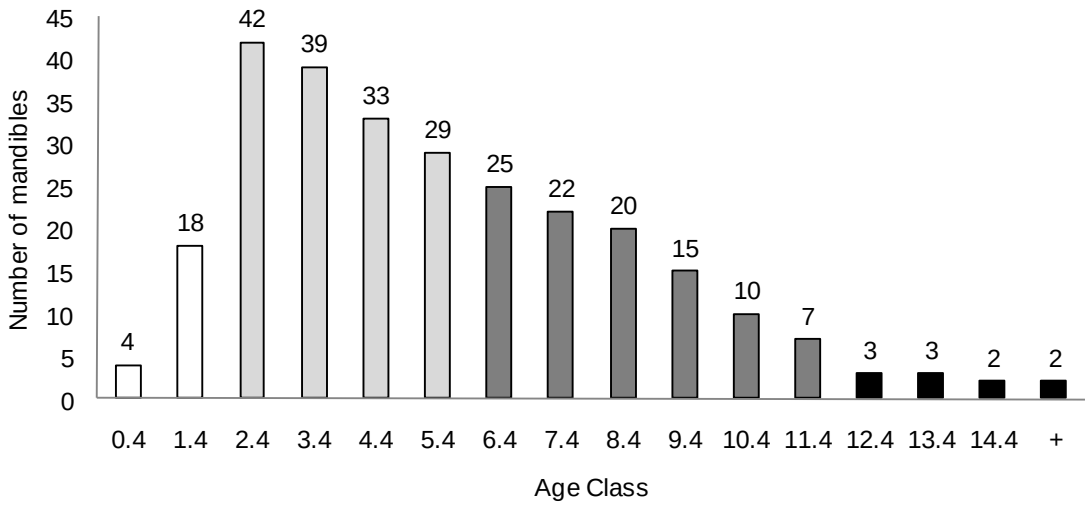



Figure 2.17. Age-class abundances from mandibles of *B. bison* at the Wardell site. Age classes 2.4–14.4+ used in the analysis (shaded bars). Shading based on age classes used in model $MS_r$ (white not included in the analysis).

Table 2.18. Akaike information criteria (AIC) and log-likelihood values (LL) from the *MS*, $MS_{y/c}$, $MS_r$, $MS_{a/o}$, and $MS_a$ models for the bison (*B. bison*) at the Wardell site, Wyoming (* indicates best-fit model).

| Model | LL | Number of parameters | AIC |
|---|---|---|---|
| *MS* | -31.9468 | 1 | 65.8936 |
| $MS_{y/c}$ | -30.7321 | 2 | 65.4641 |
| $MS_r$* | -28.0740 | 3 | 62.1479 |
| $MS_{a/o}$ | -26.4619 | 11 | 74.9239 |
| $MS_a$ | -26.4212 | 13 | 78.8423 |

Table 2.19. Maximum likelihood estimates of annual survival and standard errors estimated by the models *MS*, $MS_{y/c}$, $MS_r$, $MS_{a/o}$, and $MS_a$ for the bison (*B. bison*) at the Wardell site, Wyoming (* indicates best-fit model).

| MS | | | $MS_{y/c}$ | | | $MS_r$* | | | $MS_{a/o}$ | | | $MS_a$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE | Parameters | Estimate | SE |
| S | 0.8110 | 0.0150 | $S_0$ | 1.0722 | 0.1960 | $S_{0-2}$ | 0.9085 | 0.0593 | $S_0$ | 0.9286 | 0.2065 | $S_0$ | 0.9286 | 0.2060 |
| | | | $S_{1-12}$ | 0.7967 | 0.0178 | | | | $S_1$ | 0.8462 | 0.2001 | $S_1$ | 0.8462 | 0.2000 |
| | | | | | | | | | $S_2$ | 0.8788 | 0.2237 | $S_2$ | 0.8788 | 0.2230 |
| | | | | | | $S_{3-7}$ | 0.8027 | 0.0342 | $S_3$ | 0.8621 | 0.2353 | $S_3$ | 0.8620 | 0.2350 |
| | | | | | | | | | $S_4$ | 0.8800 | 0.2572 | $S_4$ | 0.8800 | 0.2570 |
| | | | | | | | | | $S_5$ | 0.9091 | 0.2809 | $S_5$ | 0.9090 | 0.2800 |
| | | | | | | | | | $S_6$ | 0.7500 | 0.2562 | $S_6$ | 0.7500 | 0.2560 |
| | | | | | | | | | $S_7$ | 0.6667 | 0.2722 | $S_7$ | 0.6666 | 0.2720 |
| | | | | | | $S_{8-12}$ | 0.6233 | 0.0954 | $S_8$ | 0.7000 | 0.3450 | $S_8$ | 0.7000 | 0.3440 |
| | | | | | | | | | $S_9$ | 0.4475 | 0.2763 | $S_9$ | 0.4286 | 0.2950 |
| | | | | | | | | | $S_{10-12}$ | 0.8511 | 0.2434 | $S_{10}$ | 1.0000 | 0.8160 |
| | | | | | | | | | | | | $S_{11}$ | 0.6666 | 0.6080 |
| | | | | | | | | | | | | $S_{12}$ | 1.0000 | 0.9935 |

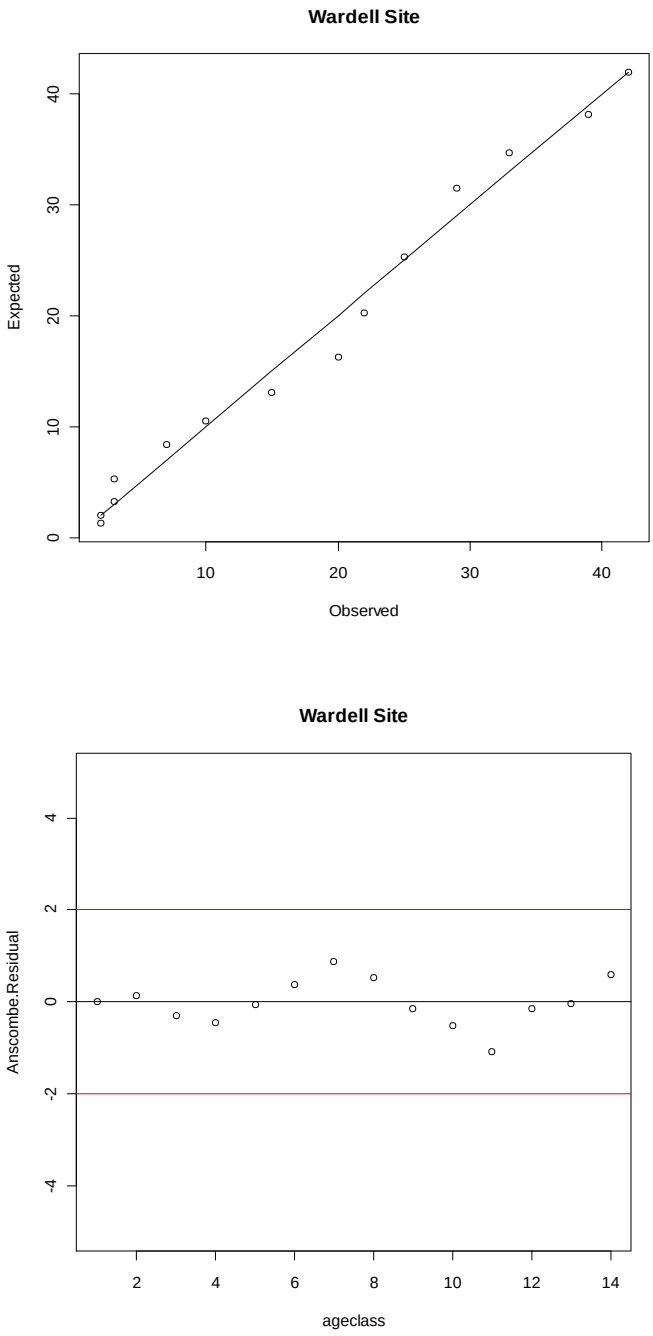



Figure 2.18. Observed vs. expected number of animals by age class and Anscombe residuals for model $MS_r$ for the bison (*B. bison*) data (age classes 2–15) at the Wardell site, Wyoming.

### 2.3.2 Bison Population Model

A Leslie matrix model was run for the population at each site using the annual survival probabilities estimated for ages 2 through 15. The model from Millspaugh et al. (2008) had 24 age classes. The data from the National Parks Service (Millspaugh et al. 2008) were used for age classes not estimated by historic data. For the Wardell site, survival probabilities were used for age classes 0–15 because of the three estimated survival probabilities of young, mature, and old.

The estimated finite population growth rates ranged from 0.95 to 1.06. Estimates for three of the six sites falling below 1.00 (a neutral population growth rate) (Table 2.20). The sites representing the bison species *B. antiquus* estimated finite population growth rates less than one. The sites representing the species *B. occidentalis* had estimated finite population growth rates between 1.06 in 7500 B.C. and 0.96 in 4500 B.C. Both sites with *B. bison* data estimated finite population growth rates of 1.06.

Table 2.20. Estimates of annual survival probabilities and population growth rate (λ), for bison (*Bison* spp.) at sites in North America.

| Site | Year (approximate) | Species | $\hat{S}$ | $\lambda$ |
|---|---|---|---|---|
| Cooper | 10,200 B.C. | *B. antiquus* | 0.6143 | 0.98 |
| Casper | 10,000 B.C. | *B. antiquus* | 0.6110 | 0.95 |
| Hudson-Meng | 7,500 B.C. | *B. occidentalis* | 0.7723 | 1.02 |
| Hawken | 4,500 B.C. | *B. occidentalis* | 0.7000 | 0.96 |
| Scoggin | 2,500 B.C. | *B. bison* | 0.6763 | 1.06 |
| Wardell | 300 A.D. | *B. bison* | 0.9085 | |
| | | | 0.8027 | 1.06 |
| | | | 0.6233 | |

## 2.4 Discussion

Life table analysis represents the simplest form of age-at-harvest analysis, making use of the most basic form of age at harvest data, a single year. Simplifying assumptions including a stable age distribution and stationary population, allowed me to obtain useful demographic information from the bison populations of pre-history. By recognizing the limitations of the data, making the necessary assumptions, and performing a transparent analysis, I present the most useful information possible from the available data. This analysis is a rare glimpse into pre-historic wildlife populations.

The estimates of declining populations for *B. antiquus* coincide with a time when they were on their way to extinction, making way for the smaller *B. occidentalis*. The population growth rates estimated for *B. occidentalis* begin showing population growth, and then a population decline as *B. occidentalis*, again paralleling the sub-species evolutionary history. The decline of *B. occidentalis* paved the way for the smaller *B. bison* to become the dominant large mammal on the open plains. This progression of population growth rates mirroring the evolution of these animals was an interesting and unintended consequence of these analyses.

Interestingly, both sites representing *B. bison* had an estimated population growth rate of 6% growth annually. Millspaugh et al. (2008) estimated a finite population growth rate of 1.16 or 16% annual growth for the bison herds found today in Wind Cave National Park, with similar estimates in other national parks. The difference in estimated finite population growth rates is driven by the difference in estimated annual survival probabilities. This means under the same fecundity values the current bison population in the National Parks grows at almost three times the rate of pre-European bison populations. The drastically higher population growth rate today may be due to more favorable conditions today in

National Parks. The predation pressure since the extirpation of wolves and grizzly bears is dramatically less than it had been historically. In National Parks today, there is greatly reduced hunting pressure, if any, unlike ancestral populations hunted by Native Americans. Millspaugh et al 2005 found population growth rates similar to those estimated here when current bison populations were modeled with historic predation pressure. Therefore, in order to manage the American bison to its "natural state," one would have to slow the population growth rate considerably through culling, hunting, or reintroduction of predators.

With the advances in statistical methodology and ever increasing availability of data, the potential for further study in the field of archaeological population reconstruction is massive. The potential wealth of information available from reconstructing historic populations could be very valuable to the future management of wildlife resources. In addition to the information analyzed here, there is information in the archaeological literature concerning sex ratios and fecundity rates. These data may be useful in an attempt to more fully reconstruct historic populations.

## 2.5 Conclusion

Given that many species in our national parks and elsewhere are often managed to natural historic conditions, the ability to evaluate prehistoric wildlife populations is quite valuable. I have demonstrated that it is possible to extract population parameters from archaeological bone assemblages, for not only bison but other large ungulate species as well. This archaeological population reconstruction offers information for managers seeking a historical perspective or benchmark from which to base management goals and policy decisions to effectively manage wildlife resources.

# Chapter 3: Pooled Age-Class Analysis

## 3.1 Introduction

The collection of age-at-harvest data is a routine activity of most state and provincial management agencies. For many wildlife agencies, an assessment of annual harvest for big game is made using hunter check stations (Rupp et al. 2000, Diefenbach et al. 2004). In addition to total harvest, data on ages of harvested animals are routinely collected at mandatory check stations or through use of postage-paid envelopes to mail a tooth to the management agency (e.g., Biederbeck et al. 2001). These harvest data are often the only wide-scale data available on an annual basis to assess the efficacy of harvest regulations, responses to management activities, and status and trends of the populations. Despite the value of such data, management agencies must make decisions regarding the level of detail required to meet their objectives. For example, managers need to determine whether animals must be aged to year or whether assignment to age classes (e.g., fawn, yearling, and adult) is sufficient.

For harvested big-game species, there are multiple options for aging animals, but each has distinct benefits and drawbacks. For many mammals, counts of cementum annuli, a technique described by Willey (1974), often provide the most accurate estimate of age (Hamlin et al. 2000). However, the process of collecting, sectioning, and counting cementum annuli can be expensive and time consuming when applied across broad geographic regions. Also, counts of cementum annuli are not error free (Harshyne et al. 1998, Hewison et al. 1999, Costello et al. 2004). Many alternative methods have been used to estimate age of harvested animals. For ungulate populations, age determination can be based on tooth eruption and wear (Severinghaus 1949, Quimby and Gaab 1957). This inexpensive aging

technique is often accurate for individuals ≤2.5 or ≤3.5 years of age, depending on species (Dimmick and Pelton 1996:190-194), but accuracy can be as low as 16% for elk (*Cervus elaphus*) ≥ 5 years of age (Hamlin et al. 2000). For this reason, most researchers are only comfortable with assigning animals, such as deer, to age-class categories of fawn, yearling, and adult (Gee et al. 2002). For other species, including some carnivores, investigators have used tooth pulp cavity metrics to assign ages. For example, Kuehn and Berg (1983) aged river otters (*Lutra canadensis*) to juvenile and adult stages using pulp cavity width through examination of radiographs. Similarly, Jenks et al. (1984) aged male and female fishers to age classes 0, 1, 2, and 3+. Therefore, although it is difficult to accurately assign animals to older age classes, it might still be possible to group animals into biologically relevant stages. An additional advantage to grouping might be cost savings (Jenks et al. 1984), particularly when considering state-wide harvest assessments. The utility of these groupings for demographic analysis, however, is dependent on their intended use.

Harvest data are commonly analyzed using population reconstruction methods (Skalski et al. 2005). Although still commonly used by state management agencies, many of the early deterministic reconstruction methods have substantial bias and make unrealistic assumptions (Millspaugh et al. 2009). In contrast, statistical population reconstruction techniques have several notable advantages, such as a flexible analysis framework which can incorporate auxiliary data (Gove et al. 2002, Skalski et al. 2005, Skalski et al. 2007), estimation of standard errors of demographic parameters, and simultaneous estimation of multiple demographic parameters such as natural survival and abundance (Skalski et al. 2005). However, statistical population reconstruction methods have typically relied on full age-class information in order to reconstruct cohort and annual abundances (Gove et al.

2002, Skalski et al. 2005). Recently Broms et al. (2010) used population reconstruction to analyze greater sage-grouse harvest data summarized at the level of young-of-year and adults. There would be practical, economical, and logistical benefits if pooled age-class data could be used in the population reconstruction analysis. However, it is unknown whether pooling results in reliable estimation of demographic parameters for big-game populations.

In this chapter, I use age-at-harvest data from a Washington State black-tailed deer population and compare reconstruction results using full age-class information (Skalski et al. 2007) and pooled age classes of 0.5, 1.5, and 2.5+. The objective of this chapter is to assess whether reliable abundance estimates can be obtained from pooled age-class data commonly collected by state agencies.

## 3.2 Study Area

I reanalyzed the black-tailed deer data previously reported by Skalski et al. (2007) with the full complement of data and after pooling ages 2.5+. All harvested female deer within the 22,079-ha King Creek block of Kapowsin Tree Farm, Pierce County, Washington, were aged. Controlled access to the area permitted complete tally of all harvested animals and hunter effort. In addition to the harvest information, a browse index of percent area surveyed with moderate-to-severe browse damage was collected concurrently.

## 3.3 Methods

### 3.3.1 Full Age-Class Analysis

With full age-at-harvest data, population reconstruction was based on estimating the annual abundance levels of the separate cohorts constituting the population (Gove et al. 2002; Skalski et al. 2005, 2007). The statistical model for the population reconstruction was based on a joint likelihood model of the form

$$L_{\text{Joint}} = L_{\text{Age-at-harvest}} \cdot L_{\text{Catch-effort}}, \tag{3.1}$$

the same used in Skalski et al. (2007). The age-at-harvest likelihood used for the reanalysis of full age class data was of the form

$$L_{\text{Age-at-harvest}} = \prod_{i=1}^{24} \cdot L_{i1} \prod_{j=2}^{13} L_{1j} \tag{3.2}$$

where $L_{ij}$ was the likelihood describing the age-at-harvest data for the cohort entering the study in year $i$ $i = 1,\ldots,24$ at age class $j$ $j = 1,\ldots,13$ and was identical to that used in Skalski et al (2007). Let

$h_{ij}$ = number of females harvested in year $i$ $i = 1,\ldots,24$ at age class $j$ $j = 1,\ldots,13$ ,

$N_{ij}$ = female deer abundance in year $i$ $i = 1,\ldots,24$ at age class $j$ $j = 1,\ldots,13$ ,

$S$ = natural survival probability for all females,

$c_{0.5}$ = vulnerability coefficient for young-of-year females (i.e., age class 0.5),

$c_{1.5+}$ = vulnerability coefficient for females 1.5 years of age or older,

$f_i$ = hunter effort in year $i$ $i = 1,\ldots,24$ .

$$L_{i1} = \binom{N_{i,1}}{h_{i,1}, h_{i+1,2....}} p_{i,J}{}^{h_{i,1}} \quad 1 - p_{i,J} \quad S p_{i+1,A}{}^{h_{i+1,2}} \quad 1 - p_{i,J} \quad 1 - p_{i+1,A} \quad S^2 p_{i+2,A}{}^{h_{i+2,3}} \ldots$$

$$L_{1j} = \binom{N_{1,j}}{h_{1,j}, h_{2,j+1....}} p_{1,A}{}^{h_{1,j}} \quad 1 - p_{1,A} \quad S p_{2,A}{}^{h_{2,j+1}} \quad 1 - p_{1,A} \quad 1 - p_{2,A} \quad S^2 p_{3,A}{}^{h_{3,j+2}} \ldots$$

where

$$p_{i,J} = 1 - e^{-c_{0.5} f_i} ,$$

$$p_{i,A} = 1 - e^{-c_{1.5+} f_i} .$$

Construction of $L_{21},\ldots,L_{Y1}$ was analogous to that of $L_{i1}$ incremented for subsequent years. Construction of $L_{12},\ldots,L_{1A}$ was analogous to that of $L_{1j}$ incremented for subsequent age classes. The catch-effort likelihood to estimate vulnerability coefficients and, in turn, capture probabilities was based on catch-per-unit-effort within a year, where

$$L_{\text{Catch-effort}} = \prod_{i=1}^{24} \binom{N_{i1}}{h_{i1}} 1-e^{-c_{0.5} f_i}{}^{h_{i1}} \; e^{-c_{0.5} f_i}{}^{N_{i1}-h_{i1}} \cdot \prod_{i=1}^{24} \binom{\sum_{j=2}^{3} N_{ij}}{\sum_{j=2}^{3} h_{ij}} 1-e^{c_{1.5+} f_i}{}^{\sum_{j=2}^{3} h_{ij}} \; e^{-c_{1.5+} f_i}{}^{\sum_{j=1}^{3} N_{ij}-h_{ij}} \tag{3.3}$$

I used the software Program USER 4.5.2 (University of Washington, http://www.cbr.washington.edu/paramest/user/) to solve for the maximum likelihood estimates. Initial abundance levels (i.e., $N_{11}, N_{12}, N_{13}, N_{21}, \ldots, N_{24,1}$) were calculated directly, while the remaining abundance levels were based on the invariance property of the maximum likelihood estimation, where

$$\hat{N}_{ij} = N_{i-1,j-1} e^{-cf_{i-1}} S \,.$$

Total annual abundance for any year was the sum of the within-year cohort abundance levels.

### 3.3.2 Pooled Age-Class Analysis

When harvest data from older age classes are pooled, the cohort information in the latter years is eliminated, leaving the cohort structured only for the youngest age classes (i.e., 0.5 and 1.5). Nevertheless, this truncated cohort structure of the data can be used to help define the population reconstruction.

In the case of pooling the harvest data from older age classes, the structure of the age-at-harvest likelihood necessarily changed. It was of the form

$$L_{\text{Age-at-harvest}} = \prod_{i=1}^{Y} L_{i1} \cdot \prod_{j=2}^{3} L_j \,, \tag{3.4}$$

where $L_{ij}$ was the likelihood describing the age-at-harvest data for the cohort entering the study in year $i \quad i = 1,\ldots,Y$ at age class $j \quad j = 1,\ldots,3$ (Figure 3.1).

Let :

$h_{ij}$ = number of females harvested in year $i \quad i = 1,\ldots,24$ at age class $j \quad j = 1,\ldots,13$ ,

$N_{ij}$ = female deer abundance in year $i \quad i = 1,\ldots,24$ at age class $j \quad j = 1,\ldots,13$ ,

$S$ = natural survival probability for all females,

$c_{0.5}$ = vulnerability coefficient for young-of-year females (i.e., age class 0.5),

$c_{1.5+}$ = vulnerability coefficient for females 1.5 years of age or older,

$f_i$ = hunter effort in year $i \quad i = 1,\ldots,24$ .

For the adults already present in the population in year 1, their likelihood contribution can be written as follows:

$$L_{13} = \binom{N_{13}}{h_{13}} \left(1 - e^{-c_{1.5+} f_i}\right)^{h_{13}} \left(e^{-c_{1.5+} f_i}\right)^{N_{13} - h_{13}} .$$

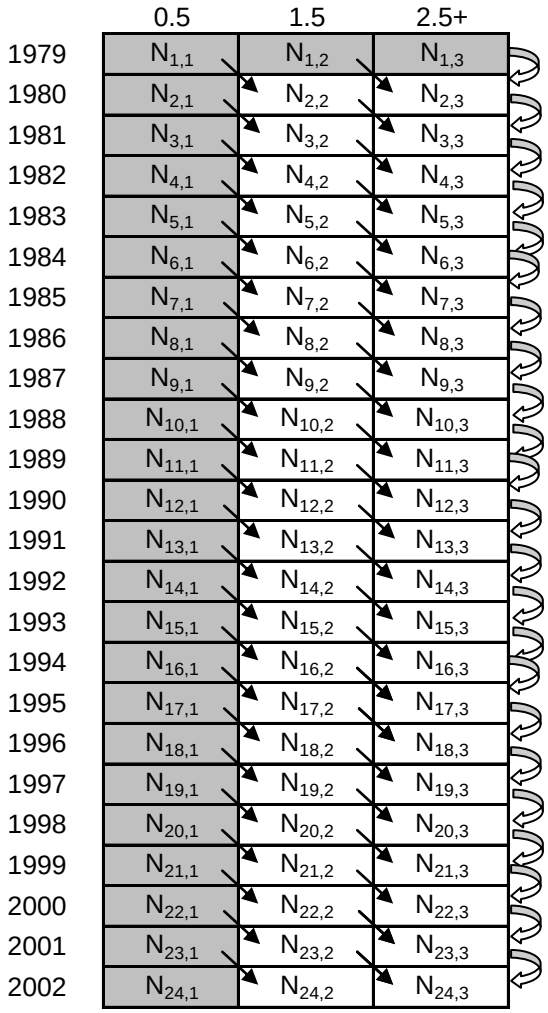



Figure 3.1. Diagram of the population reconstruction with pooled age class data (Eq. 3.4). Shaded cells were directly estimated. Arrows represent cohorts exploited in the model.

For the yearlings present in the population in year 1, their harvest in the first year and their harvest with other adults in the next year were modeled, based on the conditional likelihood, as follows:

$$L_{12} = \binom{h_{12\bullet}}{h_{12}, h_{23}} \left( \frac{E\ h_{12}}{E\ h_{12} + E\ h_{23}} \right)^{h_{12}} \left( \frac{E\ h_{23}}{E\ h_{12} + E\ h_{23}} \right)^{h_{23}}$$

where

$$E\ h_{12} = N_{12}\ 1 - e^{-c_{1.5+} f_1}$$
$$E\ h_{23} = \left[ N_{12}\ e^{-c_{1.5+} f_1}\ S + N_{13}\ e^{-c_{1.5+} f_1}\ S \right] 1 - e^{-c_{1.5+} f_2}$$

and where $h_{12\bullet} = h_{12} + h_{23}$. For the juveniles present in the first year, the likelihood can be written as follows:

$$L_{11} = \binom{h_{11\bullet}}{h_{11}, h_{22,} h_{33}} \left( \frac{E\ h_{11}}{E\ h_{11} + E\ h_{22} + E\ h_{33}} \right)^{h_{11}} \left( \frac{E\ h_{22}}{E\ h_{11} + E\ h_{22} + E\ h_{33}} \right)^{h_{22}}$$
$$\cdot \left( \frac{E\ h_{33}}{E\ h_{11} + E\ h_{22} + E\ h_{33}} \right)^{h_{33}},$$

where

$$E\ h_{11} = N_{11}\ 1 - e^{-c_{0.5} f_1}\ ,$$
$$E\ h_{22} = N_{11}\ e^{-c_{0.5} f_1}\ S\ 1 - e^{-c_{1.5+} f_2}\ ,$$
$$E\ h_{33} = \left[ N_{11}\ e^{-c_{0.5} f_1}\ S\ e^{-c_{1.5+} f_2}\ S + N_{12}\ e^{-c_{1.5+} f_1}\ S\ e^{-c_{1.5+} f_2}\ S \right.$$
$$\left. + N_{13}\ e^{-c_{1.5+} f_1}\ S\ e^{-c_{1.5+} f_2}\ S_A \right] 1 - e^{-c_{1.5+} f_3}\ ,$$

and where $h_{11\bullet} = h_{11} + h_{22} + h_{33}$. Construction of $L_{21}, \ldots, L_{Y1}$ was analogous to that of $L_{11}$ incremented for subsequent years. The pooled catch-effort likelihood was identical to the



(3.5)

unpooled catch-effort likelihood where

$$L_{\text{Catch-effort}} = \prod_{i=1}^{24} \binom{N_{i1}}{h_{i1}} \left(1 - e^{-c_{0.5} f_i}\right)^{h_{i1}} \left(e^{-c_{0.5} f_i}\right)^{N_{i1} - h_{i1}}$$

$$\cdot \prod_{i=1}^{24} \binom{\sum_{j=2}^{3} N_{ij}}{\sum_{j=2}^{3} h_{ij}} \left(1 - e^{c_{1.5+} f_i}\right)^{\sum_{j=2}^{3} h_{ij}} \left(e^{-c_{1.5+} f_i}\right)^{\sum_{j=1}^{3} N_{ij} - h_{ij}} .$$

I used the software USER 4.5.2 (University of Washington, http://www.cbr.washington.edu/paramest/user/) to solve for the maximum likelihood estimates. Initial abundance levels (i.e., $N_{11}, N_{12}, N_{13}, N_{21}, \ldots, N_{24,1}$) were calculated directly while the remaining abundance levels were based on the invariance property of the maximum likelihood estimation, where

$$\hat{N}_{ij} = N_{i-1,j-1} e^{-c f_{i-1}} S .$$

Total annual abundance for any year was the sum of the within-year cohort abundance levels.

I calculated standard errors from the inverse hessian, which was numerically estimated. The reported asymptotic $1-\alpha$ 100% confidence intervals were expanded by the scale parameter based on a goodness-of-fit to the age-at-harvest matrix where

$$\text{Scale Parameter} = \sqrt{\frac{\chi^2_{\text{df}}}{\text{df}}}, \qquad \chi^2_{\text{df}} = \sum \left( \frac{\text{Observed}_i - \text{Expected}_i}{\sqrt{\text{Expected}_i}} \right)^2,$$

df = # cells in the age-at-harvest matrix – number of parameters estimated.

Residual plots and scale parameters were compared to assess the affect of pooling on model fitness. Two kinds of residuals were compared, standardized residuals were calculated as an

approximate $Z$-statistic where $Z = \left( \frac{\text{Observed} - \text{Expected}}{\sqrt{\text{Expected}}} \right)$, and Anscombe residuals were calculated (Anscombe 1953).

## 3.4 Results

### 3.4.1 Effect of Pooling on Precision

In the prior analysis (Skalski et al. 2007), a likelihood model was fit to the full data with a common natural survival probability and separate vulnerability coefficients ($c_{0.5}, c_{1.5+}$) for the young-of-year and older does (Table 3.1). The same parameterization was therefore used in my full reanalysis and pooled analysis for purposes of direct comparison (Table 3.1). Vulnerability coefficients and survival probability decreased from the original analysis (Skalski et al. 2007).

Table 3.1. Comparison of natural survival ($S$) and vulnerability coefficients ($c_{0.5}, c_{1.5+}$) for reconstruction models using all age-at-harvest data and pooling of adult age classes (2.5+ years).

| Parameter | Skalski et al (2007) | Full data | Pooled adult age classes |
|---|---|---|---|
| $S$ | 0.7293 ( 0.0097) | 0.7220 (0.0172) | 0.6953 (0.0197) |
| $c_{0.5}$ | 0.0980 (0.0190) | 0.0869 (0.0279) | 0.0677 (0.0212) |
| $c_{1.5+}$ | 0.1840 (0.0220) | 0.1615 (0.0502) | 0.1357 (0.0420) |

Cohort-specific and annual abundance levels were estimated from the reconstruction (Table 3.2). Graphical plots from the original full age-at-harvest analysis (Skalski et al. 2007), my full age-at-harvest reanalysis and pooled adult age-class analysis show very similar time trends in annual abundance (Figure 3.2). My reanalysis estimated around 14% more female deer annually on average than the original analysis; the pooled analysis estimated on average 20% more females annually than my unpooled analysis. The residual plots did not reveal any additional lack-of-fit from my full analysis to my pooled analysis (Figure 3.3, Figure 3.4). Anscombe residuals were more normally distributed than the standardized residuals in the case of the full age-class data. However, the Anscombe and standardized residuals were almost identical for the pooled age-class data. Skalski et al. (2007) reported annual abundance estimates with an average coefficient of variation (CV) of 4.6%. The full age-class analysis produced annual abundance estimates with an average CV of 31.01%. The pooled age-class analysis produced annual abundance estimates with similar precision, CV = 31.61%. Consequently, pooling had virtually no effect on the precision of the population reconstruction.

Table 3.2. Estimates of female black-tailed deer abundance by age class and year in Pierce County, Washington, USA, 1979–2002, based on a pooled adult age-class population reconstruction.

| Year | 0.5 | 1.5 | 2.5+ | Annual abundance | 95% CI | |
|---|---|---|---|---|---|---|
| 1979 | 985.3 | 511.6 | 2,587.3 | 4,084.3 | 2,414.4 | 8,816.5 |
| 1980 | 862.6 | 677.1 | 2,104.7 | 3,644.4 | 2,194.4 | 7,945.5 |
| 1981 | 616.6 | 594.5 | 1,900.4 | 3,111.5 | 1,905.3 | 6,845.9 |
| 1982 | 1,113.2 | 421.5 | 1,677.1 | 3,211.9 | 1,980.6 | 7,093.9 |
| 1983 | 561.2 | 758.1 | 1,399.5 | 2,718.8 | 1,683.4 | 6,018.2 |
| 1984 | 524.0 | 374.4 | 1,380.9 | 2,279.4 | 1,386.2 | 4,996.4 |
| 1985 | 456.2 | 349.1 | 1,120.7 | 1,926.0 | 1,152.2 | 4,184.3 |
| 1986 | 728.2 | 307.7 | 961.9 | 1,997.9 | 1,198.0 | 4,346.0 |
| 1987 | 492.8 | 490.5 | 828.3 | 1,811.6 | 1,083.1 | 3,934.4 |
| 1988 | 700.3 | 332.6 | 863.8 | 1,896.7 | 1,138.0 | 4,127.2 |
| 1989 | 651.9 | 472.6 | 783.6 | 1,908.2 | 1,146.7 | 4,155.8 |
| 1990 | 554.4 | 439.6 | 821.5 | 1,815.5 | 1,083.5 | 3,939.2 |
| 1991 | 620.6 | 372.5 | 819.0 | 1,812.2 | 1,066.5 | 3,902.5 |
| 1992 | 899.0 | 418.2 | 778.1 | 2,095.4 | 1,219.8 | 4,486.3 |
| 1993 | 956.5 | 607.4 | 785.3 | 2,349.3 | 1,350.4 | 4,996.1 |
| 1994 | 1,756.9 | 653.5 | 934.9 | 3,345.4 | 1,921.7 | 7,111.9 |
| 1995 | 940.8 | 1,204.3 | 1,073.3 | 3,218.3 | 1,861.9 | 6,867.5 |
| 1996 | 836.9 | 647.3 | 1,550.6 | 3,034.8 | 1,761.8 | 6,487.9 |
| 1997 | 1,662.5 | 575.7 | 1,495.8 | 3,734.0 | 2,134.2 | 7,917.1 |
| 1998 | 1,459.4 | 1,144.7 | 1,412.3 | 4,016.3 | 2,317.6 | 8,558.9 |
| 1999 | 488.2 | 1,005.4 | 1,745.1 | 3,238.7 | 1,898.4 | 6,959.5 |
| 2000 | 956.1 | 337.4 | 1,888.7 | 3,182.2 | 1,851.2 | 6,810.6 |
| 2001 | 259.4 | 659.0 | 1,520.7 | 2,439.1 | 1,422.7 | 5,227.7 |
| 2002 | 304.4 | 179.2 | 1,496.4 | 1,980.1 | 1,149.0 | 4,232.0 |

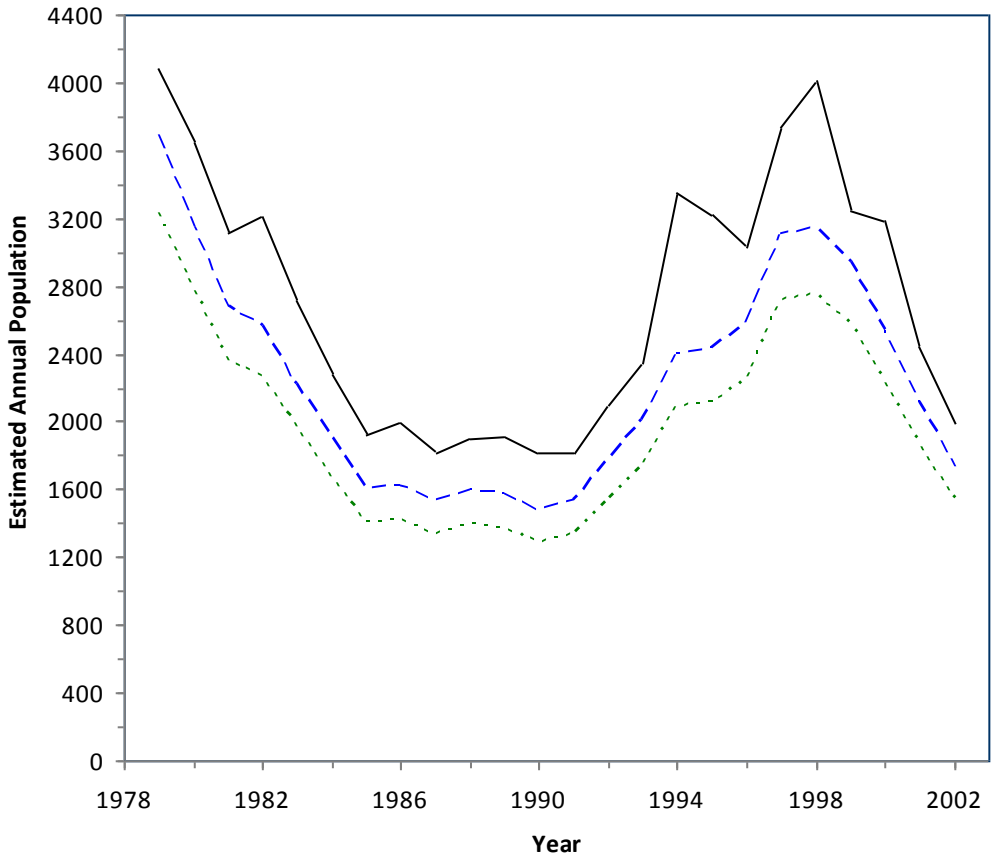
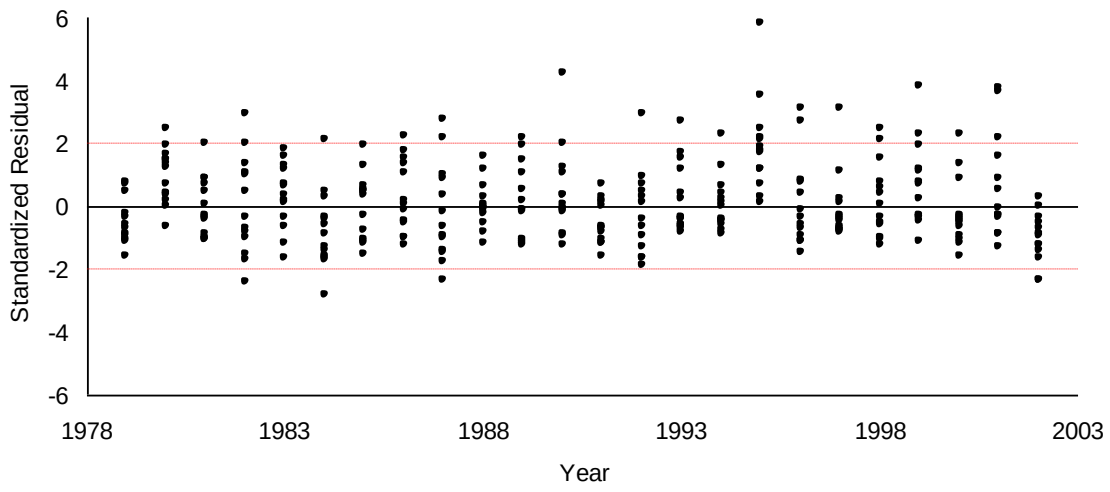



Figure 3.2. Time trends (1979–2002) for the females of a Washington State black-tailed deer population reconstruction from Skalski et al. 2007 (dotted line), analysis based on full age classes (dashed line) and pooled adult age classes (solid line).

a. Full age class




b. Pooled age class

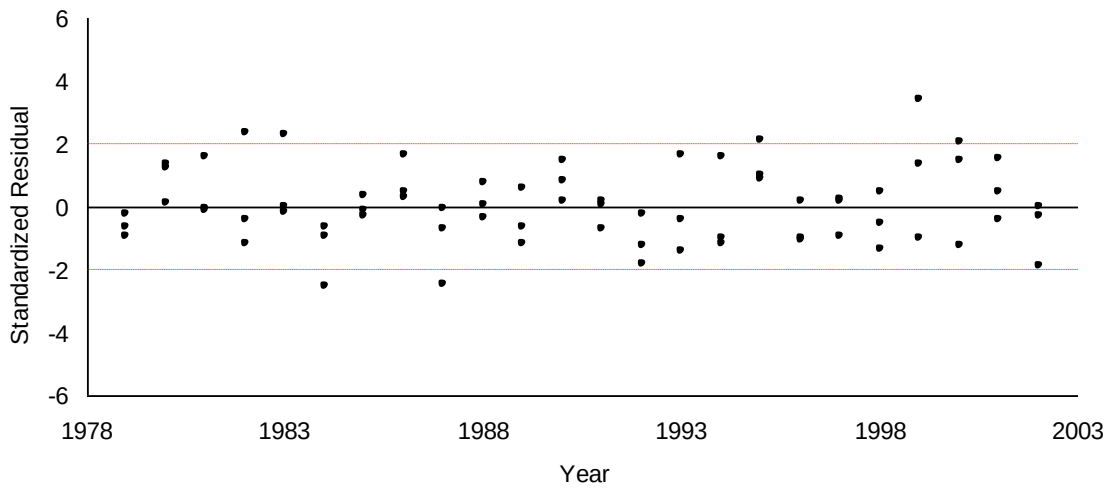
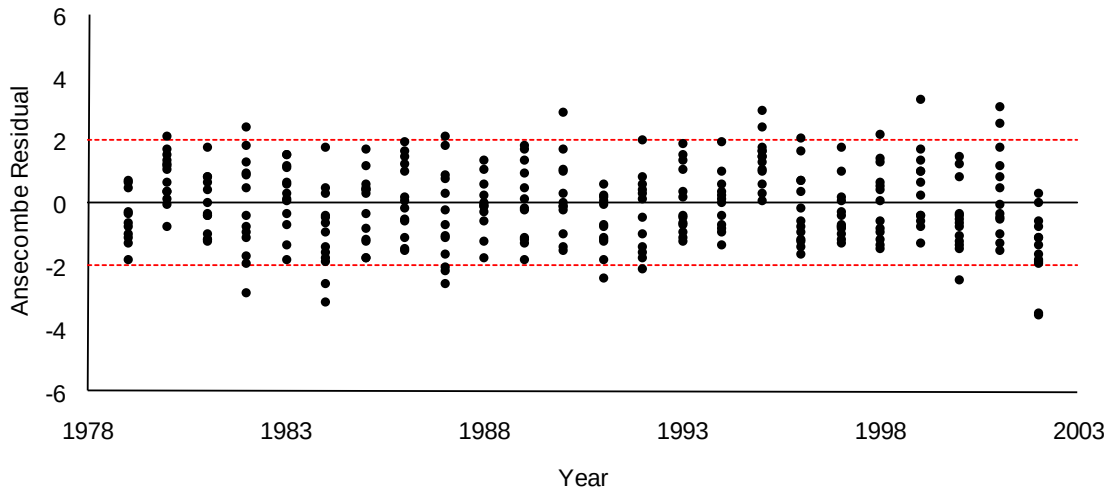



Figure 3.3. Standardized residuals graphed by time for the reanalyzed (a) full age-class analysis and (b) pooled age class analysis of the females of a Washington State black-tailed deer population reconstruction.

a. Full age class




b. Pooled age class

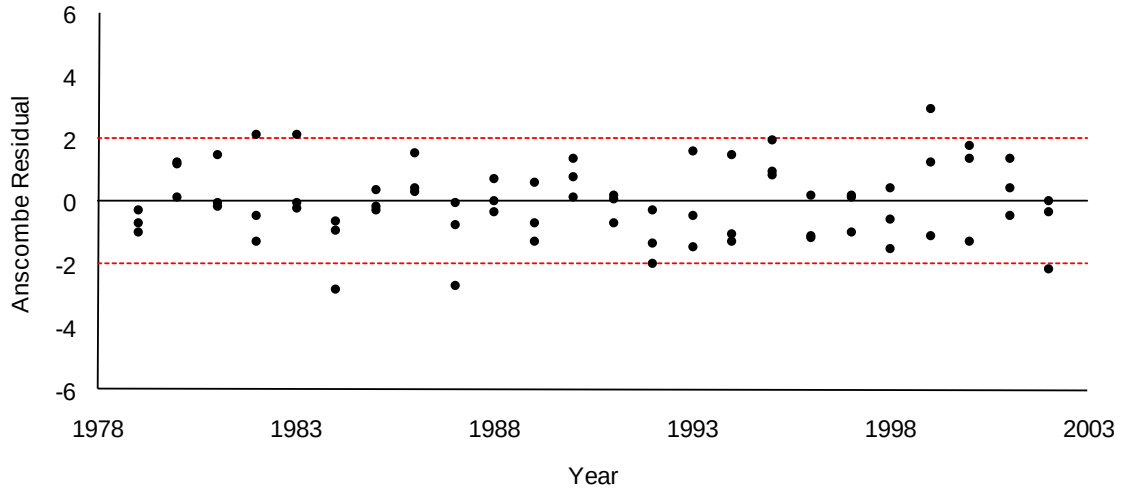



Figure 3.4. Anscombe residuals graphed by time for the reanalyzed (a) full age-class analysis and (b) pooled age-class analysis of the females of a Washington State black-tailed deer population reconstruction.

### 3.4.2 Senescence Correction

When comparing the unpooled and pooled reconstructions, there was an apparent positive bias in the pooled reconstruction. In an attempt to correct for the positive bias in the pooled reconstruction estimates, a method to correct for senescence was developed. In the original pooled model, all animals in the 2.5+ age class were not differentiated by age. Essentially, the model treated all the animals ≥2.5 years old as the same age. This theoretically allowed animals to live beyond the maximum observed age of 13. To correct for senescence, cohorts with a known starting age ($N_{11}$, $N_{12}$, $N_{21}$, …, $N_{241}$) were tracked individually through the entire abundance matrix, including once they entered adulthood. Cohorts were then removed once they reached the maximum age. For the cohort with animals of unknown age, cohort $N_{13}$, a senescence correction was developed. The senescence correction for their cohort for year $y$ was as follows:

$$SC_y = \frac{1 - S^{c-y+2}}{1 - S^{c+1}}$$

where

$y$ = the year of the study,

$k$ = maximum number of years lived,

$p$ = age at which pooled age class is entered,

$c = k - p$, maximum number of years an animal can live in the pooled age class for years 2 through $k - 1$.

The senescence correction was based on two simplifying assumptions. One, the population was stable and stationary before the study, with a common initial adult abundance

($N_0$). Two, there was no harvest, or negligible harvest, before the study. The mathematical derivation of the senescence correction was as follows:

The 2.5+ age-class abundance ($N_{13}$) in the first year of the study was equal to the sum of the abundance of each adult age class. Each adult age class was expressed as a function of the common initial adult abundance ($N_0$) and common survival probability:

$$N_{13} = N_0 + N_0 S + N_0 S^2 ... + N_0 S^c. \tag{3.6}$$

The common initial adult abundance was then factored out of the sum

$$N_{13} = N_0 \;\; 1 + S + S^2 ... + S^c \;\; . \tag{3.7}$$

The initial adult abundance was multiplied by the sum of an infinite series of common survival probabilities:

$$\frac{1}{1-S} N_0 = N_0 \;\; 1 + S + S^2 ... + S^\infty \;\; , \tag{3.8}$$

$$\left[ \frac{1}{1-S} = \;\; 1 + S + S^2 ... + S^\infty \;\; \right]. \tag{3.9}$$

The appropriate number of survival terms were factored out of the infinite series, resulting in the common initial adult abundance multiplied times the initial series of survival terms, and an additional survival term times another infinite series:

$$\frac{N_0}{1-S} = N_0 \;\; 1 + S + S^2 ... + S^c + S^{c+1} \;\; 1 + S + S^2 ... + S^\infty \quad , \tag{3.10}$$

$$\frac{N_0}{1-S} = N_0 \left( 1 + S + S^2 ... + S^c + S^{c+1} \left( \frac{1}{1-S} \right) \right). \tag{3.11}$$

Terms were rearranged to leave a known quantity on one side of the equality statement:

$$\frac{N_0}{1-S} - \frac{N_0 S^{c+1}}{1-S} = N_0 \;\; 1 + S + S^2 ... + S^c \tag{3.12}$$

The equality statement was re-expressed in terms of the known quantity:

$$N_0 \frac{1-S^{c+1}}{1-S} = N_0 \;\; 1+S+S^2 ... + S^c \;\; = N_{13}, \qquad (3.13)$$

where

$N_{13}$ = initial abundance of the cohort,

$N_0$ = common initial adult abundance,

$S$ = common survival probability,

$c$ = the maximum number of years an animal can live in the pooled age class.

The estimated abundance $N_{13}$, expressed as a function of a common survival probability, was then:

$$N_{13} = N_0 \frac{1-S^{c+1}}{1-S} \;.$$

The proportion of this cohort that remained as part of the pooled age class in year two was:

$$\frac{N_{23r}}{N_{13}}$$

where:

$$N_{13} = N_0 \frac{1-S^{c+1}}{1-S},$$

$$N_{23r} = N_0 \frac{1-S^{c}}{1-S},$$

so,

$$SC_2 = \frac{N_{23r}}{N_{13}} = \frac{N_0 \dfrac{1-S^c}{1-S}}{N_0 \dfrac{1-S^{c+1}}{1-S}} = \frac{1-S^c}{1-S^{c+1}},$$

where

$N_{23r}$ = the remaining animals alive in the cohort,

$N_{13}$ = initial abundance of the cohort,

$SC_2$ = proportion of $N_{13}$ that survives to year two because of senescence.

In general, the senescence correction for a given year $y$ was $SC_y = \frac{1-S^{c-y+2}}{1-S^{c+1}}$. This senescence correction was incorporated into the model when calculating the adult abundances ($N_{23}$, $N_{33}$, $N_{43}$, …, $N_{k-13}$). Without the senescence correction, the adult abundances were calculated by:

$$N_{i3} = N_{(i-1)3}S\ \ 1-p_{(i-1)A}\ \ + N_{(i-1)2}S\ \ 1-p_{(i-1)A}$$

for $i$ = 2 to 24. With the senescence correction, the adult abundances were calculated by:

$$\begin{aligned}
N_{23} &= N_{13}SC_2S\ \ 1-p_{1A}\ \ + N_{12}S\ \ 1-p_{1A}\ \ , \\
N_{33} &= N_{13}SC_3S\ \ 1-p_{1A}\ \ S\ \ 1-p_{2A}\ \ + N_{12}S\ \ 1-p_{1A}\ \ S\ \ 1-p_{2A}\ \ + N_{11}S\ \ 1-p_{1J}\ \ S\ \ 1-p_{2A}\ \ , \\
N_{43} &= N_{13}SC_4S\ \ 1-p_{1A}\ \ S\ \ 1-p_{2A}\ \ S\ \ 1-p_{3A}\ \ + N_{12}S\ \ 1-p_{1A}\ \ S\ \ 1-p_{2A}\ \ S\ \ 1-p_{3A} \\
&\quad + N_{11}S\ \ 1-p_{1J}\ \ S\ \ 1-p_{2A}\ \ S\ \ 1-p_{3A}\ \ + N_{21}S\ \ 1-p_{2J}\ \ S\ \ 1-p_{3A}\ \ .
\end{aligned}$$

The remaining adult abundances were calculated analogously, adding an additional cohort each year (Figure 3.4).

When the senescence correction included with a maximum life expectancy of 12 years, the population estimates declined 42 animals on average, from an overall positive bias of 459 animals on average. The senescence correction was tested with several maximum life expectancies (8–14). Shorter maximum life expectancies did not necessarily result in lower population estimates (Figure 3.5).

The senescence correction in the best case only slightly lowered abundance estimates, while increasing model instability. The senescence correction was therefore not included in my final analysis.

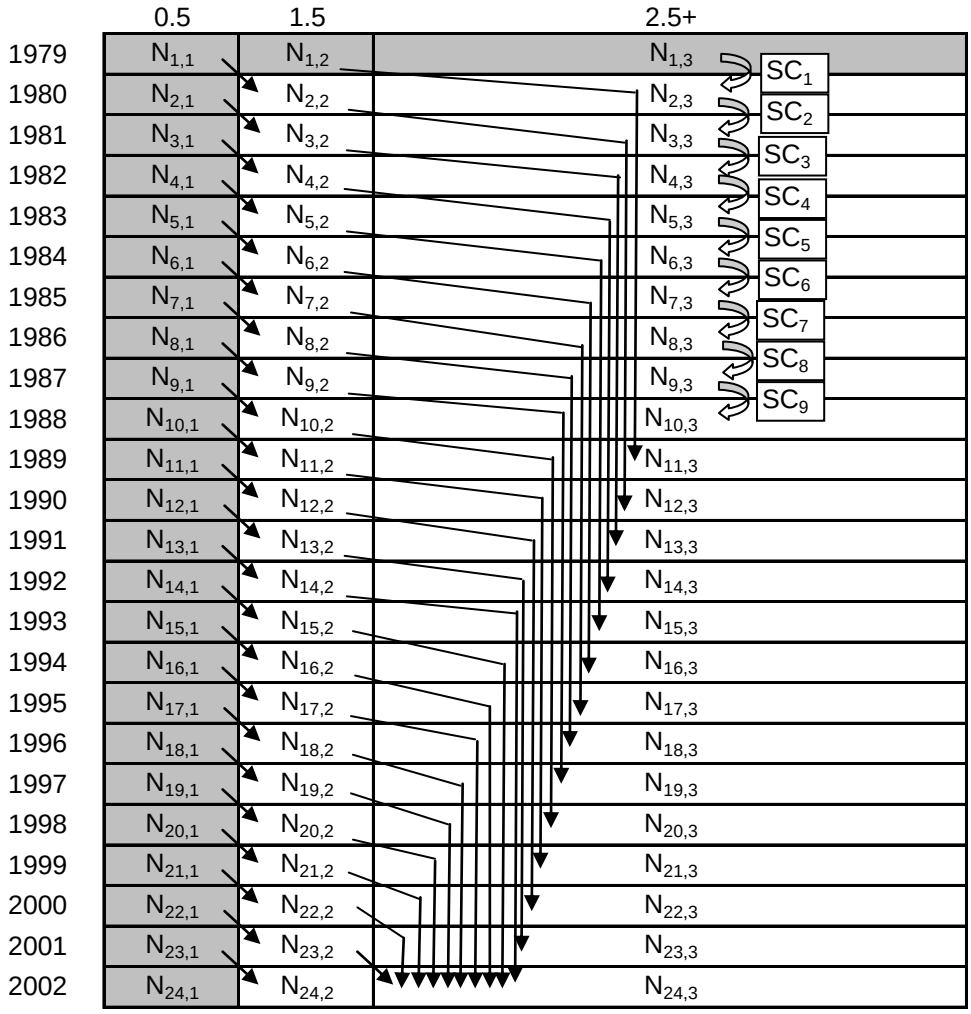



Figure 3.5. Diagram of the population reconstruction with pooled age-class data including a correction for senescence. Shaded cells were directly estimated. Arrows represent cohorts exploited in the model. $SC_y$ represents the year-specific senescence correction applied to $N_{1,3}$.

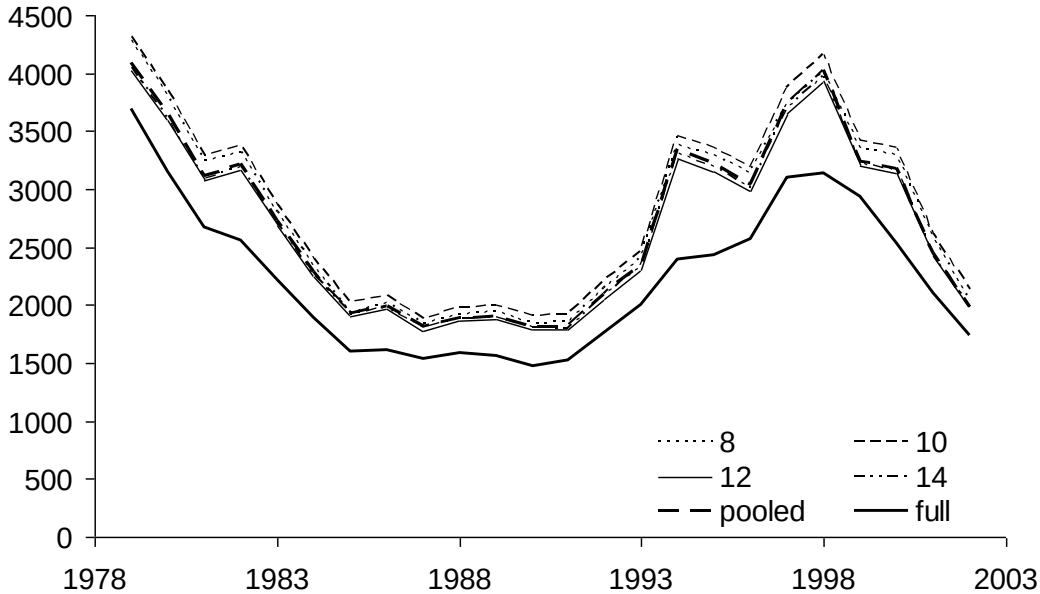



Figure 3.6. Time trends (1979–2002) for the females of a Washington State black-tailed deer population using both a full and a pooled reconstruction with a senescence correction with a maximum age of 8,10,12,14.

### 3.4.3 Additional Pooling Structure

In another attempt to correct for the positive bias of the original pooling structure, a second pooled model structure was tested. With the second model structure, the age-at-harvest likelihood was of the form

$$L_{\text{Age-at-harvest}} = \prod_{i=1}^{Y} L_{i1} \cdot L_{12} \cdot \prod_{i=1}^{y} L_{i3} \ , \tag{3.14}$$

where $L_{ij}$ was the likelihood describing the age-at-harvest data for the cohort entering the study in year $i \quad i = 1, \ldots, Y$ at age class $j \quad j = 1, \ldots, 3$ (Figure 3.6). In this model structure, Eq. (3.13), the annual abundance in both the juvenile and adult age classes, was directly estimated unlike previous model structures Eqs. (3.2, 3.4).

| | 0.5 | 1.5 | 2.5+ |
|---|---|---|---|
| 1979 | $N_{1,1}$ | $N_{1,2}$ | $N_{1,3}$ |
| 1980 | $N_{2,1}$ | $N_{2,2}$ | $N_{2,3}$ |
| 1981 | $N_{3,1}$ | $N_{3,2}$ | $N_{3,3}$ |
| 1982 | $N_{4,1}$ | $N_{4,2}$ | $N_{4,3}$ |
| 1983 | $N_{5,1}$ | $N_{5,2}$ | $N_{5,3}$ |
| 1984 | $N_{6,1}$ | $N_{6,2}$ | $N_{6,3}$ |
| 1985 | $N_{7,1}$ | $N_{7,2}$ | $N_{7,3}$ |
| 1986 | $N_{8,1}$ | $N_{8,2}$ | $N_{8,3}$ |
| 1987 | $N_{9,1}$ | $N_{9,2}$ | $N_{9,3}$ |
| 1988 | $N_{10,1}$ | $N_{10,2}$ | $N_{10,3}$ |
| 1989 | $N_{11,1}$ | $N_{11,2}$ | $N_{11,3}$ |
| 1990 | $N_{12,1}$ | $N_{12,2}$ | $N_{12,3}$ |
| 1991 | $N_{13,1}$ | $N_{13,2}$ | $N_{13,3}$ |
| 1992 | $N_{14,1}$ | $N_{14,2}$ | $N_{14,3}$ |
| 1993 | $N_{15,1}$ | $N_{15,2}$ | $N_{15,3}$ |
| 1994 | $N_{16,1}$ | $N_{16,2}$ | $N_{16,3}$ |
| 1995 | $N_{17,1}$ | $N_{17,2}$ | $N_{17,3}$ |
| 1996 | $N_{18,1}$ | $N_{18,2}$ | $N_{18,3}$ |
| 1997 | $N_{19,1}$ | $N_{19,2}$ | $N_{19,3}$ |
| 1998 | $N_{20,1}$ | $N_{20,2}$ | $N_{20,3}$ |
| 1999 | $N_{21,1}$ | $N_{21,2}$ | $N_{21,3}$ |
| 2000 | $N_{22,1}$ | $N_{22,2}$ | $N_{22,3}$ |
| 2001 | $N_{23,1}$ | $N_{23,2}$ | $N_{23,3}$ |
| 2002 | $N_{24,1}$ | $N_{24,2}$ | $N_{24,3}$ |

Figure 3.7. Diagram of a population reconstruction with pooled age-class data (Eq. 3.14). Shaded cells were directly estimated. Arrows represent cohorts exploited in the model.

Let

$h_{ij}$ = number of females harvested in year $i$ $i = 1, \ldots, 24$ at age class $j$ $j = 1, 2, 3$ ,

$N_{ij}$ = female deer abundance in year $i$ $i = 1, \ldots, 24$ at age class $j$ $j = 1, 2, 3$ ,

$S$ = natural survival probability for all females,

$c_{0.5}$ = vulnerability coefficient for young-of-year females (i.e., age class 0.5),

$c_{1.5+}$ = vulnerability coefficient for females 1.5 years of age or older,

$f_i$ = hunter effort in year $i$ $i = 1, \ldots, 24$ .

For the adults already present in the population in year 1, their likelihood contribution was written as follows:

$$L_{13} = \binom{N_{13}}{h_{13}} \left(1 - e^{-c_{1.5+} f_i}\right)^{h_{13}} \left(e^{-c_{1.5+} f_i}\right)^{N_{13} - h_{13}} .$$

For the yearlings present in the population in year 1, their likelihood was written as follows

$$L_{12} = \binom{N_{12}}{h_{12}} \left(1 - e^{-c_{1.5+} f_1}\right)^{h_{12}} \left(e^{-c_{1.5+} f_1}\right)^{h_{23}}$$

For the juveniles present in the first year, the likelihood was written as follows:

$$L_{11} = \binom{N_{11}}{h_{11}, h_{22}} \left(1 - e^{-c_{0.5} f_1}\right)^{h_{11}} \left(e^{-c_{0.5} f_1} \cdot S \cdot \left(1 - e^{-c_{1.5+} f_1}\right)\right)^{h_{22}}$$
$$\cdot \left(1 - \left(1 - e^{-c_{0.5} f_1}\right) - e^{-c_{0.5} f_1} \cdot S \cdot \left(1 - e^{-c_{1.5+} f_1}\right)\right)^{N_{11} - h_{11} - h_{22}}$$

Construction of $L_{21}, \ldots, L_{Y1}$ was analogous to that of $L_{11}$ incremented for subsequent years.

Construction of $L_{23}, \ldots, L_{Y3}$ was analogous to that of $L_{13}$ incremented for subsequent years.

The catch-effort likelihood was identical to the original pooled and unpooled catch-effort likelihood.

Juvenile and adult abundance levels (i.e., $N_{11}, N_{21} \ldots, N_{24,1}$ and $N_{12}, N_{13}, N_{23}, \ldots, N_{24,1}$) were calculated directly, while yearling abundance levels were based on the invariance property of the maximum likelihood estimation, where

$$\hat{N}_{i2} = N_{i-1,1} e^{-c_{0.5} f_{i-1}} S \, .$$

Total annual abundance for any year was the sum of the within-year cohort abundance levels.

Use of the second likelihood structure for pooling resulted in abundance estimates that were, on average, 1443 animals higher than the full model (Figure 3.8). These results suggest model (3.14) is not the preferred approach to pooling age-at-harvest data and is therefore not recommended.

### 3.5 Discussion

The black-tailed deer example demonstrates that big-game reconstruction is feasible using as few as three age classes. There was enough age-structure information to perform a partial cohort analysis and estimate initial abundance of each recruitment class. The difference in parameter and precision estimates between Skalski et al. (2007) and my reanalysis is attributed to improved numerical optimization techniques. The difference in abundance estimates from my reanalysis and the pooled analysis are likely due simply to the loss of information associated with pooling. However, there was little corresponding loss in precision of demographic parameters between my analyses when data were pooled. The survival and vulnerability parameter estimates are inversely correlated with the estimated abundance (Table 3.1, Table 3.2).

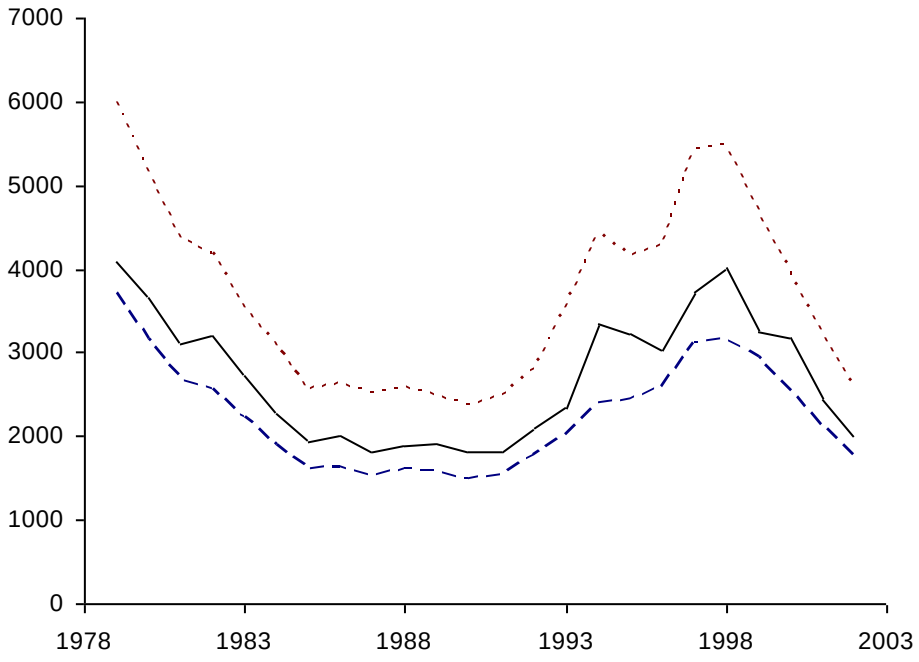



Figure 3.8. Time trends (1979–2002) for the females of a Washington State black-tailed deer population reconstruction based on full age-class data (dashed line), pooled adult age classes (solid line) based on Eq. (3.4) and a second pooled adult age-class model structure (dotted line) based on Eq. (3.14).

For species like white-tailed deer, mule deer and wild turkey, which are readily aged to young-of-year, subadults, and adults, the pooled age-class reconstruction method should provide useful abundance estimates. One tangible benefit to pooling age classes would be reduced cost and fewer logistical issues with estimating adult age classes. Additionally, the use of age-class grouping means that other species, such as wild turkey, which cannot be aged beyond broad age-class categories, can now be analyzed with statistical population reconstruction methods. Also, a senescence correction may be more useful in a model stabilized by additional information.

It was possible to perform population reconstruction with pooled age-class data; in the black-tailed deer example, it was feasible because of the many years of data (i.e., 24). In Chapter 5, I suggested that it is advisable to have additional auxiliary data, beyond the age-at-harvest and hunter effort data when doing statistical population reconstruction, even without pooling. The additional loss of information associated with pooling makes having reliable auxiliary information all the more important. Broms et al. (2010) examined the potential of extending the pooling concept to only two age classes (e.g., young-of-year and adults) for applications such as small game species (e.g., greater sage-grouse, mourning doves [Z*enaida macroura*]). Their results suggest, with appropriate auxiliary information, it is possible to use the statistical reconstruction method with as few as two age classes, provided appropriate auxiliary data exist. Furthermore, Broms et al. (2010) found that additional auxiliary data were essential in their reconstruction analysis. The lack of the cohort structure of the data required multiple sources of auxiliary demographic data before annual abundance could be reconstructed. Both catch-per-unit-effort and radiotelemetry

information were necessary for model selection and estimability in the greater sage-grouse, pooled age-class population reconstruction (Broms et al. 2010).

Given the flexibility in model construction and incorporation of auxiliary information, statistical population reconstruction could be applied to situations where (1) historically only pooled age-class data are available; (2) collection of specific age-class data is costly; (3) logistical constraints dictate the collection of pooled age-class data; (4) animals can only be reliably classified into pooled age classes due to errors in aging. With increasingly tight budgets, it is more and more difficult to continue collection of data that are expensive, such as cementum annuli counts. The reconstruction methods described herein offer one alternative technique for demographic assessment that might reduce costs. Ultimately, managers should consider the intended purpose, the necessary accuracy, precision of demographic values, and feasibility of data collection when deciding on whether to pool age classes or not.

### 3.6 Management Implications

Population reconstruction using pooled adult age classes can provide a cost-effective supplement to existing inventory methods, and in some cases, could provide the primary method of inventorying hunted game populations over large geographic areas. Tooth eruption and wear data are relatively easy and inexpensive to collect from harvested ungulates, and in most cases, can be used to accurately age individuals to young-of-year, subadults, and adults 2.5+ years. This analysis indicates reliable population trends can be reconstructed with minimal precision loss without the need for expensive tooth extraction and cementum annuli analyses. Aging by tooth eruption and wear is already commonly used by many wildlife agencies, and this chapter suggests a useful means of analyzing this often

collected and neglected demographic data.  Besides ungulate species, the same type of population reconstruction could also be used for species like wild turkey, which are also commonly classified into three age classes based on plumage and spur length (Kelly 1975).

# Chapter 4: Population Reconstruction of Marten and Fisher Populations in Upper Michigan

## 4.1 Introduction

Estimating furbearer population abundance, particularly for harvested populations, is necessary for effective management. However, monitoring terrestrial carnivores is challenging because of their comparatively low densities and elusive behavior which makes observations difficult. Marten and fisher abundance has been estimated or inferred using track surveys (Raphael 1994), mark recapture from samples collected at hair snares (Mowat and Paetkau 2002, Williams et al. 2009), and radiotelemetry (Belant 2007). However, there is no cost-effective technique currently available to estimate marten and fisher abundance over large geographic areas. Consequently, for harvested populations, sex and age-structure data derived from harvested animals are generally used to monitor trends in age and sex ratios of these species (Douglas and Strickland 1987, Strickland and Douglas 1987). Such data summaries often provide a useful first approximation of demographic trends, but new analytical developments (Gove et al. 2002) that make use of age-at-harvest data, routinely collected by management agencies over extensive areas, might offer alternative opportunities for assessment.

Statistical population reconstruction (SPR) has emerged as a useful and robust alternative in modeling age-at-harvest data for many wildlife species (Gove et al. 2002; Skalski et al. 2005, 2007; Broms et. al. 2010). For many management agencies, data derived from hunters and trappers, including age-at-harvest and hunter effort, are the historical backbone of data collection because such information is relatively easy to collect, offers extensive information over broad spatial scales, and does not require intensive and expensive

sampling (Skalski et al. 2005, Millspaugh et al. 2009). Statistical population reconstruction takes advantage of these commonly collected data, while offering the flexibility of combining data from other intensive survey approaches, such as radiotelemetry (e.g., Broms et al. 2010). Such flexibility in data types that can be combined and the ability to refine the model as more auxiliary data becomes available offers an adaptive framework for managers. In addition to estimating abundance, SPR approaches simultaneously estimate natural survival, harvest mortality, and recruitment. This additional information offers a more robust assessment of status and trends than abundance alone.

Martens and fishers historically were present throughout Michigan's Upper Peninsula (Williams et al. 2007). Populations of both species declined during the late 1800s and early 1900s, presumably from overharvest and habitat change (e.g., Hagmeier 1956, Powell 1993). Martens and fishers were extirpated in Upper Peninsula Michigan in 1936 and 1939, respectively (Manville 1948, Williams et al. 2007). Martens and fishers were restored across much of the area between 1959–1992 through a series of reintroductions and translocations (Williams et al. 2007). Populations of both species increased and a trapping season for fishers was reinstated in the western Upper Peninsula in 1989 (Cooley et al. 1990) and expanded to the entire Upper Peninsula, excluding Drummond Island and Pictured Rocks National Lakeshore, in 1996 (Williams et al. 2007). Martens were listed as a state threatened species in 1978, later becoming a 'Species of Concern' until March 1999; in 2000, they were legally harvested throughout the Upper Peninsula during the same trapping season as fisher (Earle et al. 2001, Frawley 2002). Michigan currently monitors population trends of martens and fishers through mandatory carcass registration to assess sex and age structure of the

harvest. Additionally, annual mail surveys are sent to trappers to provide estimates of harvest effort. These data are sufficient for SPR and form the basis of my analysis.

My objective was to apply SPR models to marten and fisher populations in the Upper Peninsula, Michigan, to estimate abundance, natural survival, harvest mortality, and recruitment. In doing so, I illustrate the first application of SPR models to furbearer data and provide an example of SPR with estimated hunter effort.

## 4.2 Study Area

The Upper Peninsula of Michigan comprises about 42,600 $km^2$ and has a human population of 310,000. Overstory vegetation is predominately conifer and northern hardwood forests with dispersed agriculture in the south-central and eastern portions. The western Upper Peninsula is characterized by rolling hills and elevations from 184–606 m. In contrast, the eastern Upper Peninsula is relatively flat, poorly drained, and includes extensive swamps and peat bogs (Albert 1995). State and federal lands comprise about 40% of the total land area.

From 1996–2002, the trapping season was 1–11 December with a maximum individual season limit of 3 fishers that could include up to 3 fishers from Unit A and 1 fisher from Unit B (Figure 4.1). The season limit for martens was 1 per trapper beginning in 2000. In 2002, the trapping season for both species was expanded to 1–15 December.

## 4.3 Methods

### 4.3.1 Age-at-Harvest and Trapper Effort Data

For both martens and fishers, my analysis relied on age-at-harvest and trapper-effort data (Table 4.1–Table 4.3). Registration of harvested martens and fisher was mandatory within 7 days of trapping season closure. At the time of registration, date of capture, location,

and sex for each animal are recorded. That information formed the basis of the age-at-harvest data used in my analysis. A tooth was extracted from each submitted skull for age determination (Strickland et al. 1982, Poole et al. 1994). To estimate annual harvest effort, The Michigan Department of Natural Resources mailed questionnaires to trappers about 1 month after season closure (e.g., Frawley 2007). Marten and fisher tag holders were requested to provide information on whether they trapped marten or fisher, the number of individuals of each species captured, and trapping effort (e.g., number of days trapped, number of trap nights [marten only]). They mailed up to two follow-up questionnaires to nonrespondents. Beginning with the 2007 trapping season, harvest information could also be submitted by trappers using an internet-based questionnaire. They calculated annual estimates of harvest effort with 95% confidence limits following Cochran (1977). Response rates were generally high (e.g., 86% and 72% for 2004 and 2007 trapping seasons, respectively; Frawley 2004, 2007).

I analyzed the marten and fisher data separately using 8 and 12 years of data, respectively. For fishers, trapping effort was expressed in terms of trap-days rather than trap-nights. Trap-days are defined here as the total number of days licensed trappers employed trap gear. Although total trap-nights (i.e., traps per night summed over the season) are a more accurate expression of trapping effort, these data were not available for fishers, in all years.

### 4.3.2 Model Construction

The marten and fisher population reconstruction models were comparable in structure because of similarities in the available data. The age-at-harvest matrix for both species was composed of multiple age classes from young-of-year to 9- or 10-year-old individuals, and 8

(marten) to 12 (fisher) years of trapping records (Table 4.1, Table 4.2). Trapping effort increased substantially during the study period, but no major shifts in trapping regulations were instituted. Although 4 days were added to the trapping season, trapper effort expressed in terms of either total trap-days or total trap-nights should accommodate the effects. Therefore, standard formulations of the age-at-harvest likelihood were applicable.

I examined two alternative models for catch-effort; $c_{0.05} \neq c_{1.5+}$, and common $c$ where $c$ is the vulnerability coefficient, $c_{0.5}$ = vulnerability coefficient for young-of-year (i.e., age class 0.5) and $c_{1.5+}$ = vulnerability coefficient for animals 1.5 years of age or older. The most general form of the catch-effort likelihood can then be written as follows:

$$L_{\text{Catch-effort}} = \prod_{i=1}^{Y} \binom{\sum_{j=1}^{A} N_{ij}}{h_{i1}, h_{i2}} \left[ \left( \frac{N_{i1}}{\sum_{j=1}^{A} N_{ij}} \right) 1 - e^{-c_{0.5} \hat{f}_i} \quad r_i \right]^{h_{i1}}$$
$$\cdot \left[ \left( \frac{N_{i2}}{\sum_{j=1}^{A} N_{ij}} \right) 1 - e^{-c_{1.5+} \hat{f}_i} \quad r_i \right]^{\sum_{j=2}^{A} h_{ij}}$$
$$\cdot \left[ 1 - \left( \frac{N_{i1}}{\sum_{j=1}^{A} N_{ij}} \right) 1 - e^{-c_{0.5} \hat{f}_i} \quad r_i - \left( \frac{N_{i2}}{\sum_{j=1}^{A} N_{ij}} \right) \left( 1 - e^{-c_{1.5+} \hat{f}_i} \right) r_i \right]^{\sum_{j=1}^{A} (N_{ij}) - h_{i1} - h_{i2}} \tag{4.1}$$

where $r_i$ = year-specific proportion of harvested animals that are aged, $h_i$ = total number of animals harvested and aged , $N_{ij}$ = abundance in year $i \quad i = 1, \ldots, Y$ at age class $j \quad j = 1, \ldots, A$ , and $f_i$ = hunter effort in year $i \quad i = 1, \ldots, Y$ . This trinomial reduces to a binomial when $c_{0.5} = c_{1.5+}$. Equation (4.1) allowed us to test whether younger animals had a

different vulnerability to trapping than older individuals. To do so, however, the age-at-harvest likelihood also must be parameterized accordingly.

An aspect of the marten and fisher data sets, which is typical of most harvested animals, was that effort was estimated by a post-season survey rather than enumerated. The Michigan Department of Natural Resources provided estimates of trapping effort $\hat{f}_i, i = 1, \ldots, Y$, along with survey sampling error, i.e., SE $\hat{f}_i$. This survey sampling error needed to be propagated to the population reconstruction. Assuming adequate survey sample sizes, the annual estimates of trapping effort can be assumed to be normally distributed with standard error equal to the estimated survey error i.e., $\sigma_i = \text{SE } \hat{f}_i$. The survey sampling error can then be incorporated into the overall likelihood model for population reconstruction based on a survey-error likelihood of the form

$$L_{\text{Survey-error}} = \prod_{i=1}^{Y} \frac{1}{\sqrt{2\pi}\sigma_i} e^{-\frac{\frac{1}{2}\varepsilon_i^2}{\sigma_i^2}}, \tag{4.2}$$

where

$\sigma_i \overset{\text{set}}{=}$ SE $\hat{f}_i$ in Table 4.1 or Table 4.2;

$\varepsilon_i$ = survey error i.e., $\hat{f}_i - f_i$ for the *i*th year $i = 1, \ldots, Y$;

such that the estimated effort $\hat{f}_i = f_i + \varepsilon_i$ represents the true trapping effort in year $i$ plus survey error. In order to take advantage of the survey-error likelihood (Eq. 4.2), the estimated effort in the age-at-harvest likelihood and catch-effort likelihood (Eq. 4.1) must also be reparameterized as $\hat{f}_i + \varepsilon_i$. The $\varepsilon_i$ $i = 1, \ldots, Y$ are $Y$ additional model parameters that must be estimated in the joint likelihood model for the population reconstruction. I

calculated standardized residuals based on the $\hat{\varepsilon}_i$'s where $Z = \frac{\hat{\varepsilon}_i}{\text{SE}\ \hat{f}_i}$ . These standardized residuals offer not only an additional measure of model fitness, they also offer a measure of accuracy in the measurement of hunter effort.

The aging likelihood accounts for less than complete aging of all animals reported harvested (Table 4.3). The form of this aging likelihood can be written as

$$L_{\text{Aging}} = \prod_{i=1}^{Y} \binom{H_i}{h_i} r_i^{h_i} \ 1 - r_i \ ^{H_i - h_i} \tag{4.4}$$

where $r_i$ = year-specific proportion of harvested animals that are aged, $H_i$ = total animals harvested in year $i$ $i = 1,...,Y$ , and $h_i$ = total number of animals aged from among the $H_i$ .

For both marten and fisher analyses, the joint likelihood model for the population reconstruction is of the form

$$L = L_{\text{Age-at-harvest}} \cdot L_{\text{Catch-effort}} \cdot L_{\text{Survey-error}} \cdot L_{\text{Aging}} \tag{4.3}$$

where $L_{\text{Aux}_1}$ and $L_{\text{Aux}_2}$ are Eqs. (4.1) and (4.2), respectively.

The age-at-harvest likelihood was constructed based on the cohort relationship. A cohort being defined as all animals born in the same year. The overall population then being simply the sum of all cohorts. Observed age-at-harvest numbers for each cohort (Table 4.1, Table 4.2) were modeled by a multinomial distribution similar to that used by Skalski et al. (2007) as a function of estimated initial recruitment, survival, harvest, and reporting probability (Skalski et al 2005, Gove et al 2002).

Table 4.1. Age-at-harvest data and estimated trapping effort (SE) for Michigan martens, 2000–2007. Trapping effort expressed in terms total trap-nights (i. e., one trap/night = 1 trap-night), along with associated sample survey standard error.

| | Age class | | | | | | | | | | | Total no. of | SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | 0.5 | 1.5 | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 | 8.5 | 9.5 | 10.5 | trap-nights | (trap-nights) |
| 2000 | 28 | 23 | 11 | 2 | 6 | 1 | 3 | 2 | 0 | 0 | 0 | 8,641 | 321.61 |
| 2001 | 23 | 19 | 12 | 8 | 4 | 4 | 3 | 2 | 0 | 0 | 0 | 7,172 | 387.73 |
| 2002 | 31 | 8 | 7 | 13 | 5 | 2 | 1 | 0 | 0 | 0 | 0 | 10,418 | 449.71 |
| 2003 | 65 | 14 | 19 | 10 | 8 | 7 | 2 | 0 | 0 | 1 | 0 | 13,822 | 589.77 |
| 2004 | 61 | 41 | 15 | 16 | 13 | 8 | 6 | 3 | 0 | 0 | 0 | 23,088 | 10,849.86 |
| 2005 | 55 | 31 | 22 | 17 | 7 | 6 | 3 | 1 | 1 | 0 | 0 | 17,578 | 895.77 |
| 2006 | 95 | 27 | 19 | 15 | 12 | 9 | 6 | 3 | 0 | 0 | 0 | 46,204 | 3,102.71 |
| 2007 | 147 | 57 | 20 | 18 | 19 | 11 | 7 | 9 | 2 | 1 | 1 | 38,131 | 4,799.23 |

Table 4.2. Age-at-harvest data and estimated trapping effort (SE) for Michigan fishers, 1996–2007. Trapping effort expressed in terms of total trap-days (i.e., 1 trapper/day = 1 trap-day), along with associated sample survey standard error.

| | Age class | | | | | | | | | | | Total no. of | SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | 0.5 | 1.5 | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 | 8.5 | 9.5 | 10.5 | trap-days | (Trap-days) |
| 1996 | 114 | 92 | 34 | 23 | 8 | 7 | 6 | 6 | 2 | 1 | 0 | 1,885 | 1,152.81 |
| 1997 | 153 | 100 | 46 | 20 | 10 | 16 | 2 | 6 | 3 | 1 | 0 | 1,991 | 1,285.71 |
| 1998 | 115 | 73 | 28 | 26 | 10 | 9 | 9 | 4 | 3 | 0 | 0 | 4,633 | 1,019.90 |
| 1999 | 85 | 55 | 24 | 15 | 6 | 3 | 1 | 1 | 0 | 0 | 0 | 2,453 | 382.65 |
| 2000 | 67 | 50 | 22 | 7 | 3 | 3 | 2 | 0 | 1 | 0 | 0 | 1,971 | 361.73 |
| 2001 | 98 | 95 | 59 | 21 | 11 | 4 | 8 | 0 | 0 | 1 | 0 | 2,173 | 373.98 |
| 2002 | 109 | 74 | 26 | 20 | 14 | 5 | 6 | 0 | 1 | 0 | 0 | 4,141 | 643.88 |
| 2003 | 162 | 75 | 45 | 44 | 25 | 5 | 7 | 4 | 1 | 1 | 0 | 4,485 | 383.16 |
| 2004 | 123 | 87 | 34 | 18 | 21 | 7 | 6 | 1 | 0 | 0 | 0 | 4,213 | 642.35 |
| 2005 | 146 | 66 | 20 | 16 | 15 | 4 | 4 | 2 | 1 | 0 | 0 | 3,829 | 596.94 |
| 2006 | 176 | 91 | 38 | 19 | 13 | 8 | 6 | 6 | 0 | 1 | 0 | 6,759 | 164.80 |
| 2007 | 133 | 52 | 24 | 7 | 10 | 5 | 6 | 7 | 2 | 0 | 0 | 5,900 | 162.76 |

Table 4.3. Numbers of martens and fishers reported harvested each year, along with numbers aged in the Upper Peninsula, Michigan, 1996-2007. The proportion of animals aged is incorporated into the reporting rate likelihoods.

| | Martens | | Fishers | |
|---|---|---|---|---|
| Season | Harvest total | Aged | Harvest total | Aged |
| 1996 | | | 471 | 293 |
| 1997 | | | 609 | 357 |
| 1998 | | | 455 | 277 |
| 1999 | | | 291 | 190 |
| 2000 | 85 | 76 | 236 | 155 |
| 2001 | 97 | 75 | 381 | 297 |
| 2002 | 85 | 67 | 348 | 255 |
| 2003 | 149 | 126 | 442 | 369 |
| 2004 | 184 | 163 | 368 | 297 |
| 2005 | 164 | 143 | 322 | 274 |
| 2006 | 196 | 186 | 399 | 358 |
| 2007 | 318 | 292 | 284 | 246 |

The age-at-harvest likelihood used for the analysis of age-at-harvest data is of the form

$$L_{\text{Age-at-harvest}} = \prod_{i=1}^{Y} \cdot L_{i1} \prod_{j=1}^{A} L_{1j} \tag{4.5}$$

where $L_{ij}$ is the likelihood describing the age-at-harvest data for the cohort entering the study in year $i \quad i = 1, \ldots, Y$ at age class $j \quad j = 1, \ldots, A$

Let

$h_{ij}$ = number of animals harvested in year $i \quad i = 1, \ldots, Y$ at age class $j \quad j = 1, \ldots, A$ ,

$N_{ij}$ = abundance in year $i \quad i = 1, \ldots, Y$ at age class $j \quad j = 1, \ldots, A$ ,

$S_j$ = age specific natural survival probability,

$c_{0.5}$ = vulnerability coefficient for young-of-year (i.e., age class 0.5),

$c_{1.5}$ = vulnerability coefficient for animals 1.5 years of age or older,

$f_i$ = hunter effort in year $i \quad i = 1, \ldots, Y$ .

$$L_{i1} = \binom{N_{i,1}}{h_{i,1}, h_{i+1,2....}} p_{i,J} r_i^{\;h_{i,1}} \quad 1 - p_{i,J} \quad S_1 p_{i+1,A} r_{i+1}^{\;h_{i+1,2}}$$
$$\cdot \quad 1 - p_{i,J} \quad 1 - p_{i+1,A} \quad S_1 S_2 p_{i+2,A} r_{i+2}^{\;h_{i+2,3}} \ldots$$

$$L_{1j} = \binom{N_{1,j}}{h_{1,j}, h_{2,j+1....}} p_{1,A} r_1^{\;h_{1,j}} \quad 1 - p_{1,A} \quad S_j p_{2,A} r_2^{\;h_{2,j+1}}$$
$$\cdot \quad 1 - p_{1,A} \quad 1 - p_{2,A} \quad S_j S_{j+1} p_{3,A} r_3^{\;h_{3,j+2}} \ldots$$

where

$$p_{i,J} = \left(1 - e^{-c_{0.5} \;\hat{f}_i + \varepsilon_i}\right),$$
$$p_{i,A} = \left(1 - e^{-c_{1.5+} \;\hat{f}_i + \varepsilon_i}\right).$$

Construction of $L_{21},\ldots,L_{Y1}$ is analogous to that of $L_{i1}$ incremented for subsequent years. Construction of $L_{12},\ldots,L_{1A}$ is analogous to that of $L_{1j}$ incremented for subsequent age classes.

The expected value of the age-at-harvest number in the first row and first column of the age-at-harvest matrix $h_{11}$ was modeled as

$$E\ h_{11} = N_{11}\ 1-e^{-c_{0.5}\ \hat{f}_i+\varepsilon_1}\ r_1 .$$

The harvest numbers of that same cohort for the next two years can be written as

$$E\ h_{22} = N_{11}\ e^{-c_{0.5}\ \hat{f}_1+\varepsilon_1}\ S_1\ 1-e^{-c_{1.5+}\ \hat{f}_2+\varepsilon_2}\ r_2$$

and

$$E\ h_{33} = N_{11}\ e^{-c_{0.5}\ \hat{f}_1+\varepsilon_1}\ S_1\ e^{-c_{1.5+}\ \hat{f}_2+\varepsilon_2} \cdot S_2\ 1-e^{-c_{1.5+}\ \hat{f}_3+\varepsilon_3}\ r_3,$$

assuming age-specific natural survival probabilities $S_i$ and age-specific vulnerability coefficients for the young-of-year and older (i.e., 1.5+).

I used Program USER to construct and analyze the age-at-harvest likelihood, along with the likelihoods for catch-effort data, survey sampling of trapper effort (Skalski and Millspaugh 2006) and aging proportion. I examined five alternative models for the martens and fishers, separately; these included $McS$, $McS_{0.5,1.5+}$, $McS_{0.5,1.5,2.5+}$, $McS_A$, and $Mc_{0.5,1.5+}S$, where:

Model $McS$: Assumed constant natural survival and harvest probability over time and across all age classes.

Model $McS_{0.5,1.5+}$: Assumed age-specific (0.5, 1.5+) natural survival probabilities that are constant over time and vulnerability coefficient that is constant over time and across all age classes.

Model $McS_{0.5,1.5,2.5+}$: Assumed age-specific (0.5, 1.5 and 2.5+) natural survival probabilities that are constant over time and vulnerability coefficient that is constant over time and across all age classes.

Model $McS_A$: Assumed age-specific natural survival probabilities that are constant over time and a vulnerability coefficient that is constant over time and across all age classes.

Model $Mc_{0.5,1.5+}S$ : Assumed constant natural survival probability over time and across all age classes and vulnerability coefficients that differ across age classes (0.5, 1.5+).

I based model selection on likelihood ratio tests (LRTs), AIC (Burnham and Anderson 2002), and residual analysis to find the most appropriate model. For martens, the reported standard errors were expanded by the scale parameter based on a goodness-of-fit to the age-at-harvest matrix where

$$\text{Scale Parameter} = \sqrt{\frac{\chi^2_{\text{df}}}{\text{df}}}, \qquad \chi^2_{\text{df}} = \sum\left(\frac{\text{Observed}_i - \text{Expected}_i}{\sqrt{\text{Expected}_i}}\right)^2,$$

df = number of cells in the age-at-harvest matrix – number of parameters estimated. For fishers, constrained optimization necessitated that standard errors be estimated using a multi-model variance estimator (Burnham and Anderson 2002:162). Alternative models were evaluated with juvenile survival i.e., $S_{0.5}$ uniformly sampled over the range 0.60 to 0.80.

Once a final model was selected a point deletion sensitivity analysis was performed (Chapter 5). The analysis was performed by running a model with the full complement of data to create a baseline for comparison. A single year of data was then removed from the data. The model was then reconstructed and run again, assuming the removed year of data never existed. The results were recorded and compared to the full-data model results. The process was then repeated several times. The purpose of the analysis was to determine the robustness of the model and its resulting parameter estimates.

## 4.4 Results

For marten, the best available population reconstruction model selected by AIC was model $McS_A$ (Table 4.4). Likelihood ratio tests largely confirmed the model selection results (Table 4.5) and residual analysis did not indicate a lack-of-fit (Figure 4.4, Figure 4.5); therefore, model $McS_A$ was selected for the marten population reconstruction. Marten abundance estimates (Table 4.6, Figure 4.1) show a general downward trend from an estimate of $\hat{N}_{2000} = 1310.8 \quad \text{SE} = 470.8$ animals in 2000 to $\hat{N}_{2007} = 920.4 \quad \text{SE} = 281.7$ in 2007. Using the fitted vulnerability coefficient and annual adjustments to trapping effort, the probability of harvest was estimated to have increased from $0.071 \quad \text{SE} = 0.0234$ to in 2000 $0.333 \quad \text{SE} = 0.0996$ in 2007 (Figure 4.2). This nearly fivefold increase in harvest probability corresponds to a nearly fivefold increase in trap-nights (Table 4.3). During the eight years of population reconstruction, annual recruitment into the trappable population ranged from 354.5(SE = 105.9) to 639.8 (SE = 199.3) with no specific discernable trend (Figure 4.3).

Table 4.4. Likelihood (ln $L$) and Akaike information criterion (AIC) values for alternative population reconstruction models for martens in the Upper Peninsula, Michigan, 2000–2007 (* indicates chosen model).

| Model | ln $L$ | No. of model parameters | AIC |
|---|---|---|---|
| $McS$ | –217.70 | 33 | 501.40 |
| $McS_{0.5,1.5+}$ | –209.51 | 34 | 487.02 |
| $McS_{0.5,1.5,2.5+}$ | –209.48 | 35 | 488.96 |
| $McS_A^*$ | –199.92 | 42 | 483.84 |
| $Mc_{0.5,1.5+}S$ | –209.08 | 34 | 486.16 |

Table 4.5. Likelihood ratio tests (LRTs) comparing alternative nested population reconstruction models for martens from the Upper Peninsula, Michigan, 2000-2007 (* indicates chosen model).

| Likelihood ratio tests | | | |
|---|---|---|---|
| Full – reduced | chi-square | df | $P$ |
| $McS_{0.5,1.5+}$ vs. $McS$ | 16.386 | 1 | 0.0001 |
| $McS_{0.5,1.5,2.5+}$ vs. $McS_{0.5,1.5+}$ | 0.0600 | 1 | 0.8065 |
| $McS_A^*$ vs. $McS_{0.5,1.5,2.5+}$ | 19.1200 | 7 | 0.0078 |
| $Mc_{0.5,1.5+}S$ vs. $McS$ | 17.2420 | 1 | 0.0000 |

Table 4.6. Annual abundance estimates $\hat{N}$ of martens and fishers from the Upper Peninsula, Michigan, 1996-2007, based on best population reconstruction model i.e., $McS_A$, $McS_{0.5,1.5,2.5+}$ and associated standard errors SE .

| Year | Marten | | Fisher | |
|---|---|---|---|---|
| | $\hat{N}$ | SE | $\hat{N}$ | SE |
| 1996 | | | 2557.5 | 1657.1 |
| 1997 | | | 2371.4 | 1555.7 |
| 1998 | | | 2056.7 | 1328.4 |
| 1999 | | | 2052.8 | 1314.1 |
| 2000 | 1310.8 | 470.8 | 2104.2 | 1378.1 |
| 2001 | 1209.0 | 406.4 | 1918.9 | 1310.5 |
| 2002 | 1171.1 | 366.8 | 1637.5 | 1140.5 |
| 2003 | 1316.8 | 389.6 | 1477.8 | 1050.7 |
| 2004 | 1142.8 | 320.9 | 1171.1 | 835.9 |
| 2005 | 947.9 | 270.0 | 1061.0 | 756.9 |
| 2006 | 950.2 | 267.2 | 939.7 | 676.9 |
| 2007 | 920.4 | 281.7 | 760.1 | 533.4 |

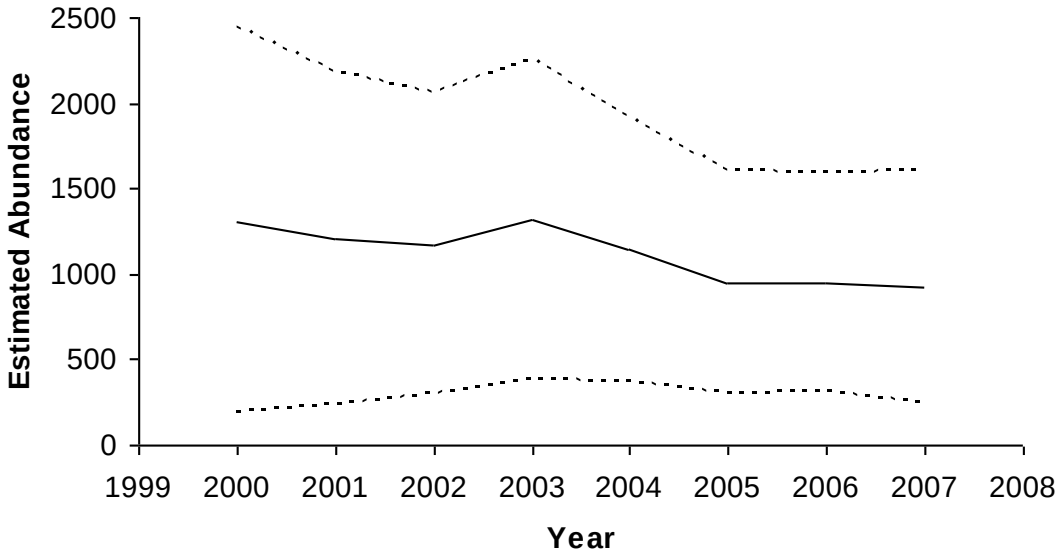



Figure 4.1. Annual trend in abundance of martens in Michigan, 2000–2007, based on the best available population reconstruction model i.e., $McS_A$ , along with associated 95% confidence intervals.

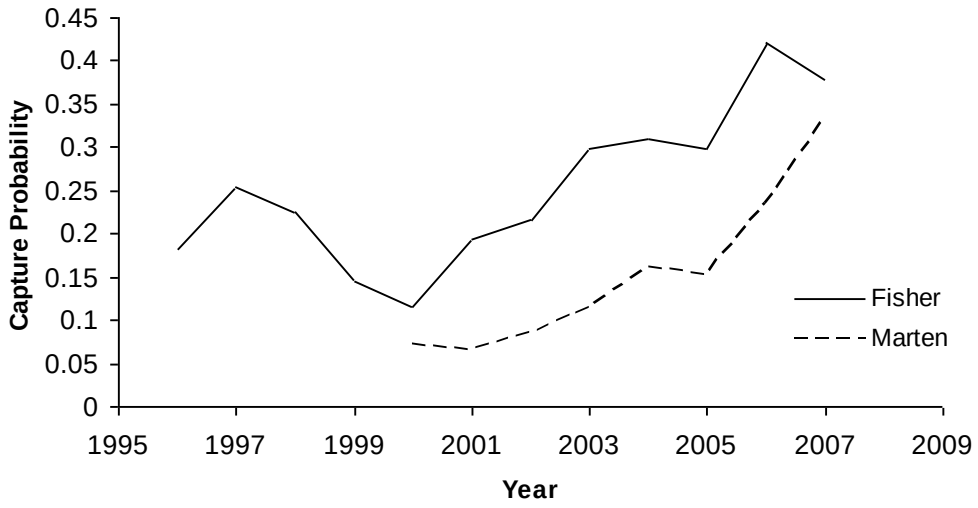



Figure 4.2. Temporal trends in estimated probabilities of annual harvest based on best available population reconstruction models i.e., $McS_A, McS_{0.5,1.5,2.5+}$ for martens and fishers respectively in the Upper Peninsula, Michigan, 1996-2007.

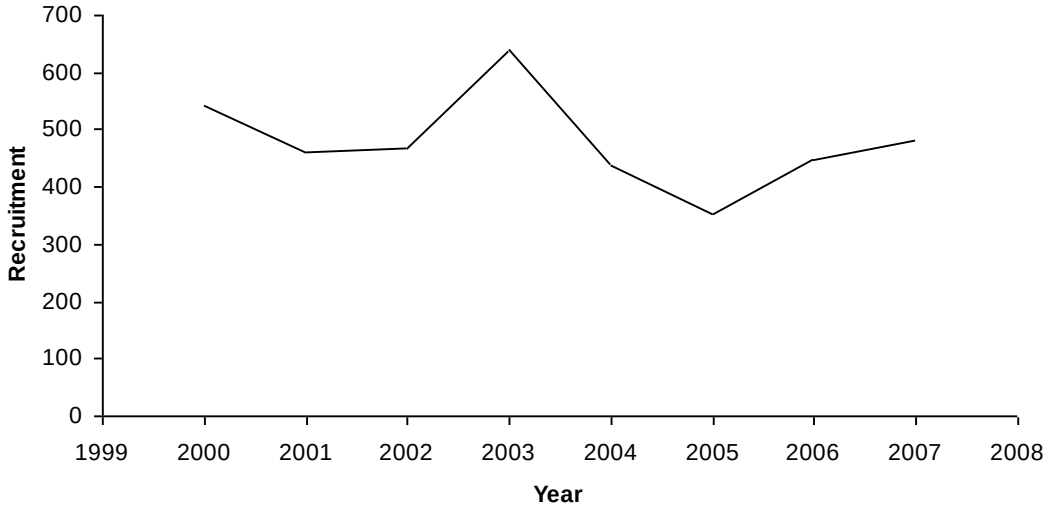



Figure 4.3. Annual trend in recruitment of martens into the trapping population in Michigan, 2000–2007, based the on best available population reconstruction model i.e., $McS_A$ .

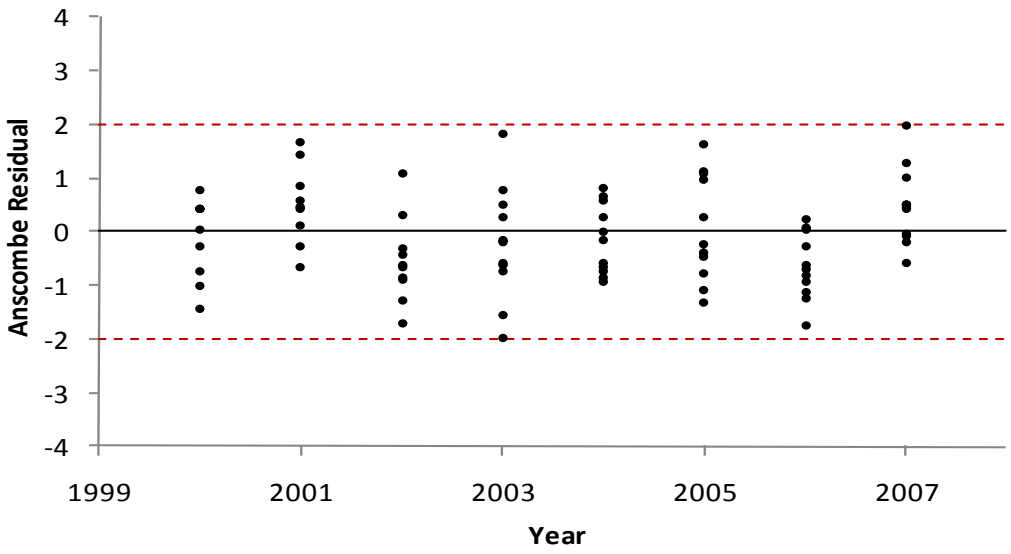



Figure 4.4 Anscombe residuals based on the best available population reconstruction model i.e., $McS_A$ for martens in Michigan, 2000–2007.

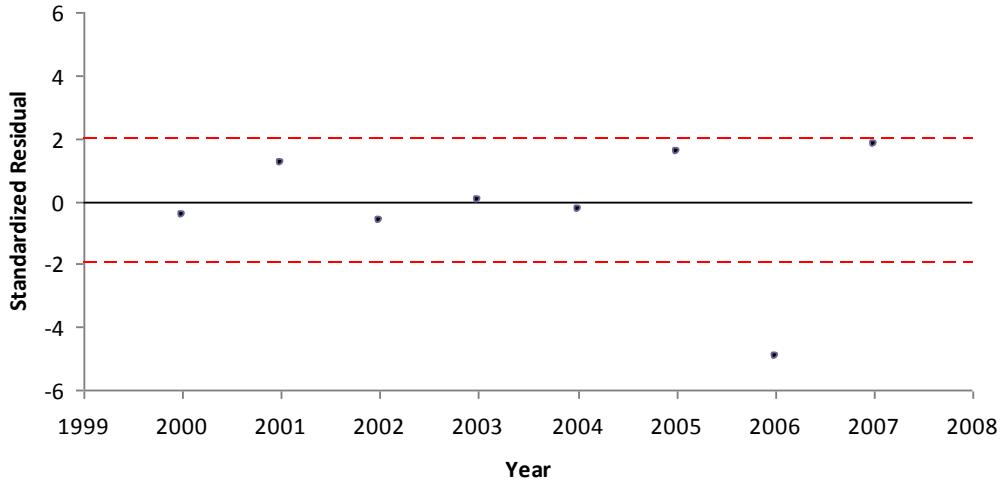



Figure 4.5. Standardized residuals for the errors $\hat{\varepsilon}_i$ in survey estimates of trapping effort (i.e., trap nights) from the best available population reconstruction model i.e., $McS_A$, for martens in Michigan, 2000–2007.

For fisher, the $McS_{0.5,1.5,2.5+}$ model was the best available model based on likelihood ratio tests and AIC criteria (Table 4.7, Table 4.8). Residual analysis did not suggest a lack of fit for the model (Figure 4.8, Figure 4.9). Model $McS_{0.5,1.5,2.5+}$ was therefore selected for the fisher population reconstruction. Differences in annual abundance were generally less than 100 animals between models all of the models tested, with model $McS_{0.5,1.5,2.5+}$ estimating the second highest annual abundance.

All of the fisher models tested estimated a juvenile survivorship of one. Obviously this is unlikely to be the true juvenile survivorship. Therefore, a sensitivity analysis was performed and a minimum chi-square estimator of $S_{0.5}$ was derived based on the goodness of fit of the age at harvest data. The chi-square statistic was minimized at a value of $S_{0.5} = 0.704$; all other parameters were estimated by maximum likelihood estimation under that constraint.

The downward population trend for Michigan fishers was estimated to be relatively precipitous, with annual abundance decreasing from a high of $\hat{N} = 2557.5 \quad \text{SE} = 1657.1$ in 1996 to a low of $\hat{N} = 760.1 \quad \text{SE} = 533.4$ in 2007 (Table 4.6, Figure 4.6). Annual harvest probabilities were higher than those of martens, sharing an increasing trend, with a low of 0.18 in 2000 to a high of 0.37 in 2006 (Figure 4.2). The annual recruitment trend in fishers showed a strong decline during the 12 years of population reconstruction unlike that of martens (Figure 4.3, Figure 4.7). Point deletion sensitivity analysis indicates, for martens and fishers alike, the parameter estimates are fairly sensitive to the number of years of data. However the trends remain the same and are robust to varying years of data (Figure 4.11).

Table 4.7 Log-likelihood and Akaike information criterion (AIC) values for alternative population reconstruction models for fishers in the Upper Peninsula, Michigan, 1996-2007. Model $McS_{0.5,1.5,2.5+}$ was selected by AIC (Burnham and Anderson 2002) (* indicates chosen model).

| Model | ln *L* | No. of model parameters | AIC |
|---|---|---|---|
| $McS$ | -357.74 | 47 | 809.48 |
| $McS_{0.5,1.5+}$ | -355.04 | 48 | 806.08 |
| $McS_{0.5,1.5,2.5+}$* | -349.53 | 49 | 797.07 |
| $McS_{A}$ | -345.18 | 55 | 800.35 |
| $Mc_{0.5,1.5+}S$ | -355.30 | 48 | 806.60 |

Table 4.8. Likelihood ratio tests (LRTs) comparing alternative nested population reconstruction models for fishers in the Upper Peninsula, Michigan, 1996–2007 (* indicates chosen model).

| Likelihood ratio tests | | | |
|---|---|---|---|
| Full – Reduced | chi-square | df | *P* |
| $McS_{0.5,1.5+}$ vs. $McS$ | 5.3980 | 1 | 0.0201 |
| $McS_{0.5,1.5,2.5+}$ vs. $McS_{0.5,1.5+}$ | 11.0140 | 1 | 0.0009 |
| $McS_{A}$ vs. $McS_{0.5,1.5,2.5+}$* | 8.7160 | 6 | 0.1902 |
| $Mc_{0.5,1.5+}S$ vs. $McS$ | 4.8800 | 1 | 0.0272 |

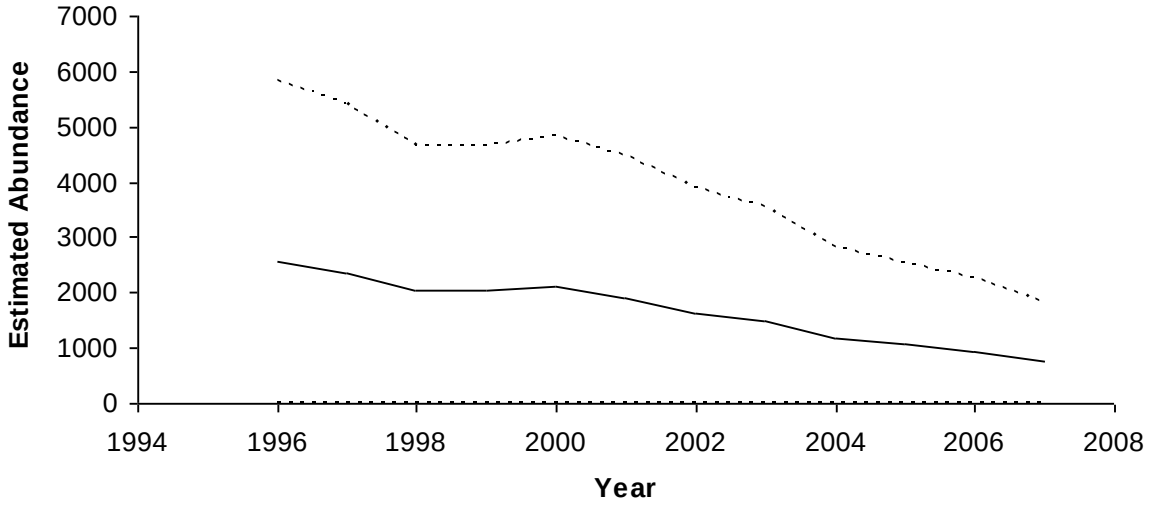



Figure 4.6. Annual trend in abundance of fishers in Michigan, 1996–2007, based the on best available population reconstruction model i.e., $McS_{0.5,1.5,2.5+}$ , along with associated 95% confidence intervals. The lower asymptotic confidence bound is zero.

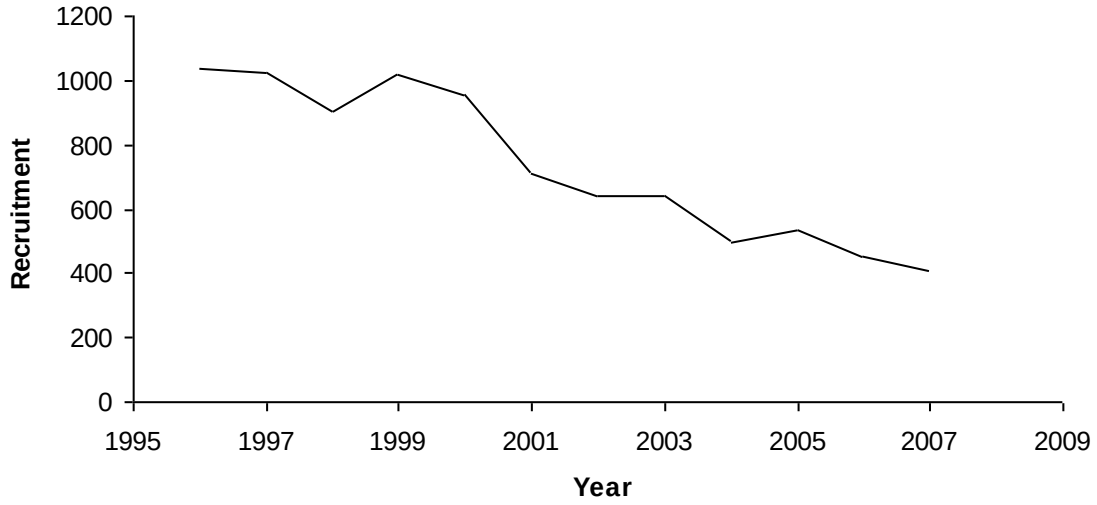



Figure 4.7. Annual trend in recruitment of fishers into the trapping population in Michigan, 1996–2007, based on the best available population reconstruction model i.e., $McS_{0.5,1.5,2.5+}$ .

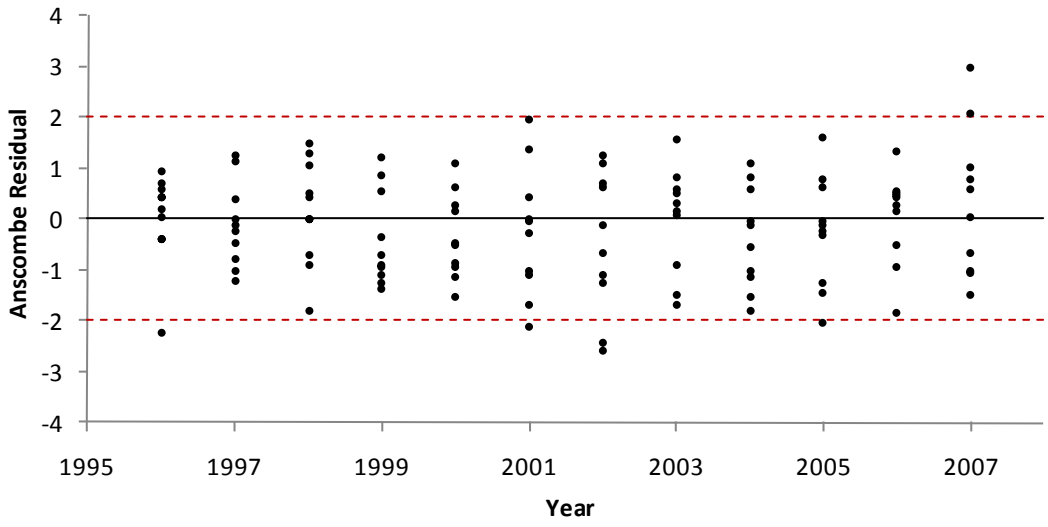



Figure 4.8. Anscombe residuals based on the best available population reconstruction model, i.e., $McS_{0.5,1.5,2.5+}$ for fishers in Michigan, 1996–2007.

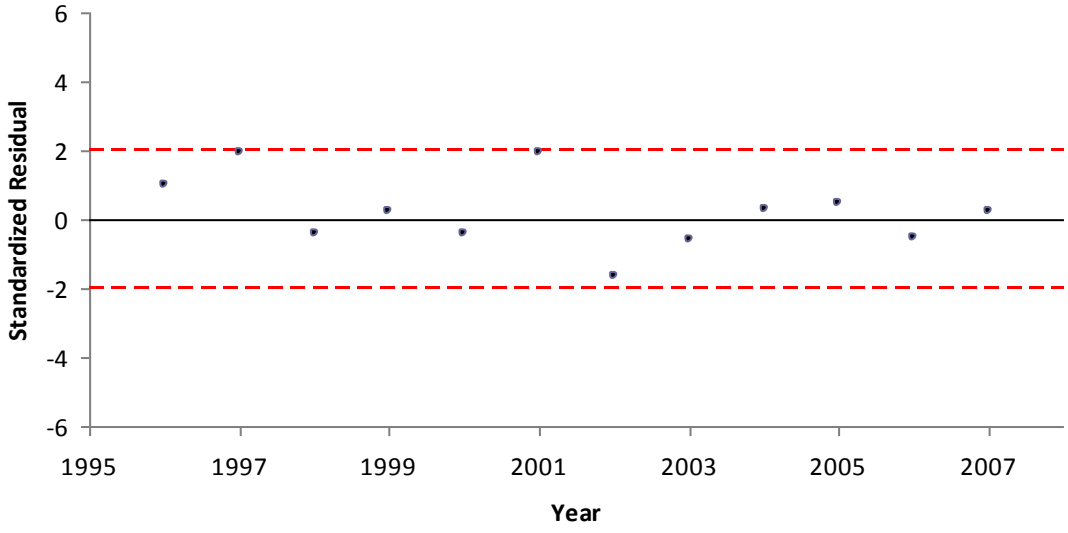



Figure 4.9. Standardized residuals for the errors $\hat{\varepsilon}_i$ in survey estimates of trapping effort (i.e., trap days) from the selected population reconstruction model i.e., $McS_{0.5,1.5,2.5+}$, for fishers in Michigan, 1996–2007.

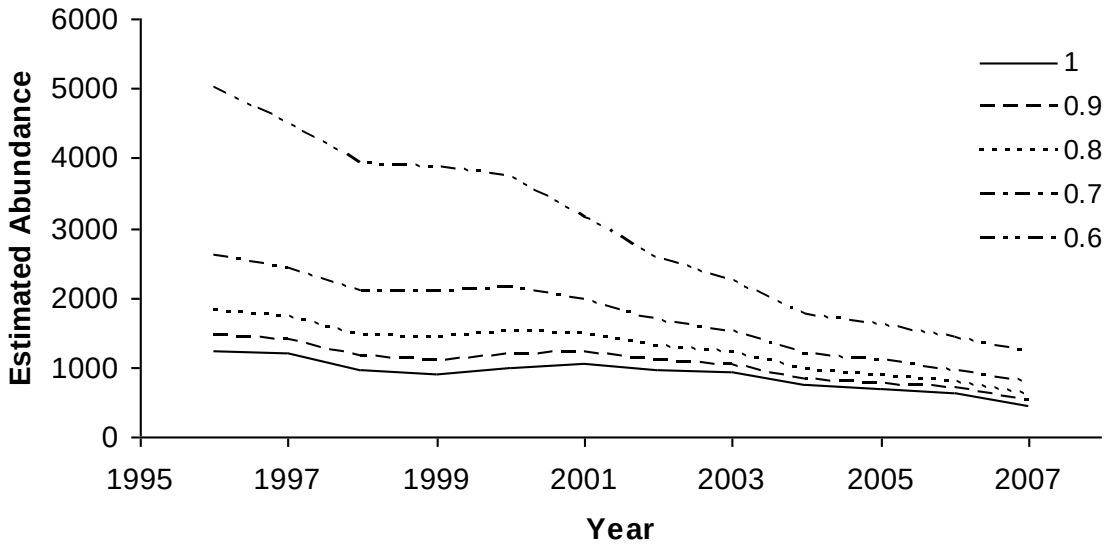



Figure 4.10. Annual abundance estimates with varying juvenile survival rates, for fishers in Michigan, 1996–2007.

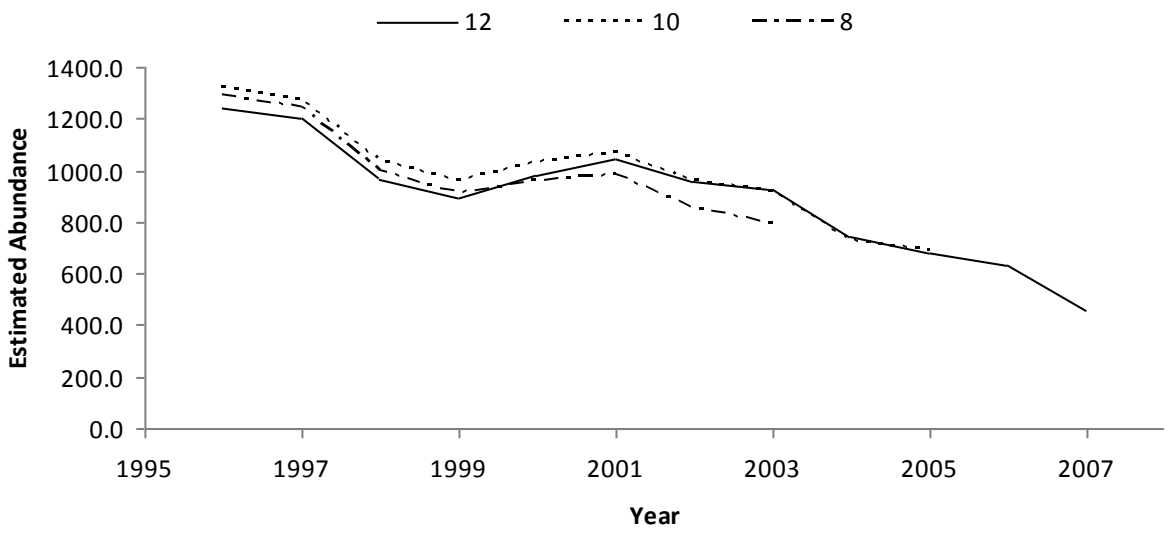



Figure 4.11. Annual abundance estimates with varying years of data for fishers in Michigan, 1996–2007, based on the point deletion sensitivity analysis.

## 4.5 Discussion

Use of SPR suggests that populations of martens and fishers are declining in Michigan's Upper Peninsula, a finding not clearly evidenced using more traditional indices of harvest. For example, sex ratios of harvested martens and fishers in this study were at least 2.7 M:1 F and 2.0 M:1 F annually, respectively. This is much higher than parity or a sex ratio skewed toward females that may result in declining populations (Strickland 1994, Douglas and Strickland 1987). Similarly, harvested marten populations with juvenile:female ($\geq$1.5 years old) ratios exceeding 3:1 are considered stable or increasing (Strickland and Douglas 1987); annual marten harvest ratios in Michigan were 1.4-3.6:1 (mean = 2.7:1). In contrast, some traditional indices of harvest suggested marten and fisher populations were potentially declining. For example, trapping effort for martens increased almost fivefold through 2006 while harvest increased only slightly more that twofold. Similarly, trapping effort for fisher increased threefold between 1996 and 2007 while the registered harvest declined 40% during this same period. Also, the annual ratio of juvenile:females $\geq$2.5 year old fishers ranged from 2.2-6.1:1, generally lower than the 6-8:1 ratio reported to maintain a stable population (Douglas and Strickland 1987, Strickland 1994). Inconsistencies in association among these traditional harvest indices and estimates of harvest obtained from SPR emphasize the need to obtain reliable and defensible population estimates, including estimates of precision. Although potentially a useful first approximation, my results draw into question the reliability of these indices as the sole technique to monitor the effects of harvest on game populations.

Given the demographic trends I observed, current harvest levels for martens and fishers in Michigan appear unsustainable. Martens and fishers are highly vulnerable to

trapping and thus susceptible to overharvest when compared with other furbearing species. However, season lengths, harvest quotas, and registered harvests for martens and fishers in Michigan are generally conservative when compared to nearby jurisdictions with harvest seasons. Although no formal population goals have been established for martens and fishers in Michigan, the goal of the Michigan Department of Natural Resources is to maintain sustainable harvests of these species with stable or increasing populations. Changes to harvest strategies, including changes in season length, timing of season, harvest limits, season or area closures or a combination of these strategies, should be considered. However, there are uncertainties in how these changes in season structure will ultimately influence harvest and a better understanding of the relationships between take and regulations would be beneficial. Alternatively, marten and fisher harvest quotas based on more spatially refined harvest units and habitat suitability could be used to refine distribution of harvest for these species.

Continued population monitoring of marten and fisher populations in Michigan is warranted and refinements to data collection and new information would assist in that effort. There are several ways in which auxiliary data used in this study could be enhanced or increased to improve demographic estimates. Improved estimates of trapper effort through promoting increased return rates of surveys or requesting trappers to maintain log books of trapping effort, increasing the proportion of harvested animals that are aged, and obtaining estimates of trap nights for fisher harvest would facilitate model performance. The inability to estimate juvenile survivorship in the fisher model is a symptom of how sensitive population reconstruction models can be when additional auxiliary demographic studies are unavailable. A sensitivity analysis in the case of the fishers indicates that juvenile survival is

an important parameter (Figure 4.10). An auxiliary study to estimate juvenile survival would therefore improve model performance. Any additional study that allows for the estimation of an annual abundance or capture probability independent of the age-at-harvest data could also greatly improve the robustness of the parameter estimates (Chapter 5). For example, the use of radio-telemetry studies has been demonstrated to improve model performance and can be used jointly with harvest effort to enhance population estimates (Broms et. al. 2010, Chapter 5). Implementing one or more of these recommendations over several years would also facilitate use of more robust models, including age-specific survival and vulnerability models for both species.

A number of state jurisdictions have been involved in legal disputes with various public groups which support banning of trapping (see Batcheller et al. 2000). Although few of these disputes have emphasized population declines of harvested species, management agencies need to ensure long-term persistence of furbearers and other harvested species. Use of SPR can provide managers with a more credible and defensible means for developing harvest strategies to ensure long-term species persistence and recreational opportunities. The use of indices as the sole metric of population status and trend is unacceptable in circumstances where available data are amenable to more robust quantitative analysis. In many cases, state agencies already routinely collect age-at-harvest data and have some measure of hunter effort. With some further consideration and collection of auxiliary information over time, most agencies could make effective use of SPR models. The impetus for robust assessment of carnivore population trends has never been greater as continued pressure from the public and anti-trapping community continues to mount. The use of SPR offers one defensible approach that has distinct advantages to commonly used indices.

Further, SPR offers a bridge between extensive data collection procedures, such as age-at-harvest, and intensive, small-scale techniques, such as mark-recapture (Amstrup et al. 2005), distance sampling (Buckland et al. 2001), and sightability models (White and Shenk 2001).

### 4.6 Management Implications

Continued monitoring of martens and fishers in Michigan is necessary, given the estimated population declines. Additionally, managers should evaluate whether overtrapping or some other factor is responsible for the decline of both populations. Given the successful application of SPR models, I recommend its use for martens and fishers in Michigan and continued collection of age-at-harvest data along with auxiliary data, such as radiotelemetry. Continued data collection might also permit modeling of both age-specific survivals and harvest in the same model, which was prevented in our evaluation because of the lack of auxiliary information. Collection of effort data in terms of trap-nights instead of trap-days for fishers might also improve model fit. Given their failure to detect population declines, I do not encourage the continued use of some common population indices, such as sex and age ratios for furbearers, as the only technique to assess status and trends. The successful application of SPR methods further demonstrates the general robustness of this technique for many harvested populations. Statistical population reconstruction offers a useful alternative to managers interested in demographic assessments over large geographic area when age-at-harvest and other auxiliary data are available.

# Chapter 5: Sensitivity Analysis of Statistical Population Reconstruction—A Black-Tailed Deer Example

## 5.1 Introduction

Statistical population reconstruction (SPR) is a powerful tool for informing wildlife management. The technique has been used extensively in fisheries management to monitor harvested populations. Basic life history reconstruction models have been used in different forms since 1949 in wildlife management, to a lesser extent. The method has been advanced to not only estimate population parameters but their variances as well. This newest form of SPR (Skalski et al. 2005) is quickly becoming the favored method to monitor harvested populations because of its flexibility and power. However, the flexible model structure can quickly become very complex. When using a complex model structure one must evaluate model adequacy and goodness-of-fit. Traditionally, model goodness-of-fit is evaluated through residual analysis and chi-square lack-of-fit tests. While sometimes helpful, these evaluation methods are not always adequate for SPR. In this chapter, I suggest a method for evaluating SPR models. I thoroughly examine how results from SPR models change with varying amounts of age-at-harvest and auxiliary input data. I examine cases with full age-class information as well as those with limited age-class information (pooling).

## 5.2 Methods

I developed a point deletion sensitivity analysis (PDSA) to evaluate SPR with varying years of data. Point deletion sensitivity analysis evaluates how annual abundance estimates change as the number of years of input data change. In PDSA, data are removed one year at a time from either the historic or recent end of the data set. Once the annual harvest data are removed, essentially creating a new data set, the age-at-harvest models are refit and

abundance re-estimated. Here data are removed in order to determine how sensitive the resulting model estimates are to varying years of input data. The removal of historic data is not unheard of; Hilborn and Walters (1992) suggest that one may want to truncate the historic years of long data sets so that the oldest data do not hide more recent trends.

The results of PDSA are evaluated both graphically and statistically. I developed a relative absolute deviance (RAD) statistic to measure the effect of data deletion on annual abundance estimates. The statistic is calculated as:

$$\mathrm{RAD}_{ik} = \frac{|A_i - T_{ik}|}{A_i},$$

where

$A_i$ = abundance estimate in year *i* with all data,

$T_{ik}$ = abundance estimate in year *i* from truncated data subset *k*,

for each truncated annual abundance. Relative absolute deviation can then be averaged across all abundance estimates in a data set, resulting in a single measure of variation in annual abundance due to data deletion.

$$\overline{\mathrm{RAD}}_{ik} = \frac{1}{y}\sum_{i=1}^{y}\frac{|A_i - T_{ik}|}{A_i}$$

These statistics can also be averaged across all data subsets to get a single overall measure of how robust the SPR is to varying years of data deletion.

$$\overline{\overline{\mathrm{RAD}}}_{ik} = \frac{1}{\sum yK}\sum_{k=1}^{K}\sum_{i=1}^{y}\frac{|A_i - T_{ik}|}{A_i}$$

These statistics are only comparable within the same data set, with the same number of estimated annual abundances and data subsets.

The PDSA was performed on an age-at-harvest data set collected from a black-tailed deer population in Washington state from 1979 to 2002 (Gilbert et. al. 2007, Skalski et. al. 2007, Chapter 3). The original data set included 24 years of age at harvest information along with a measurement of annual hunter effort. For the PDSA 14 data subsets were created, seven subsets removing 0,2,4,6,8,10,12 years of historic data and seven subsets 0,2,4,6,8,10,12 removing years of recent data. This data set was evaluated first with the full complement of age-class data. It was then reanalyzed with age classes 0.5, 1.5 and 2.5+, pooling all of the older age classes, analogous to the pooling presented in Chapter 3.

## 5.3 Full Age-Class Data with No Auxiliary Likelihood

### 5.3.1 Likelihood Model

Statistical population reconstruction with complete age-class information was based on a joint likelihood model of the form

$$L_{\text{Joint}} = L_{\text{Age-at-harvest}} \cdot L_{\text{Effort}}, \tag{5.1}$$

the same as Skalski et al. (2007) and Chapter 3. The age-at-harvest likelihood for the analysis of full age class data was of the form

$$L_{\text{Age-at-harvest}} = \prod_{i=1}^{24} \cdot L_{i1} \prod_{j=2}^{13} L_{1j} \tag{5.2}$$

where $L_{ij}$ was the likelihood describing the age-at-harvest data for the cohort entering the study in year $i$ $i = 1,\ldots,24$ at age class $j$ $j = 1,\ldots,13$ and was identical to that used in Skalski et al (2007). Let

$h_{ij}$ = number of females harvested in year $i$ $i = 1,\ldots,24$ at age class $j$ $j = 1,\ldots,13$ ,

$N_{ij}$ = female deer abundance in year $i$ $i = 1,\ldots,24$ at age class $j$ $j = 1,\ldots,13$ ,

$S$ = natural survival probability for all females,

$c_{0.5}$ = vulnerability coefficient for young-of-year females (i.e., age class 0.5),

$c_{1.5+}$ = vulnerability coefficient for females 1.5 years of age or older,

$f_i$ = hunter effort in year $i$ $i = 1, \ldots, 24$ , such that.

$$L_{i1} = \binom{N_{i,1}}{h_{i,1}, h_{i+1,2....}} p_{i,J}{}^{h_{i,1}} \quad 1 - p_{i,J} \quad Sp_{i+1,A}{}^{h_{i+1,2}} \quad 1 - p_{i,J} \quad 1 - p_{i+1,A} \quad S^2 p_{i+2,A}{}^{h_{i+2,3}} \ldots$$

and

$$L_{1j} = \binom{N_{1,j}}{h_{1,j}, h_{2,j+1....}} p_{1,A}{}^{h_{1,j}} \quad 1 - p_{1,A} \quad Sp_{2,A}{}^{h_{2,j+1}} \quad 1 - p_{1,A} \quad 1 - p_{2,A} \quad S^2 p_{3,A}{}^{h_{3,j+2}} \ldots$$

where

$$p_{i,J} = 1 - e^{-c_{0.5} f_i}$$

$$p_{i,A} = 1 - e^{-c_{1.5+} f_i} \quad .$$

Construction of $L_{21}, \ldots, L_{Y1}$ was analogous to that of $L_{i1}$ incremented for subsequent years. Construction of $L_{12}, \ldots, L_{1A}$ was analogous to that of $L_{1j}$ incremented for subsequent age classes. The catch-effort likelihood to estimate vulnerability coefficients and in turn capture probabilities was based on catch-per-unit-effort within a year, where

$$L_{\text{Catch-effort}} = \prod_{i=1}^{24} \binom{N_{i1}}{h_{i1}} 1 - e^{-c_{0.5} f_i}{}^{h_{i1}} \quad e^{-c_{0.5} f_i}{}^{N_{i1} - h_{i1}}$$
$$\cdot \prod_{i=1}^{24} \binom{\sum_{j=2}^{3} N_{ij}}{\sum_{j=2}^{3} h_{ij}} 1 - e^{c_{1.5+} f_i}{}^{\sum_{j=2}^{3} h_{ij}} \quad e^{-c_{1.5+} f_i}{}^{\sum_{j=1}^{3} N_{ij} - h_{ij}} \quad . \tag{5.3}$$

Initial abundance levels (i.e., $N_{11}, N_{12}, N_{13}, N_{21}, \ldots, N_{24,1}$) were estimated directly from the likelihood model, while the remaining abundance levels were based on the invariance property of the maximum likelihood estimation, where

$$\hat{N}_{ij} = N_{i-1,j-1} e^{-cf_i} S \; .$$

Total annual abundance for any year was the sum of the within-year cohort abundance levels.

### 5.3.2 Sensitivity Analysis Results

Based on the PDSA, the black-tailed deer population reconstruction was very sensitive to the number of years of data input (Table 5.1). I removed historic data and the abundance estimates in 2002 (the last year of the reconstruction) ranged from 1,644 females (2 years removed) to over one million females (12 years removed), with the full data estimate being 1,721 females (Figure 5.1). The relative absolute deviation from the full data set ranged from 7.5% to 66,998.5% with an average of 13,513.5% when historic data were removed (Table 5.1). I removed recent data and the abundance estimates for 1979 (the first year of the reconstruction) ranged from 3662 females (0 years removed) to 519 females (6 years removed) (Figure 5.1). The relative absolute deviation from the full data set ranged from 79.9% to 25.5% with an average of 57.5% when recent data was removed (Table 5.1).

These drastic changes in annual abundance estimates suggest that this population reconstruction was highly sensitive to the number of years of data available. Annual abundance estimates changed dramatically depending on the number of available years of data. The same abundance trends were evident regardless of the degree of data deletion (Figure 5.1).

Table 5.1. Relative absolute deviation $\overline{\text{RAD}}$ statistics from a point deletion sensitivity analyses performed on a statistical population reconstruction of female black-tailed deer. Models had either, no auxiliary data, an auxiliary that estimated abundance (1979 or 2002) or an auxiliary that estimated capture probability (1979 or 2002), either with (a) historic or (b) recent data removed.

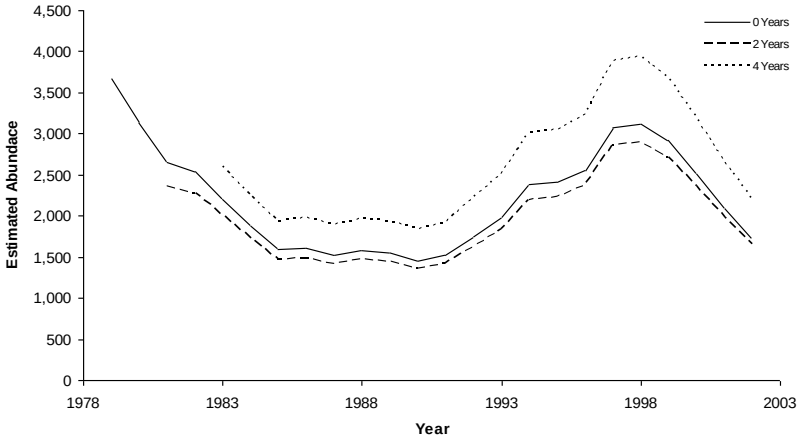
a. Historic data removed

| Years removed | No Auxiliary | Abundance auxiliary | | | | Vulnerability coefficient auxiliary | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | CV = 0.05 | CV = 0.125 | CV = 0.25 | CV = 0.50 | CV = 0.05 | CV = 0.125 | CV = 0.25 | CV = 0.50 |
| 2 | 7.50% | 3.18% | 3.40% | 4.39% | 6.12% | 0.93% | 0.96% | 1.49% | 3.65% |
| 4 | 24.94% | 3.35% | 1.76% | 3.07% | 9.71% | 1.80% | 1.55% | 1.74% | 5.82% |
| 6 | 152.35% | 0.34% | 2.77% | 10.81% | 27.10% | 1.25% | 0.95% | 2.71% | 14.21% |
| 8 | 23943.66% | 1.52% | 4.33% | 22.25% | 69.35% | 2.89% | 1.75% | 7.48% | 35.81% |
| 10 | 14386.01% | 2.77% | 5.52% | 15.83% | 40.43% | 1.79% | 2.33% | 1.79% | 17.91% |
| 12 | 66998.46% | 2.12% | 6.32% | 21.97% | 69.13% | 2.16% | 1.88% | 4.44% | 31.29% |
| Mean | 13513.50% | 2.17% | 3.75% | 11.70% | 32.57% | 3.05% | 1.48% | 1.71% | 16.04% |

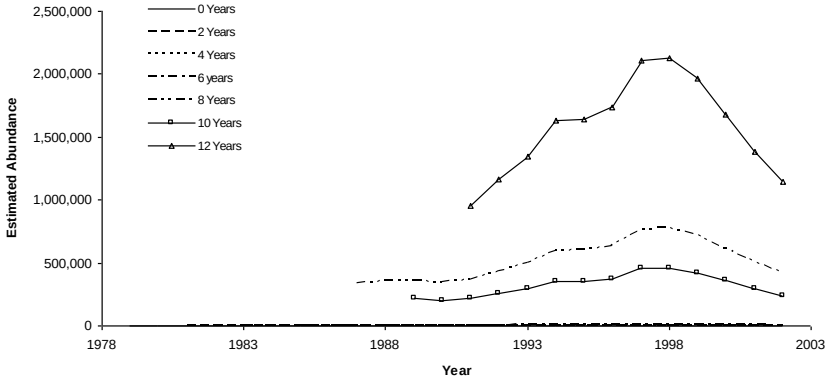
b. Recent data removed

| Years removed | No Auxiliary | Abundance auxiliary | | | | Vulnerability coefficient auxiliary | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | CV = 0.05 | CV = 0.125 | CV = 0.25 | CV = 0.50 | CV = 0.05 | CV = 0.125 | CV = 0.25 | CV = 0.50 |
| 2 | 53.50% | 1.75% | 4.77% | 18.69% | 39.50% | 2.07% | 3.89% | 12.07% | 32.47% |
| 4 | 64.45% | 1.11% | 5.69% | 21.76% | 47.37% | 1.16% | 3.23% | 13.47% | 38.49% |
| 6 | 79.97% | 1.60% | 5.17% | 19.49% | 47.72% | 1.65% | 2.30% | 11.05% | 36.42% |
| 8 | 63.59% | 3.65% | 6.22% | 14.32% | 35.38% | 2.21% | 2.33% | 6.30% | 22.24% |
| 10 | 45.33% | 5.57% | 6.74% | 10.48% | 22.44% | 4.57% | 5.36% | 4.28% | 9.13% |
| 12 | 25.57% | 1.26% | 1.65% | 3.48% | 10.57% | 2.78% | 4.16% | 3.32% | 1.23% |
| Mean | 57.50% | 2.36% | 5.15% | 15.83% | 36.10% | 2.27% | 3.47% | 9.16% | 25.86% |

a. 0, 2 and 4 years of historic data removed




b. 6, 8, 10 and 12 years of historic data removed




c. 0, 2, 4, 6, 8, 10 and 12 years of recent data removed

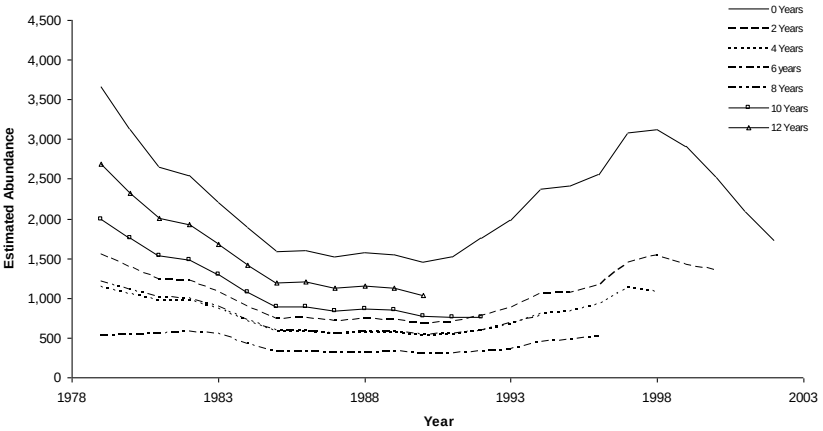



Figure 5.1. Annual abundance trends from the statistical population reconstruction of female black-tailed deer, with varying numbers of historic (a and b) and recent (c) years of age-at-harvest data removed.

I examined the residuals for all 14 data subsets (seven subsets removing 0,2,4,6,8,10,12 years of historic data and seven subsets 0,2,4,6,8,10,12 removing years of recent data) (Figure 5.2). All of the residual plots looked nearly identical; there were no discernable trends, no additional points fell outside +/–2, and the dispersion about 0 was about the same. I examined the residuals to determine if I could have diagnosed the abundance estimate problem through residual analysis. I would not have been able to diagnose the unreasonable abundance estimate from the residuals alone. In addition, the chi-square scale parameter used by Skalski et al (2007) to account for lack of model fit did not differ greatly between data subsets (Table 5.2). This means that an investigator could perform a statistical population reconstruction, and residual analysis, and not be able to discern a problem.

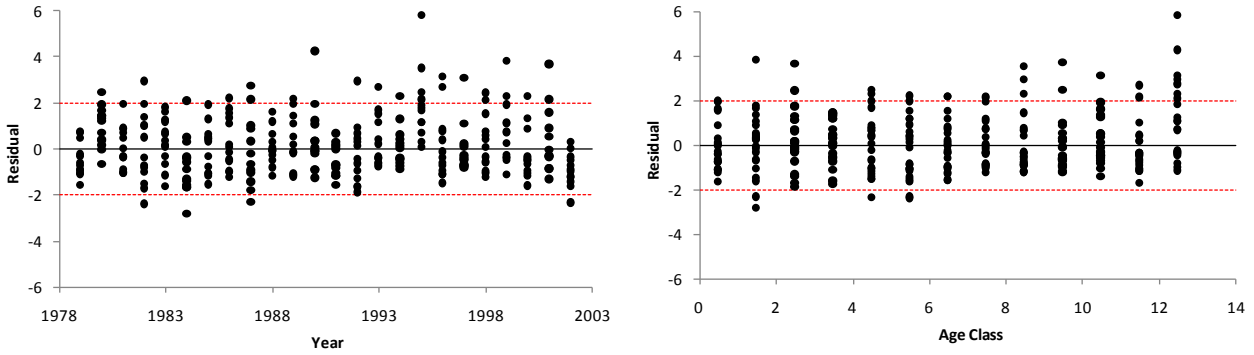
The above PDSA suggests population reconstruction based solely on age-at-harvest and catch effort data are very sensitive to the number of years of data collection. Investigators should be very cautious when interpreting statistical population results in these circumstances and PDSA should always be performed.

## 5.4 Full Age-Class Data with an Auxiliary Likelihood

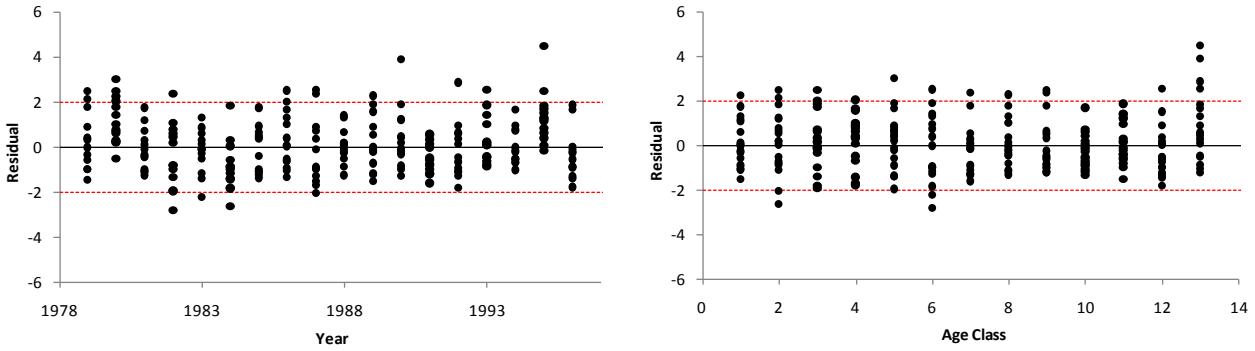
The above results lead to two conclusions. One, it is necessary to perform some sort of point deletion sensitivity analysis or other non-residual based form of model sensitivity evaluation. Two, auxiliary data may help statistical population reconstruction to produce more reliable results. To explore whether auxiliary data improved model accuracy, I simulated auxiliary data in order to answer three questions. What is the effect of the type of auxiliary data on the stability of population reconstruction? How precise do the auxiliary information need to be?

What effect does the timing of the auxiliary study have on the stability of population reconstruction?

a. All data




b. 6 years of recent data removed




c. 12 years of recent data removed

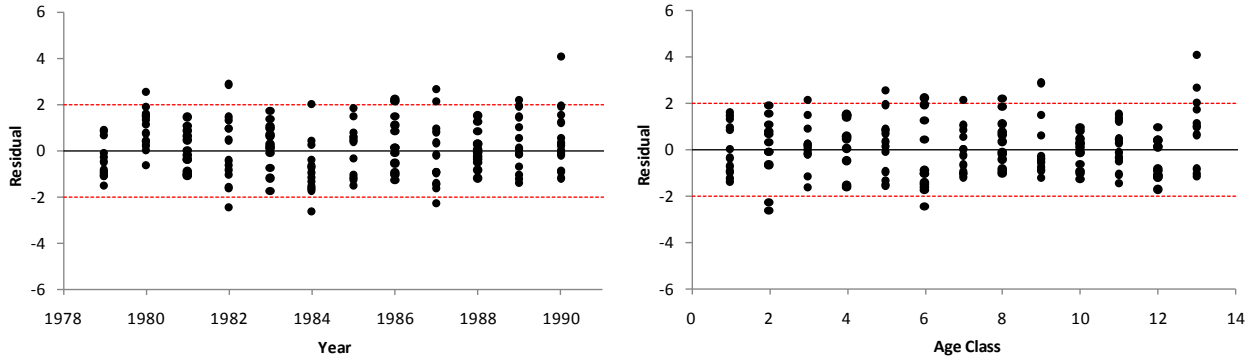



Figure 5.2. Standardized residuals plotted by year and age class from a point deletion sensitivity analyses of female, black-tailed deer, age-at-harvest data with (a) all data, (b) 6 years of recent data removed, and (c) 12 years of recent data removed.

Table 5.2. Scale parameters from point deletion sensitivity analyses with either historic or recent years removed, performed on a statistical population reconstruction of female black-tailed deer.

| | Scale parameter | |
|---|---|---|
| Years removed | Historic data removed | Recent data removed |
| 0 | 1.380 | 1.380 |
| 2 | 1.373 | 1.325 |
| 4 | 1.366 | 1.309 |
| 6 | 1.362 | 1.314 |
| 8 | 1.366 | 1.264 |
| 10 | 1.424 | 1.276 |
| 12 | 1.583 | 1.297 |

### 5.4.1 Likelihood Model

Auxiliary data were simulated and incorporated into the original model structure resulting in a joint likelihood model of the form:

$$L_{\text{Joint}} = L_{\text{Age-at-harvest}} \cdot L_{\text{Catch-effort}} \cdot L_{\text{Simulated auxiliary}} \tag{5.4}$$

Studies were simulated to estimate parameter values at varying levels of precision. The auxiliary data were simulated to produce parameter estimates with CV's of 0.05, 0.125 and 0.250. The CV values of 0.05, 0.125 and 0.250 correspond to three levels of precision suggested by Robson and Regier (1964): research, accurate management and rough management. Two types of auxiliary data were generated; a single mark-recapture (Seber 1982:59) was simulated to estimate total annual abundance of the form:

$$L_{\text{Simulated auxiliary}} = \binom{N_i}{n_{10}, n_{01}, n_{11}} p_1 \; 1-p_2 \;^{n_{10}} \; 1-p_1 \; p_2 \;^{n_{01}} \; p_1 p_2 \;^{n_{11}}$$

$$\cdot \; 1-p_1 \; 1-p_2 \;^{N_i - n_{10} - n_{01} - n_{11}}, \tag{5.5}$$

where

$N_i$ = abundance in year i to be estimated,

$p_1$ = capture probability in first period of the study,

$p_2$ = capture probability in second period of the study,

$n_{10}$ = number of female deer caught in the first period only,

$n_{01}$ = number of female deer caught in the second period only,

$n_{11}$ = number of female deer caught in both periods.

In a single mark-recapture survey (i.e., Lincoln/Petersen index) the variance of the abundance estimate is $\text{Var}\ \hat{N} = \frac{N\ 1-p_1\ \ 1-p_2}{p_1 p_2}$. A second auxiliary study was simulated in the form of a mark-harvest study to estimate vulnerability coefficients (i.e., $c_j$ and $c_a$) of the form:

$$L_{\text{Simulated auxiliary}} = \binom{n_J}{x_j} 1-e^{-c_j f_i}\ \ ^{x_j}\ \ e^{-c_j f_i}\ \ ^{n_j-h_j} \cdot \binom{n_A}{x_a} 1-e^{-c_a f_i}\ \ ^{x_a}\ \ e^{-c_a f_i}\ \ ^{n_a-x_a}, \tag{5.6}$$

where

$n_J$ = number of marked juveniles released into the population,

$x_j$ = number of marked juveniles harvested,

$n_A$ = number of marked adults released into the population,

$x_a$ = number of marked adults harvested,

$c_j$ = vulnerability coefficient for juveniles,

$c_a$ = vulnerability coefficient for adults,

$f_i$ = hunter effort in year $i$.

Variance of the estimation of the vulnerability coefficients would depend on the mark-harvest sample size ($n_J$ and $n_A$) and the overall probability of harvest.

When historic data were removed, the auxiliary data were simulated to estimate abundance or vulnerability coefficients in 2002. When the most recent data were removed, auxiliary data were simulated to estimate abundance or vulnerability coefficients in 1979. Auxiliary data were also simulated in years 1990 and 1991 to determine if the timing of an auxiliary study changed its effectiveness. For each simulated auxiliary study, a relative absolute deviation statistic $\overline{\text{RAD}}$ was calculated.

### 5.4.2 Sensitivity Analysis Results

I removed historic data and included a simulated auxiliary study to estimate abundance in 2002 (Table 5.3). The 2002 abundance estimates ranged from 1719 to 1740 females with a simulated auxiliary CV of 0.05, 1706 to 1829 females with a simulated auxiliary CV of 0.125, and 1715 to 2178 females with a simulated auxiliary CV of 0.250 (Figure 5.3). The $\overline{\text{RAD}}$ ranged from 2.2% with an auxiliary CV of 0.05 to 32.6% with an auxiliary CV of 0.5 (Table 5.1). I also removed historic data and included a simulated auxiliary study in 2002 to estimate the vulnerability coefficients (Table 5.4). The 2002 abundance estimates ranged from 1693 to 1767 females with a simulated auxiliary CV of 0.05, 1666 to 1783 females with a simulated auxiliary CV of 0.125, and 1674 to 1887 females with a simulated auxiliary CV of 0.250 (Figure 5.4). The $\overline{\text{RAD}}$ ranged from 1.7% with an auxiliary CV of 0.05 to 16.0% with an auxiliary CV of 0.5 (Table 5.1) When no auxiliary data was included the average deviation was 13,513.5% (Table 5.1).

Table 5.3. Auxiliary data to estimate abundance in 1979 (recent data removed) or 2002 (historic data removed).

| CV | Historic data removed | | | Recent data removed | | |
|---|---|---|---|---|---|---|
| | $N$ | $P_1$ | $P_2$ | $N$ | $P_1$ | $P_2$ |
| 0.05 | 1720 | 0.325 | 0.325 | 3662 | 0.248 | 0.248 |
| 0.1 | 1720 | 0.194 | 0.194 | 3662 | 0.142 | 0.142 |
| 0.125 | 1720 | 0.162 | 0.162 | 3662 | 0.117 | 0.117 |
| 0.2 | 1720 | 0.108 | 0.108 | 3662 | 0.076 | 0.076 |
| 0.25 | 1720 | 0.088 | 0.088 | 3662 | 0.062 | 0.062 |
| 0.3 | 1720 | 0.074 | 0.074 | 3662 | 0.052 | 0.052 |
| 0.4 | 1720 | 0.057 | 0.057 | 3662 | 0.040 | 0.040 |
| 0.5 | 1720 | 0.046 | 0.046 | 3662 | 0.032 | 0.032 |

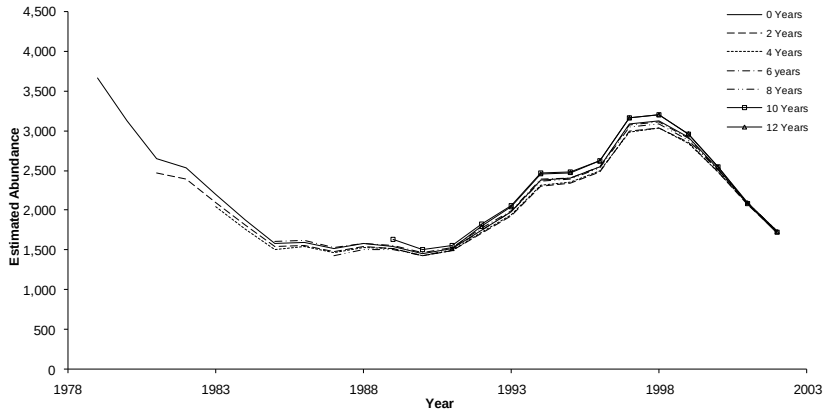
Table 5.4. Auxiliary data to estimate vulnerability coefficients in 1979 (recent data removed) or 2002 (historic data removed).

| | Historic data removed | | | | | | Recent data removed | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CV | $P_j$ | $n_j$ | $x_j$ | $P_a$ | $n_a$ | $x_a$ | $P_j$ | $n_j$ | $x_j$ | $P_a$ | $n_a$ | $x_a$ |
| 0.05 | 0.013 | 30488 | 395 | 0.024 | 16336 | 390 | 0.015 | 26200 | 394 | 0.028 | 14006 | 389 |
| 0.1 | 0.013 | 7622 | 99 | 0.024 | 4084 | 98 | 0.015 | 6550 | 98 | 0.028 | 3501 | 97 |
| 0.125 | 0.013 | 4878 | 63 | 0.024 | 2614 | 62 | 0.015 | 4192 | 63 | 0.028 | 2241 | 62 |
| 0.2 | 0.013 | 1906 | 25 | 0.024 | 1021 | 24 | 0.015 | 1637 | 25 | 0.028 | 875 | 24 |
| 0.25 | 0.013 | 1220 | 16 | 0.024 | 653 | 16 | 0.015 | 1048 | 16 | 0.028 | 560 | 16 |
| 0.3 | 0.013 | 847 | 11 | 0.024 | 454 | 11 | 0.015 | 728 | 11 | 0.028 | 389 | 11 |
| 0.4 | 0.013 | 476 | 6 | 0.024 | 255 | 6 | 0.015 | 409 | 6 | 0.028 | 219 | 6 |
| 0.5 | 0.013 | 305 | 4 | 0.024 | 163 | 4 | 0.015 | 262 | 4 | 0.028 | 140 | 4 |

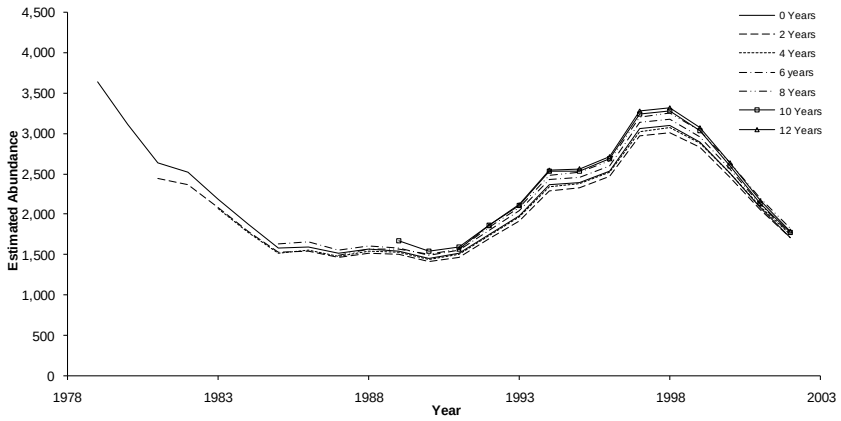
Table 5.5. Relative absolute deviation $\overline{\text{RAD}}$ statistics from a point deletion sensitivity analysis of female black-tailed deer. Comparing auxiliary studies simulated at the beginning and the end of the study (1979 and 2002) with those simulated in the center of the study (1990 and 1991).

| | Historic data removed | | | | Recent data removed | | | |
|---|---|---|---|---|---|---|---|---|
| | Abundance auxiliary | | Vulnerability coefficient auxiliary | | Abundance auxiliary | | Vulnerability coefficient auxiliary | |
| CV | 2002 | 1991 | 2002 | 1991 | 1979 | 1990 | 1979 | 1990 |
| 0.05 | 2.17% | 1.76% | 1.71% | 1.75% | 2.36% | 3.44% | 2.27% | 2.29% |
| 0.125 | 3.75% | 3.76% | 1.48% | 1.52% | 5.15% | 6.60% | 3.47% | 3.54% |
| 0.25 | 11.70% | 11.77% | 3.05% | 3.36% | 15.83% | 17.28% | 9.16% | 9.42% |

a. Auxiliary study to estimate abundance with a CV of 0.05 in year 2002




b. Auxiliary study to estimate abundance with a CV of 0.125 in year 2002




c. Auxiliary study to estimate abundance with a CV of 0.250 in year 2002

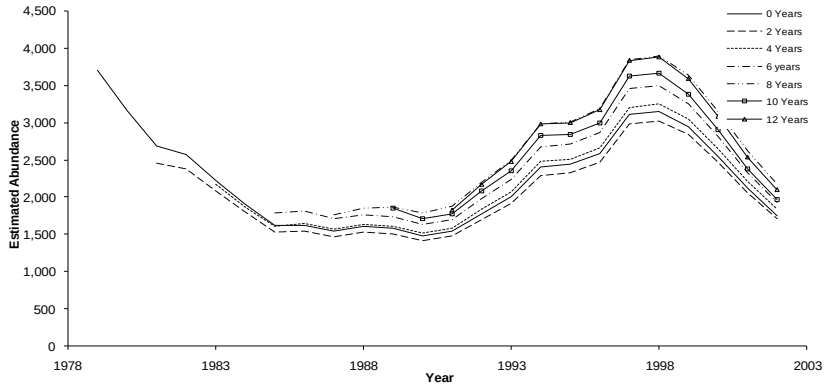
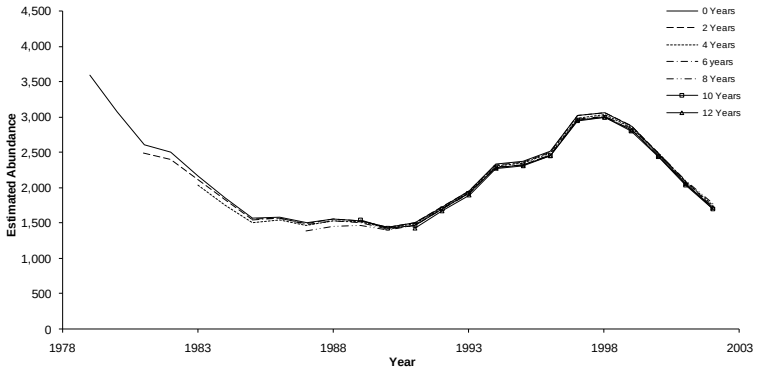
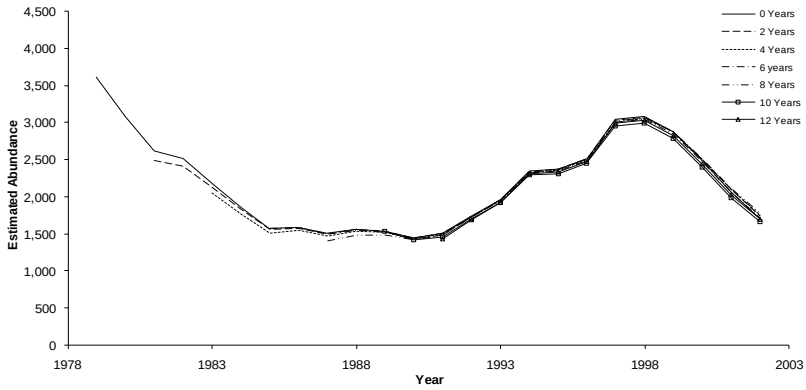



Figure 5.3. Annual abundance trends from a point deletion sensitivity analysis, historic data removed, on a statistical population reconstruction of female black-tailed deer, with a simulated auxiliary study to estimate abundance in 2002 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

a. Auxiliary study to estimate vulnerability coefficients with a CV of 0.05 in year 2002




b. Auxiliary study to estimate vulnerability coefficients with a CV of 0.125 in year 2002




c. Auxiliary study to estimate vulnerability coefficients with a CV of 0.250 in year 2002

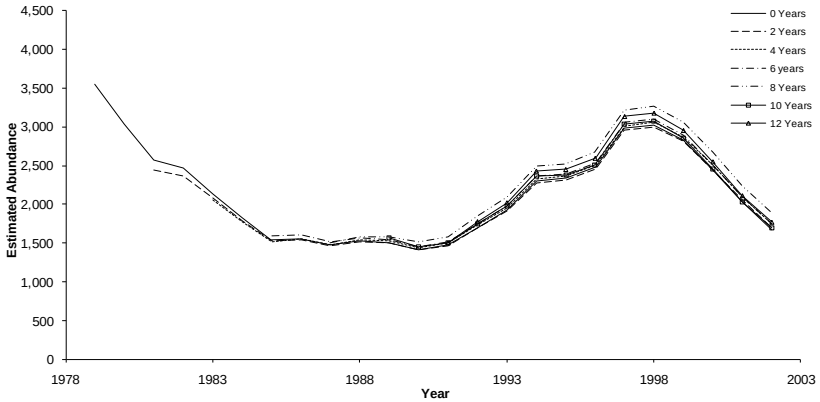
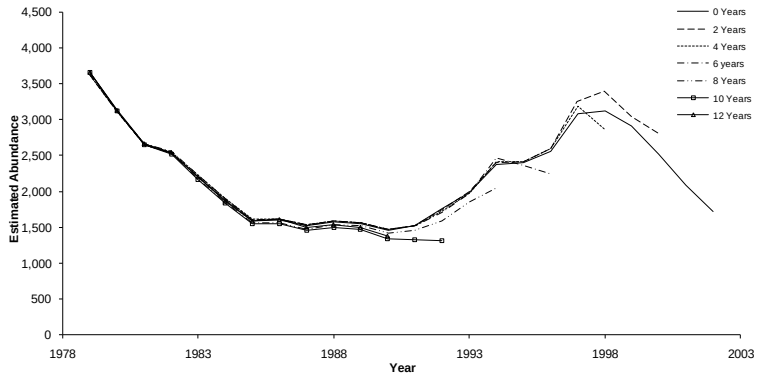



Figure 5.4. Annual abundance trends from a point deletion sensitivity analysis, historic data removed, on a statistical population reconstruction of female black-tailed deer, with a simulated auxiliary study to estimate vulnerability coefficients in 2002 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

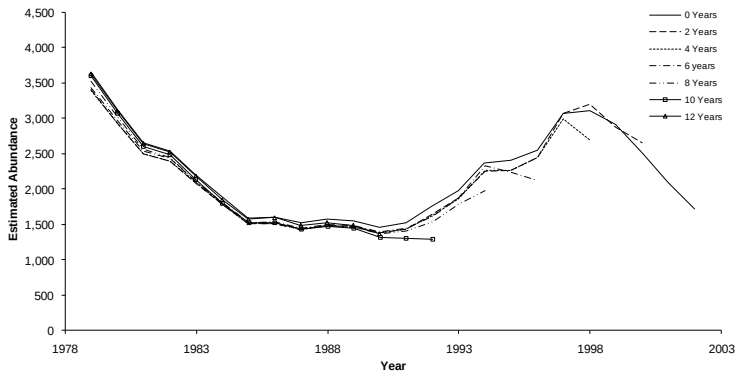
I also removed recent data and included a simulated auxiliary study to estimate abundance in 1979 (Table 5.3). The 1979 abundance estimates ranged from 3618 to 3661 females with a simulated auxiliary CV of 0.05, 3402 to 3659 females with a simulated auxiliary CV of 0.125, and 2797 to 3671 females with a simulated auxiliary CV of 0.250 (Figure 5.5). The $\overline{\text{RAD}}$ ranged from 2.4% with an auxiliary CV of 0.05 to 36.1% with an auxiliary CV of 0.5 (Table 5.1). I also removed recent data and included a simulated auxiliary study to estimate vulnerability coefficients (Table 5.4). The 1979 abundance estimates ranged from 3556 to 3905 females with a simulated auxiliary CV of 0.05, 3452 to 3943 females with a simulated auxiliary CV of 0.125, and 3029 to 3909 females with a simulated auxiliary CV of 0.250 (Figure 5.6). The $\overline{\text{RAD}}$ ranged from 2.27% with an auxiliary CV of 0.05 to 25.86% with an auxiliary CV of 0.5 (Table 5.1). When no auxiliary data were included $\overline{\text{RAD}}$ was 57.5% (Table 5.1) Auxiliary studies added in the middle of the data collection period, years 1990 and 1991 produced $\overline{\text{RAD}}$s that were very similar to when studies were simulated for either end of the 24 years of data (Table 5.5).

Estimating harvest probability always produced lower $\overline{\text{RAD}}$ than estimating abundance, all other factors being equal (Figure 5.7). Auxiliary information, even with a CV of 0.5 produced drastically better precision than studies with no auxiliary information (Figure 5.8). Timing of the auxiliary study had little or no affect on the precision of the population reconstruction, all other factors being equal.

a. Auxiliary study to estimate abundance with a CV of 0.05 in 1972




b. Auxiliary study to estimate abundance with a CV of 0.125 in 1972




c. Auxiliary study to estimate abundance with a CV of 0.250 in 1972

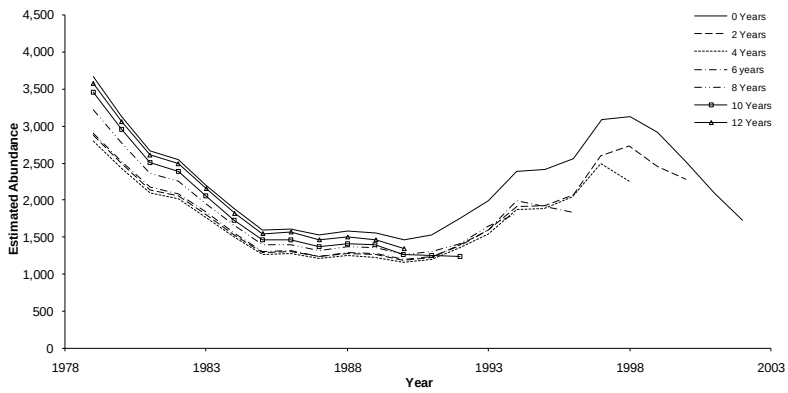
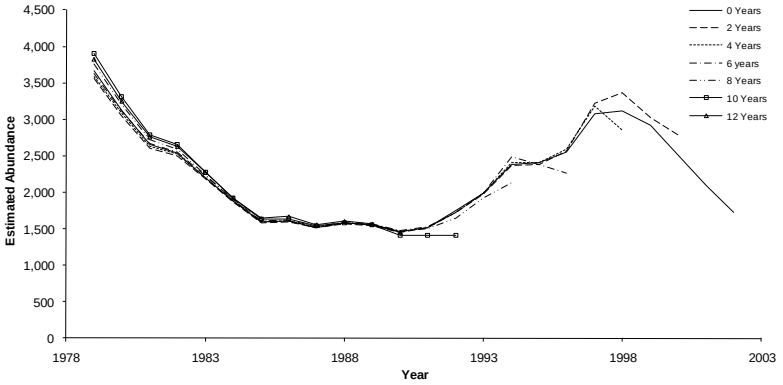
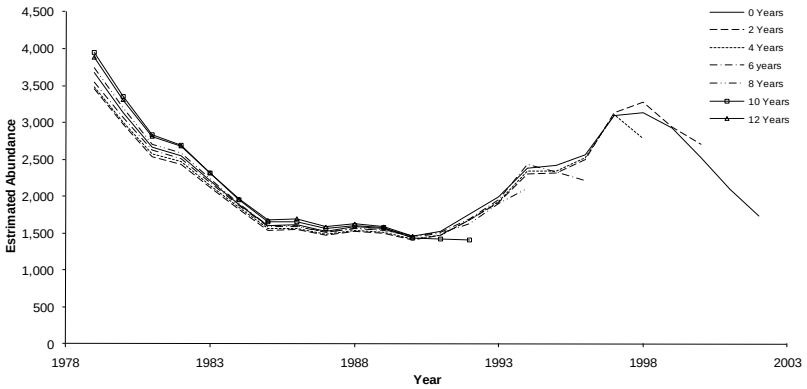



Figure 5.5. Annual abundance trends from a point deletion sensitivity analysis, recent data removed, on a statistical population reconstruction of female black-tailed deer, with an auxiliary study to estimate abundance in 1979 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

a. Auxiliary study to estimate vulnerability coefficients with a CV of 0.05 in 1972




b. Auxiliary study to estimate vulnerability coefficients with a CV of 0.125 in 1972




c. Auxiliary study to estimate vulnerability coefficients with a CV of 0.250 in 1972

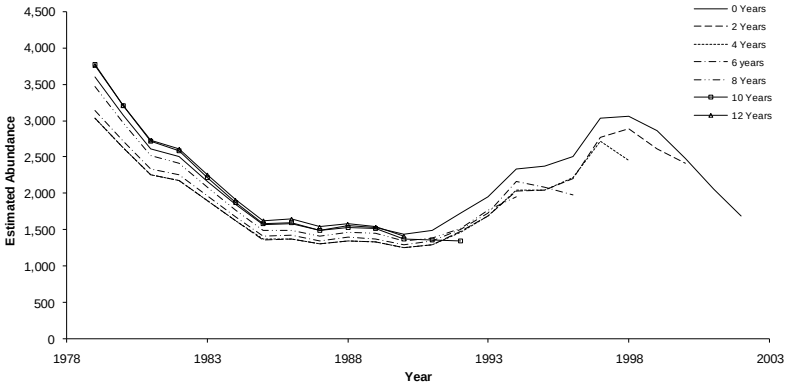



Figure 5.6. Annual abundance trends from a point deletion sensitivity analysis, recent data removed, on a statistical population reconstruction of female black-tailed deer, with an auxiliary study to estimate vulnerability coefficients in 1979 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

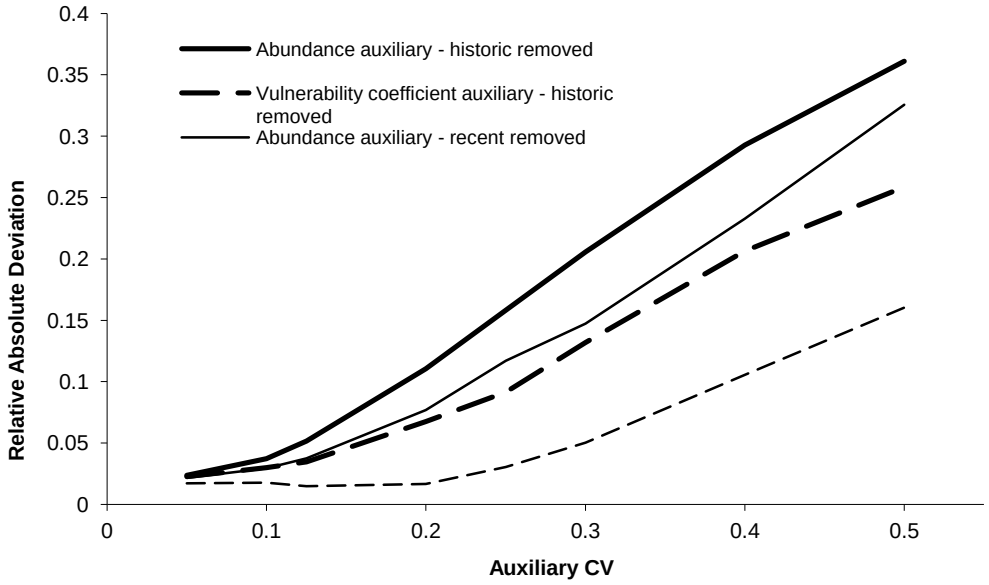



Figure 5.7. Relative absolute deviance ( $\overline{RAD}$ ) versus the CV of the auxiliary studies estimating abundance (solid lines) and vulnerability coefficients (dashed lines) for a point deletion sensitivity analysis, with historic (bold lines) or recent (thin lines) data removed, of female black-tailed deer.

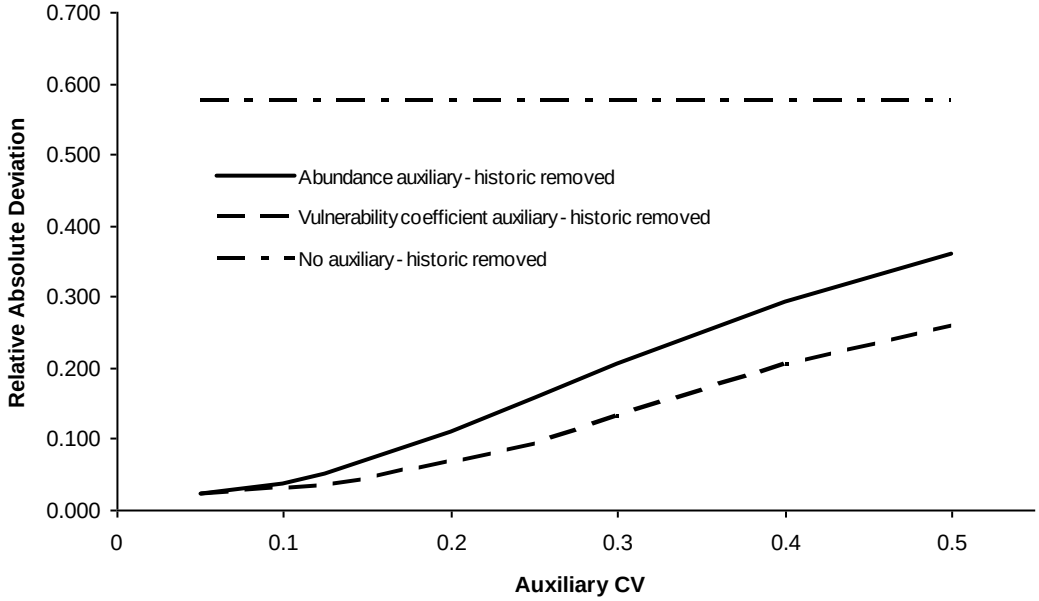



Figure 5.8. Relative absolute deviance ( $\overline{RAD}$ ) with respect to the CV of simulated auxiliary studies estimating abundance (solid line) and vulnerability coefficients (dashed line) for a point deletion sensitivity analysis, with historic (bold lines) data removed of female black-tailed deer. Including a line for relative deviance for the model without any auxiliary information included.

## 5.5 Pooled Age-Class Data with No Auxiliary Likelihood

### 5.5.1 Likelihood Model

The statistical model for the population reconstruction with limited age-class information (pooling the harvest data from older age classes) was based on a joint likelihood model of the form:

$$L_{\text{Joint}} = L_{\text{Age-at-harvest}} \cdot L_{\text{Catch-effort}} \tag{5.7}$$

The age-at-harvest likelihood used for the analysis of pooled age class data was of the form:

$$L_{\text{Age-at-harvest}} = \prod_{i=1}^{Y} L_{i1} \cdot \prod_{j=2}^{3} L_{1j} \tag{5.8}$$

where $L_{ij}$ was the likelihood describing the age-at-harvest data for the cohort entering the study in year $i$ $i = 1, \ldots, Y$ at age class $j$ $j = 1, 2, 3$ .

Let

$h_{ij}$ = number of females harvested in year $i$ $i = 1, \ldots, 24$ at age class $j$ $j = 1, 2, 3$ ,

$N_{ij}$ = female deer abundance in year $i$ $i = 1, \ldots, 24$ at age class $j$ $j = 1, 2, 3$ ,

$S$ = natural survival probability for all females,

$c_{0.5}$ = vulnerability coefficient for young-of-year females (i.e., age class 0.5),

$c_{1.5}$ = vulnerability coefficient for females 1.5 years of age or older,

$f_i$ = hunter effort in year $i$ $i = 1, \ldots, 24$ .

For the adults already present in the population in year 1, their likelihood contribution was written as follows:

$$L_{13} = \binom{N_{13}}{h_{13}} \; 1 - e^{-c_{1.5+} f_i} \;^{h_{13}} \; e^{-c_{1.5+} f_i} \;^{N_{13} - h_{13}} .$$

For the yearlings present in the population in year 1, their harvest in the first year and their harvest with other adults in the next year was modeled, based on the conditional likelihood, as follows:

$$L_{12} = \binom{h_{12\bullet}}{h_{12}, h_{23}} \left( \frac{E \;\; h_{12}}{E \;\; h_{12} \;\; + E \;\; h_{23}} \right)^{h_{12}} \left( \frac{E \;\; h_{23}}{E \;\; h_{12} \;\; + E \;\; h_{23}} \right)^{h_{23}}$$

where

$$\begin{aligned} E \;\; h_{12} \;\; &= N_{12} \;\; 1 - e^{-c_{1.5+} f_1} \\ E \;\; h_{23} \;\; &= \left[ N_{12} \;\; e^{-c_{1.5+} f_1} \;\; S + N_{13} \;\; e^{-c_{1.5+} f_1} \;\; S \right] 1 - e^{-c_{1.5+} f_2} \end{aligned}$$

and where $h_{12\bullet} = h_{12} + h_{23}$. For the juveniles present in the first year, the likelihood can be written as follows:

$$L_{11} = \binom{h_{11\bullet}}{h_{11}, h_{22,} h_{33}} \left( \frac{E \;\; h_{11}}{E \;\; h_{11} \;\; + E \;\; h_{22} \;\; + E \;\; h_{33}} \right)^{h_{11}} \left( \frac{E \;\; h_{22}}{E \;\; h_{11} \;\; + E \;\; h_{22} \;\; + E \;\; h_{33}} \right)^{h_{22}}$$
$$\cdot \left( \frac{E \;\; h_{33}}{E \;\; h_{11} \;\; + E \;\; h_{22} \;\; + E \;\; h_{33}} \right)^{h_{33}} ,$$

where

$$\begin{aligned} E \;\; h_{11} \;\; &= N_{11} \;\; 1 - e^{-c_{0.5+} f_1} \\ E \;\; h_{22} \;\; &= N_{11} \;\; e^{-c_{0.5+} f_1} \;\; S \;\; 1 - e^{-c_{1.5+} f_2} \\ E \;\; h_{33} \;\; &= \left[ N_{11} \;\; e^{-c_{0.5+} f_1} \;\; S \;\; e^{-c_{1.5+} f_2} \;\; S + N_{12} \;\; e^{-c_{1.5+} f_1} \;\; S \;\; e^{-c_{1.5+} f_2} \;\; S \right. \\ &\qquad \left. + N_{13} \;\; e^{-c_{1.5+} f_1} \;\; S \;\; e^{-c_{1.5+} f_2} \;\; S_A \right] 1 - e^{-c_{1.5+} f_3} \;\; , \end{aligned}$$

and where $h_{11\bullet} = h_{11} + h_{22} + h_{33}$. Construction of $L_{21}, \ldots, L_{Y1}$ was analogous to that of $L_{11}$ incremented for subsequent years. The pooled catch-effort likelihood was identical to the unpooled catch-effort likelihood, where:

$$L_{\text{Catch-effort}} = \prod_{i=1}^{24} \binom{N_{i1}}{h_{i1}} \left(1 - e^{-c_{0.5} f_i}\right)^{h_{i1}} \left(e^{-c_{0.5} f_i}\right)^{N_{i1} - h_{i1}}$$

$$\cdot \prod_{i=1}^{24} \binom{\sum_{j=2}^{3} N_{ij}}{\sum_{j=2}^{3} h_{ij}} \left(1 - e^{c_{1.5+} f_i}\right)^{\sum_{j=2}^{3} h_{ij}} \left(e^{-c_{1.5+} f_i}\right)^{\sum_{j=1}^{3} N_{ij} - h_{ij}} . \qquad (5.9)$$

Initial abundance levels (i.e., $N_{11}, N_{12}, N_{13}, N_{21}, \ldots, N_{24,1}$) were estimated directly from the likelihood model while the remaining abundance levels were calculated from the invariance property of the maximum likelihood estimation, where

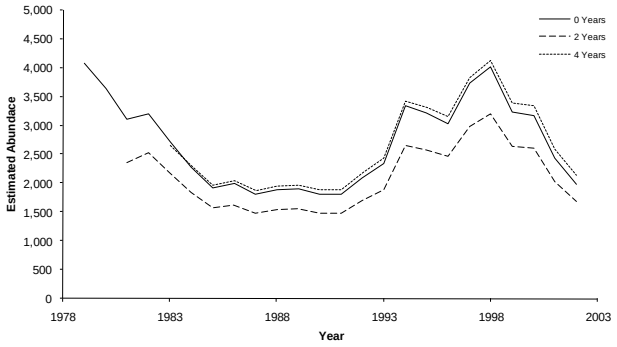
$$\hat{N}_{ij} = N_{i-1,j-1} e^{-cf_i} S .$$

Total annual abundance for any year was the sum of the within-year cohort abundance levels

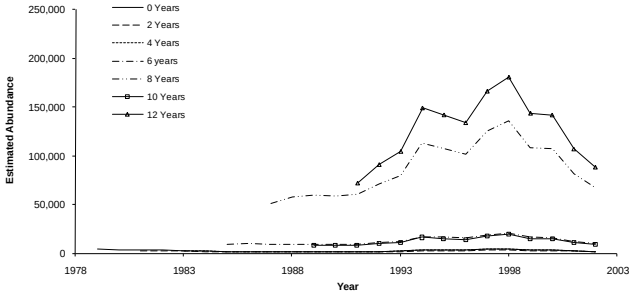
### 5.5.2 Sensitivity Analysis Results

Based on the PDSA, the pooled black-tailed deer population reconstruction was very sensitive to the number of years of data input (Figure 5.9). I removed historic data and the abundance estimates for 2002 (the last year of reconstruction) range from 1,721 females (0 years removed) to 88,791 females (12 years removed) (Figure 5.9). The $\overline{RAD}$ ranged from 3.52% to 4,314.68% with an average of 1,119.19% when historic data were removed (Table 5.6). When recent data were removed the abundance estimates in 1979 (the first year of reconstruction) ranged from 1,685 females (2 yrs removed) to 219,124 females (12 years removed), with 4,086 females estimated with 0 years removed (Figure 5.9). The $\overline{RAD}$ from the entire pooled data set ranged from 38.2% to 4,943.48% with an average of 949.39% when recent years of data were removed (Table 5.6).

a. 0, 2 and 4 years of historic data removed




b. 6, 8, 10 and 12 years of historic data removed




c. 0, 2, 4 and 6 years of recent data removed

d. 8, 10 and 12 years of recent data removed

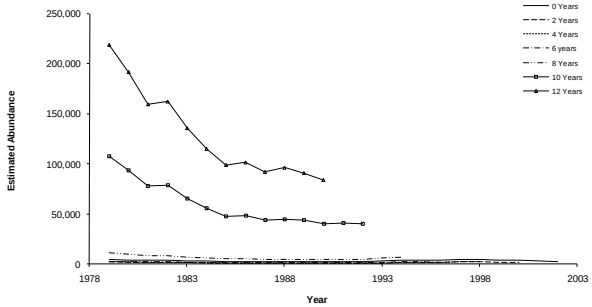



Figure 5.9. Annual abundance trends from the pooled statistical population reconstruction of female black-tailed deer, with varying numbers of historic (a and b) and recent (c and d) years of age at harvest data removed.

Table 5.6. Relative absolute deviation ( $\overline{RAD}$ ) statistics from a point deletion sensitivity analysis performed on a pooled statistical population reconstruction of female black-tailed deer. Models had no auxiliary data, an auxiliary that estimated abundance (1979 or 2002) or an auxiliary that estimated a vulnerability coefficient (1979 or 2002), either with historic (a) or recent (b) data removed.

a. Historic data removed

| Years removed | No auxiliary | Abundance auxiliary | | | | Vulnerability coefficient auxiliary | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | CV = 0.05 | CV = 0.125 | CV = 0.250 | CV = 0.50 | CV = 0.05 | CV = 0.125 | CV = 0.250 | CV = 0.50 |
| 2 | 19.08% | 3.79% | 4.50% | 6.42% | 9.46% | 1.01% | 1.07% | 1.63% | 5.95% |
| 4 | 3.53% | 4.54% | 4.37% | 3.64% | 2.33% | 1.62% | 1.61% | 1.56% | 1.84% |
| 6 | 392.21% | 1.82% | 0.86% | 3.89% | 15.28% | 1.59% | 1.58% | 0.79% | 6.35% |
| 8 | 3179.55% | 2.81% | 2.31% | 10.41% | 39.45% | 3.92% | 3.45% | 3.22% | 17.06% |
| 10 | 368.21% | 3.19% | 4.13% | 8.04% | 17.94% | 2.15% | 3.79% | 2.82% | 2.71% |
| 12 | 4314.69% | 1.44% | 3.40% | 12.07% | 42.05% | 3.67% | 3.33% | 1.48% | 15.92% |
| Mean | 1119.94% | 3.05% | 3.28% | 6.87% | 18.61% | 2.14% | 2.26% | 1.85% | 7.61% |

b. Recent data removed

| Years removed | No auxiliary | Abundance auxiliary | | | | Vulnerability coefficient auxiliary | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | CV = 0.05 | CV = 0.125 | CV = 0.250 | CV = 0.50 | CV = 0.05 | CV = 0.125 | CV = 0.250 | CV = 0.50 |
| 2 | 55.81% | 1.34% | 2.84% | 12.21% | 33.51% | 1.29% | 2.37% | 6.93% | 23.94% |
| 4 | 53.01% | 1.96% | 2.68% | 9.13% | 26.44% | 1.81% | 1.84% | 4.31% | 16.53% |
| 6 | 38.24% | 2.08% | 1.92% | 4.38% | 13.39% | 2.06% | 2.60% | 2.07% | 6.19% |
| 8 | 157.94% | 3.19% | 3.28% | 4.30% | 8.67% | 3.93% | 5.65% | 6.98% | 9.98% |
| 10 | 2286.63% | 5.05% | 4.63% | 5.67% | 17.63% | 4.99% | 7.30% | 9.94% | 18.18% |
| 12 | 4943.49% | 1.79% | 2.78% | 7.28% | 26.04% | 3.83% | 7.41% | 11.57% | 23.16% |
| Mean | 949.39% | 2.44% | 2.95% | 7.50% | 21.62% | 2.75% | 4.09% | 6.53% | 16.28% |

Table 5.7. Scale parameters from point deletion sensitivity analysis with either historic or recent years removed, performed on a pooled statistical population reconstruction of female black-tailed deer.

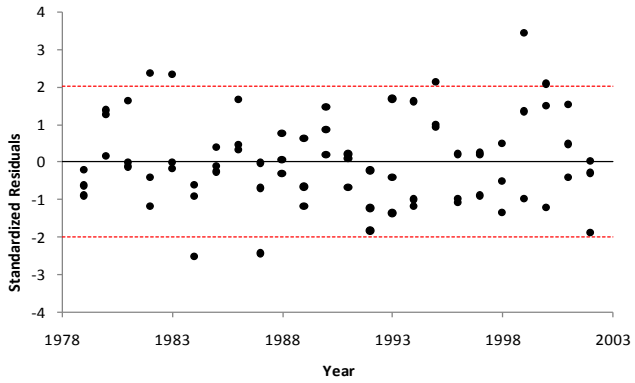
| Years removed | Scale parameter | |
|---|---|---|
| | Historic data removed | Recent data removed |
| 0 | 1.518 | 1.518 |
| 2 | 1.540 | 1.465 |
| 4 | 1.555 | 1.332 |
| 6 | 1.473 | 1.396 |
| 8 | 1.465 | 1.342 |
| 10 | 1.520 | 1.312 |
| 12 | 1.650 | 1.400 |

These drastic changes in annual abundance estimates suggest that this pooled population reconstruction was highly sensitive to the number of years of data. Annual abundance estimates changed dramatically depending on the number of available years of data (Figure 5.9). However the same abundance trends were evident regardless of the degree of data deletion (Figure 5.9).

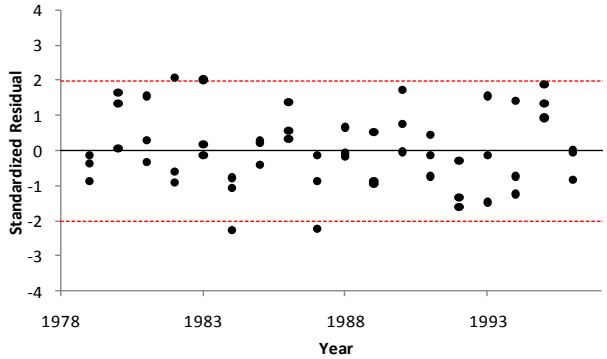
I examined the residuals for all 14 data subsets ( seven subsets removing 0,2,4,6,8,10,12 years of historic data and seven subsets 0,2,4,6,8,10,12 removing years of recent data) (Figure 5.10). All of the residual plots looked nearly identical; there were no discernable trends, no additional points fell outside +/–2, and the dispersion about 0 was the same. I examined the residuals to determine if I could have diagnosed the abundance estimate problem through residual analysis. I would not have been able to diagnose the unreasonable abundance estimate from the residuals alone. In addition, the Chi-square scale parameter used by Skalski et al (2007) to account for lack of model fit did not differ greatly between data subsets (Table 5.7). This means that an investigator could perform a pooled SPR, and residual analysis, and not be able to discern a problem.

The above PDSA suggests pooled population reconstruction based solely on age-at-harvest and catch effort data are very sensitive to the number of years of data collection. Investigators should be very cautious when interpreting pooled statistical population results in these circumstances and PDSA should always be performed.

a. All data




b. Six years of recent data removed




c. Twelve years of recent data removed

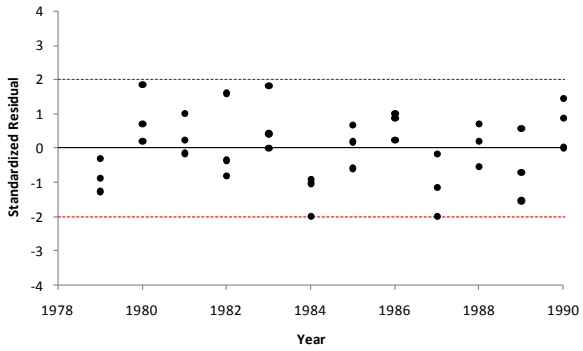



Figure 5.10. Standardized residuals plotted by year from a point deletion sensitivity analysis, recent data removed, on a pooled statistical population reconstruction of female black-tailed deer. 0, 6 and 12 years removed shown as examples.

## 5.6 Pooled Age-Class Data with an Auxiliary Likelihood

The above results lead to the same two conclusions as with the full age class data. One, it is necessary to perform some sort of point deletion sensitivity analysis or other non-residual based form of model sensitivity evaluation. Two, auxiliary data may help SPR produce more reliable results. To explore the concept of auxiliary data improving model accuracy, I incorporated auxiliary data in order to answer three questions. What is the affect of the type of auxiliary data on the stability of pooled population reconstruction? How precise does the auxiliary information need to be? What effect does the timing of the auxiliary study have on the stability of pooled population reconstruction?

### 5.6.1 Likelihood Model

Auxiliary data were simulated and incorporated into the original pooled model structure, resulting in a joint likelihood model of the form:

$$L_{\text{Joint}} = L_{\text{Age-at-harvest}} \cdot L_{\text{Catch-effort}} \cdot L_{\text{Simulated Auxiliary}} \,. \tag{5.10}$$

Studies were simulated to estimate parameter values at varying levels of precision. The auxiliary data were simulated to produce parameter estimates with CVs of 0.05, 0.125, and 0.250 (Section 5.3.1). Two types of auxiliary data were generated; a single mark-recapture (Seber 1982:59) was simulated to estimate an annual abundance (Eq. 5.5). The second auxiliary study simulated was in the form of a mark-harvest study to estimate vulnerability coefficients (Eq. 5.6)

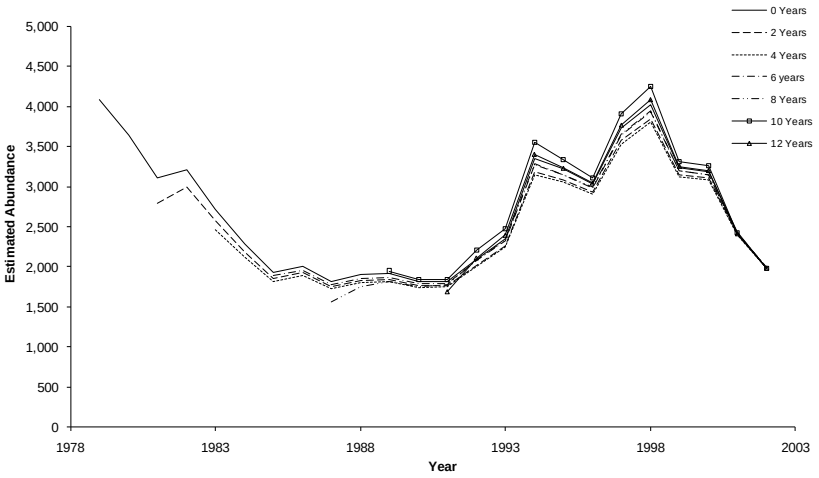
When historic data were removed, the auxiliary data were simulated to estimate abundance or vulnerability coefficients in 2002. When the most recent data were removed, auxiliary data were simulated to estimate abundance or vulnerability coefficients in 1979. Auxiliary data were also simulated in years 1990 and 1991 to determine if the timing of an

auxiliary study changed its effectiveness. For each simulated auxiliary study, relative deviation statistics were calculated.

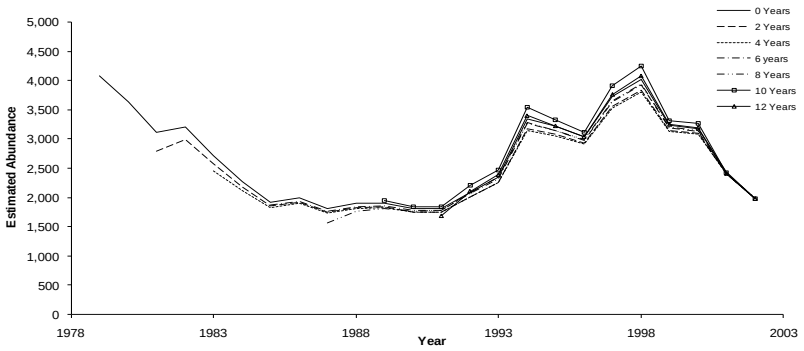
### 5.6.2 Sensitivity Analysis Results

I removed historic data and incorporated an auxiliary study to estimate abundance in 2002 (Table 5.8). The 2002 abundance estimates ranged from 1,979 to 1,993 females with an auxiliary CV of 0.05, 1,962 to 2,047 females with a simulated auxiliary CV of 0.125, and 1,969 to 2,308 females with a simulated auxiliary CV of 0.250 (Figure 5.11). The $\overline{\mathrm{RAD}}$ ranged from 3.0% with an auxiliary CV of 0.05 to 18.6% with an auxiliary CV of 0.5 (Table 5.6). I also removed historic data and incorporated an auxiliary study in 2002 to estimate vulnerability coefficients (Table 5.9). The 2002 abundance estimates ranged from 1,981 to 2,112 females with a simulated auxiliary CV of 0.05, 1,908 to 2,062 females with a simulated auxiliary CV of 0.125, and 1,876 to 2,101 females with a simulated auxiliary CV of 0.250 (Figure 5.12). The $\overline{RAD}$ ranged from 2.1% with an auxiliary CV of 0.05 to 7.6% with an auxiliary CV of 0.5 (Table 5.6). When no auxiliary data were included the average deviation was 1,119.94% (Table 5.6).

a. Auxiliary study to estimate abundance with a CV of 0.05 in 2002




b. Auxiliary study to estimate abundance with a CV of 0.125 in 2002




c. Auxiliary study to estimate abundance with a CV of 0.250 in 2002

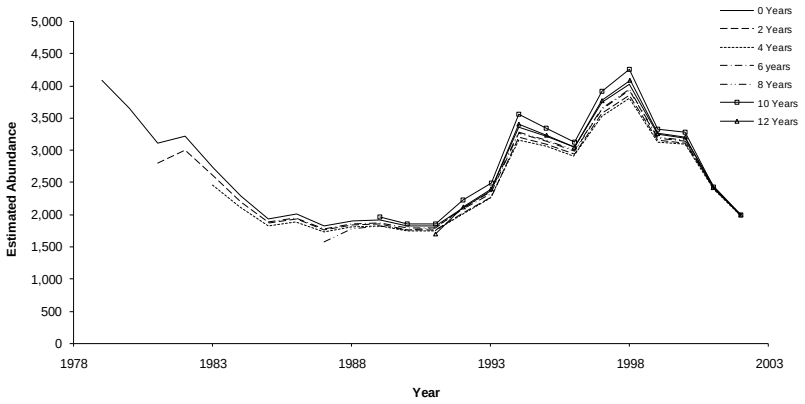
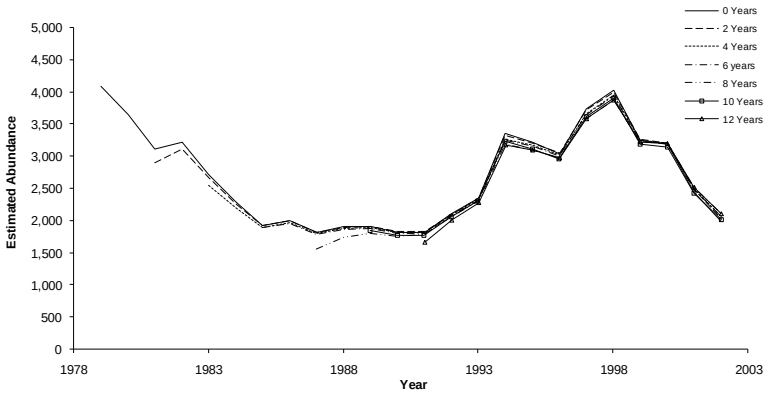
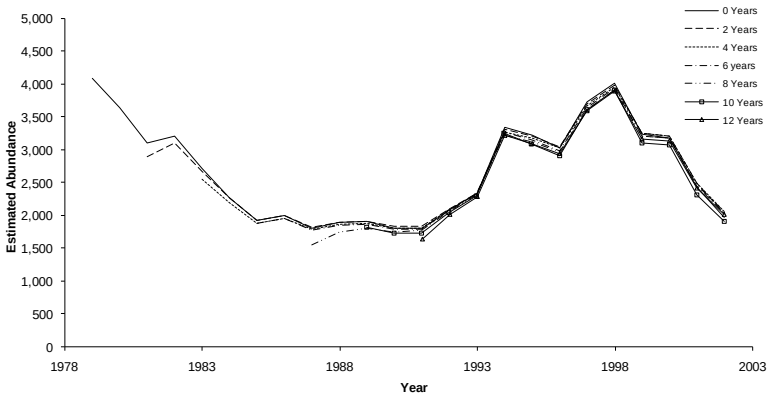



Figure 5.11. Annual abundance trends from a point deletion sensitivity analysis, historic data removed, on a pooled statistical population reconstruction of female black-tailed deer, with an auxiliary study to estimate abundance in 2002 with a CV of a) 0.05, b) 0.125, and c) 0.250.

a. Auxiliary study to estimate vulnerability coefficients with a CV of 0.05 in 2002




b. Auxiliary study to estimate vulnerability coefficients with a CV of 0.125 in 2002




c. Auxiliary study to estimate vulnerability coefficients with a CV of 0.250 in 2002

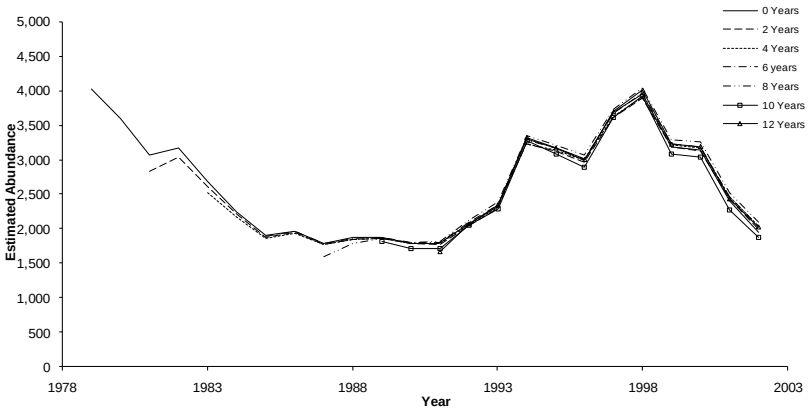



Figure 5.12. Annual abundance trends from a point deletion sensitivity analysis, historic data removed, on a pooled statistical population reconstruction of female black-tailed deer, with an auxiliary study to estimate vulnerability coefficients in 2002 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

Table 5.8. Auxiliary data used to estimate abundance in 1979 (recent data removed) or 2002 (historic data removed).

| | Historic data removed | | | Recent data removed | | |
|---|---|---|---|---|---|---|
| CV | $N$ | $P_1$ | $P_2$ | $N$ | $P_1$ | $P_2$ |
| 0.05 | 1981 | 0.310 | 0.310 | 4086 | 0.238 | 0.238 |
| 0.1 | 1981 | 0.183 | 0.183 | 4086 | 0.135 | 0.135 |
| 0.125 | 1981 | 0.152 | 0.152 | 4086 | 0.111 | 0.111 |
| 0.2 | 1981 | 0.101 | 0.101 | 4086 | 0.073 | 0.073 |
| 0.25 | 1981 | 0.082 | 0.082 | 4086 | 0.059 | 0.059 |
| 0.3 | 1981 | 0.070 | 0.070 | 4086 | 0.050 | 0.050 |
| 0.4 | 1981 | 0.053 | 0.053 | 4086 | 0.038 | 0.038 |
| 0.5 | 1981 | 0.043 | 0.043 | 4086 | 0.030 | 0.030 |

Table 5.9 Auxiliary data used to estimate the vulnerability coefficients in 1979 (Recent data removed) or 2002 (historic data removed).

| | Historic data removed | | | | | | Recent data removed | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CV | $P_j$ | $n_j$ | $x_j$ | $P_a$ | $n_a$ | $x_a$ | $P_j$ | $n_j$ | $x_j$ | $P_a$ | $n_a$ | $x_a$ |
| 0.05 | 0.013 | 30488 | 395 | 0.024 | 16336 | 390 | 0.015 | 26200 | 394 | 0.028 | 14006 | 389 |
| 0.1 | 0.013 | 7622 | 99 | 0.024 | 4084 | 98 | 0.015 | 6550 | 98 | 0.028 | 3501 | 97 |
| 0.125 | 0.013 | 4878 | 63 | 0.024 | 2614 | 62 | 0.015 | 4192 | 63 | 0.028 | 2241 | 62 |
| 0.2 | 0.013 | 1906 | 25 | 0.024 | 1021 | 24 | 0.015 | 1637 | 25 | 0.028 | 875 | 24 |
| 0.25 | 0.013 | 1220 | 16 | 0.024 | 653 | 16 | 0.015 | 1048 | 16 | 0.028 | 560 | 16 |
| 0.3 | 0.013 | 847 | 11 | 0.024 | 454 | 11 | 0.015 | 728 | 11 | 0.028 | 389 | 11 |
| 0.4 | 0.013 | 476 | 6 | 0.024 | 255 | 6 | 0.015 | 409 | 6 | 0.028 | 219 | 6 |
| 0.5 | 0.013 | 305 | 4 | 0.024 | 163 | 4 | 0.015 | 262 | 4 | 0.028 | 140 | 4 |

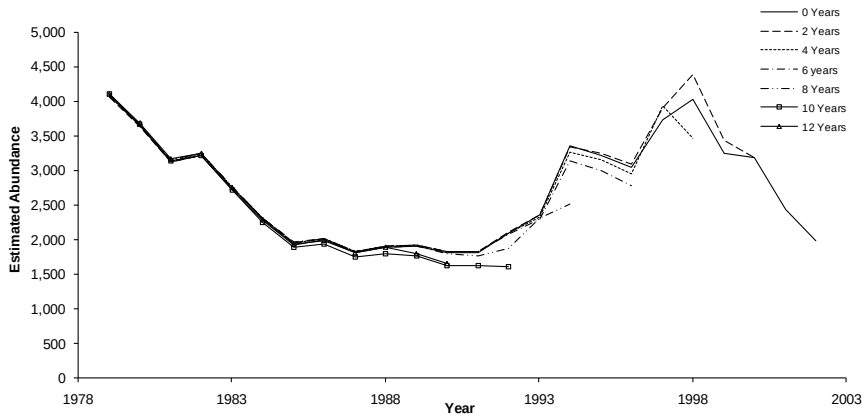
I removed recent data and included an auxiliary study to estimate abundance in 1979 (Table 5.8). The 1979 abundance estimates ranged from 4,059 to 4,100 females with an auxiliary study with a CV of 0.05; 3,894 to 4,139 females with an auxiliary study with a CV of 0.125; and 3,517 to 4,455 females with an auxiliary study with a CV of 0.250 (Figure 5.13). The $\overline{\text{RAD}}$ ranged from 2.4% with an auxiliary CV of 0.05 to 21.6% with an auxiliary CV of 0.5 (Table 5.6). I also removed recent data and included an auxiliary study to estimate vulnerability coefficients (Table 5.9). The 1979 abundance estimates ranged from 3,992 to 4,412 females with an auxiliary study with a CV of 0.05; 3,917 to 4,544 females with an auxiliary study with a CV of 0.125; and 3,632 to 4,623 females with an auxiliary study with a CV of 0.250 (Figure 5.14). The $\overline{\text{RAD}}$ ranged from 2.75% with an auxiliary CV of 0.05 to 16.28% with an auxiliary CV of 0.5 (Table 5.6). When no auxiliary data were included, the average deviation was 949.39% (Table 5.6). Auxiliary studies simulated in the middle of the data collection period, years 1990 and 1991, produced $\overline{\text{RAD}}$'s that were very similar to those produced when auxiliary studies were added at either end (Table 5.10).

Estimating vulnerability coefficients always produced lower $\overline{\text{RAD}}$'s than estimating abundance, all other factors being equal (Table 5.10). Auxiliary information, even with a CV of 0.5, produced drastically better precision than studies with no auxiliary information (Table 5.6). Timing of the auxiliary study had little or no effect on the precision of the pooled population reconstruction, all other factors being equal.

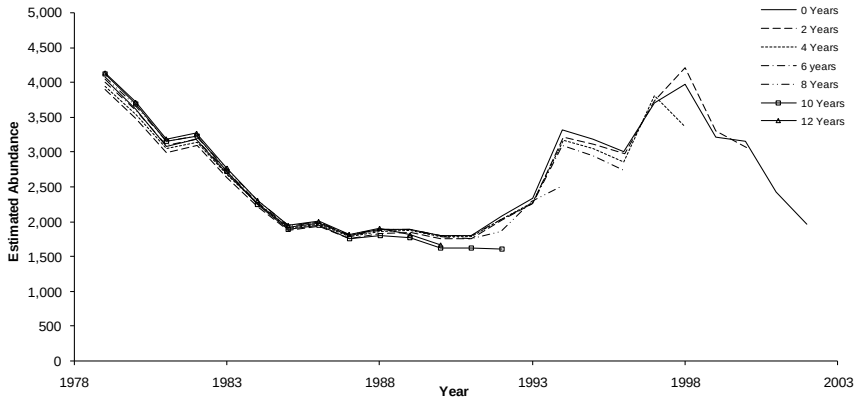
Table 5.10. Relative absolute deviation ($\overline{RAD}$) statistics from a point deletion sensitivity analysis of female black-tailed deer. Comparing auxiliary studies simulated at the beginning and the end of the study (1979 and 2002) with those simulated in the center of the study (1990 and 1991).

| Historic data removed | | | | Recent data removed | | | |
|---|---|---|---|---|---|---|---|
| Abundance auxiliary | | Vulnerability coefficient auxiliary | | Abundance auxiliary | | Vulnerability coefficient auxiliary | |
| 2002 | 1991 | 2002 | 1991 | 1979 | 1990 | 1979 | 1990 |
| 3.05% | 2.67% | 2.14% | 2.16% | 2.44% | 4.39% | 2.75% | 2.79% |
| 3.28% | 3.63% | 2.26% | 2.26% | 2.95% | 5.90% | 4.09% | 4.19% |
| 6.87% | 7.64% | 1.85% | 1.89% | 7.50% | 11.69% | 6.53% | 6.75% |

a. Auxiliary study to estimate abundance with a CV of 0.05 in 1979




b. Auxiliary study to estimate abundance with a CV of 0.125 in 1979




c. Auxiliary study to estimate abundance with a CV of 0.250 in 1979

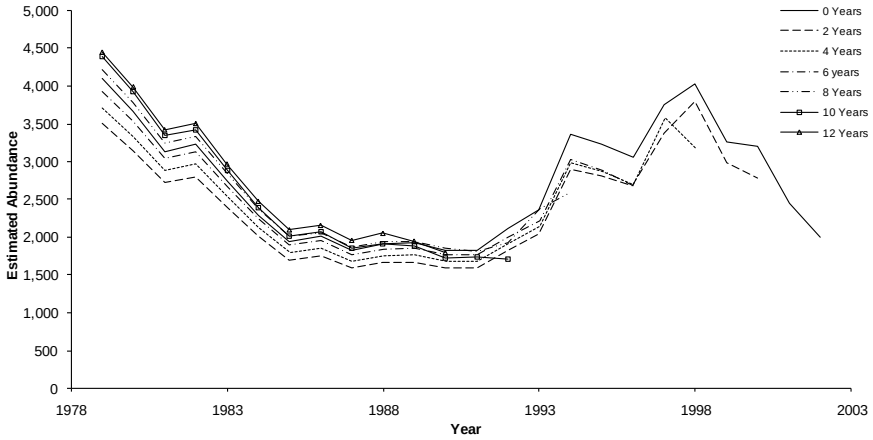
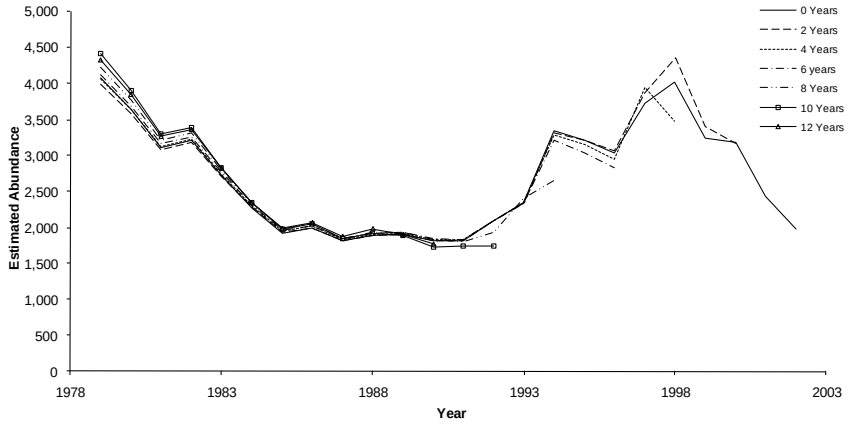
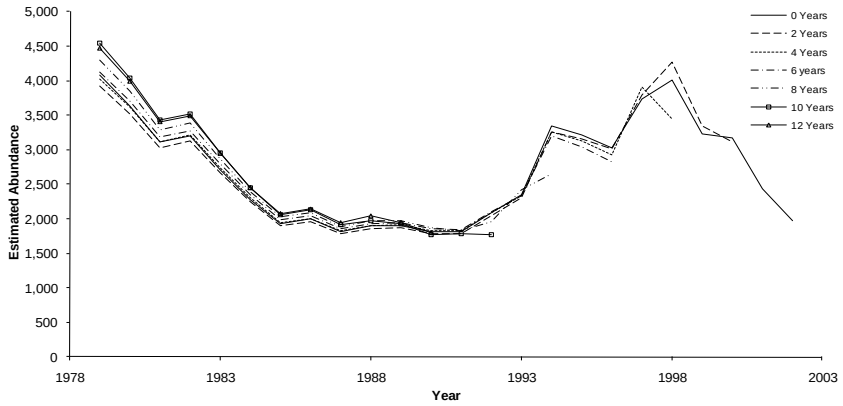



Figure 5.13. Annual abundance trends from a point deletion sensitivity analysis, recent data removed, on a pooled statistical population reconstruction of female black-tailed deer, with an auxiliary study to estimate abundance in 1979 with a CV of ( a) 0.05, (b) 0.125, and (c) 0.250.

a. Auxiliary study to estimate vulnerability coefficients with a CV of 0.05 in 1979




b. Auxiliary study to estimate vulnerability coefficients with a CV of 0.125 in 1979




**c.** Auxiliary study to estimate vulnerability coefficients with a CV of 0.250 in 1979

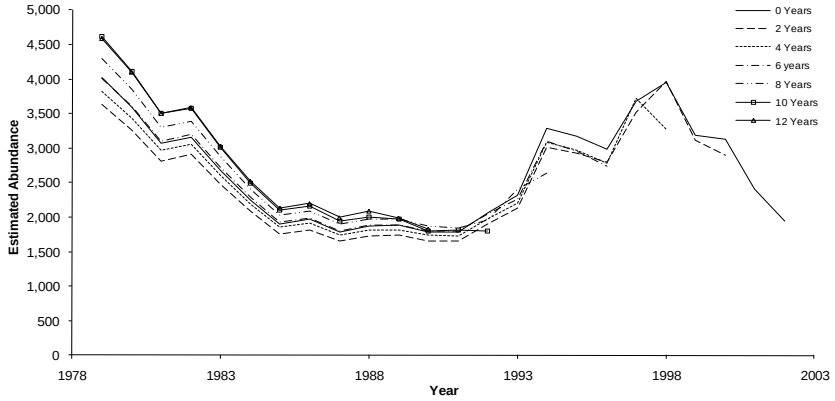



Figure 5.14. Annual abundance trends from a point deletion sensitivity analysis, recent data removed, on a pooled statistical population reconstruction of female black-tailed deer, with an auxiliary study to estimate vulnerability coefficients in 1979 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

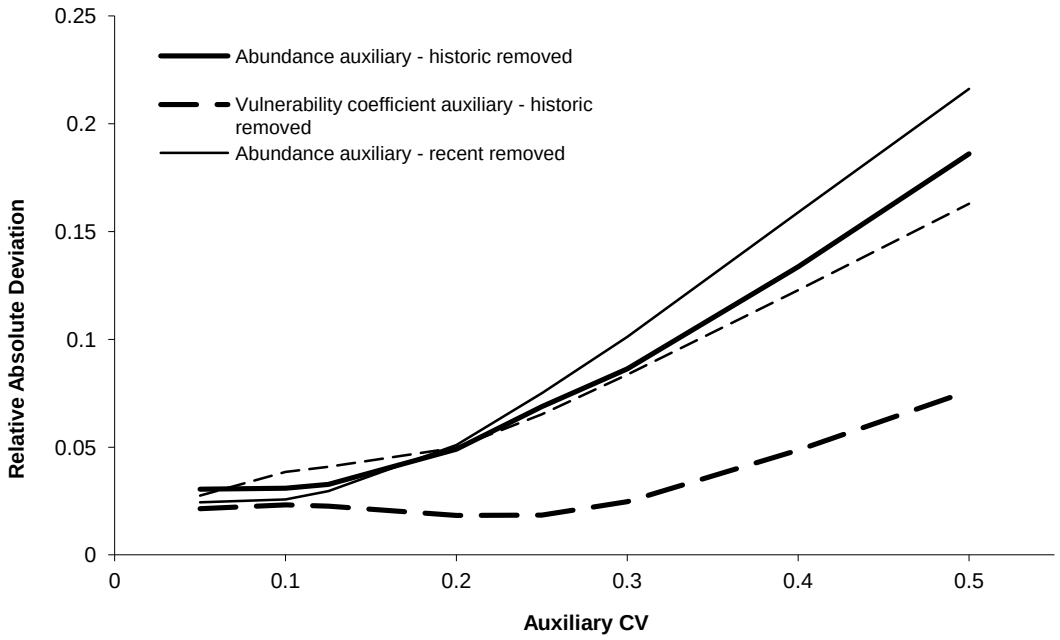



Figure 5.15. Relative absolute deviance ($\overline{\text{RAD}}$) with respect to the CV of simulated auxiliary studies estimating abundance (solid lines) and vulnerability coefficients (dashed lines) for a point deletion sensitivity analysis, with historic (bold lines) or recent (thin lines) data removed, of female black-tailed deer.

## 5.7 Discussion

Auxiliary data that independently estimate a model parameter, such as an abundance or capture probability, improve model performance and reliability, regardless of the number of years of data. Auxiliary data not only improve model reliability but are often necessary to obtain reasonable abundance estimates (Broms et. al. 2010). Auxiliary data stabilize pooled and unpooled age-class models equally well.

Point deletion sensitivity analysis (PDSA) is a method for further evaluating SPR models. I have laid out the particulars of PDSA and showed its usefulness when other model evaluation methods have failed. Point deletion sensitivity analysis is not the sole method for SPR model evaluation, nor should it be. It is simply another tool to evaluate complex population reconstruction models. It should be used along with residual analysis, chi-square lack-of-fit tests, Monte Carlo analysis, or other techniques for model evaluation. Factors outside of the amount of age-at-harvest data available may affect how data can be modeled with SPR. These can include effort being estimated instead of measured, changes in population size during the study period, changes in hunter effort over the study period, and many more variables. Additionally, when using pooled age class data, the number of age classes that are pooled relative to the animal's life span may be a factor of great importance. In Broms' (2008) thesis on SPR of small-game species, she used Monte Carlo analysis to evaluate model efficiency and robustness. She found that auxiliary information vastly improved model accuracy; models with low harvest mortality that did not include auxiliary information had unstable abundance estimates with extremely high standard errors. In addition, she set forth a list of factors that influence model performance. My results support

Broms (2008) and indicate that auxiliary data are necessary when age-at-harvest data are coupled with catch-effort information.

This chapter evaluated auxiliary data that estimated either annual abundance or harvest probability. These parameters were chosen because they were determined to be the most sensitive, based on the PDSA. However, survival or recruitment could have been independently estimated through auxiliary data and may have provided additional benefits. The benefits of more auxiliary data sources have yet to be explored. For this reason, auxiliary studies, in conjunction with population reconstruction, are highly recommended. Even auxiliary studies that estimated parameter values within +/–100% of their value, 95% of the time, tremendously improved the reliability of the model.

### 5.7.1 Conclusions

Statistical population reconstruction may be the future gold standard of broad-scale wildlife monitoring of game species because of its power and flexibility to include several types of data, some of which are often already available. However, it is not without its limitations. Attempts at modeling with SPR should use all available data, preferably several years of age-at-harvest and catch-effort data, augmented with some form(s) of auxiliary information. In addition, PDSA should be performed to determine model stability and evaluate the most effective and efficient auxiliary studies to augment the models as needed.

## 5.8 Management Implications

Statistical population reconstruction is recommended for managers who currently have age-at-harvest information or who want to begin collecting age-at-harvest information. If age-at-harvest and catch-effort information already exist, I recommend a preliminary analysis be done, similar to the one preformed here. This analysis would determine the

amount of additional information needed and the most effective type of auxiliary study to augment the existing data. If age-at-harvest and catch-effort information does not already exist, I recommend the collection of either pooled or unpooled age-at-harvest and catch-effort information (whichever is more feasible) with the most detailed hunter effort information available. This information is inexpensive and provides the basis for, not only SPR, but other wildlife population metrics. In addition, I would recommend a study to independently estimate harvest probability at a rough management level. While SPR is not a panacea for the challenges facing wildlife populations and their managers, it is a powerful tool to be used, in conjunction with other population evaluation methods, to more completely inform management decisions.

# Chapter 6: Population Reconstruction of Cougar in Northeastern Oregon

## 6.1 Introduction

Inventorying terrestrial predator populations such as bear, cougar, and bobcat is among the most challenging of abundance studies. Difficulties exist because of the large spatial areas of concern, low animal densities, large home ranges, elusive behavior, and the risks and costs of capturing and handling individuals. These difficulties have resulted in the widespread use of indices or noninvasive sampling techniques, including the use of scent stations, track-plates surveys, snow-track sampling, scat surveys and camera trapping (Gompper et al 2006). Generally, the indices generated by indirect sampling of carnivores do not provide enough information to estimate abundance or other demographic parameters (Gompper et al 2006). Camera trapping may be useful in estimating abundance for individually identifiable animals, but is far less useful for animals which cannot be individually identified in a photograph (Heilburn et al 2006). McDonald et al. (1999) used aerial line transect surveys to monitor polar bears (*Ursus maritimus*) on pack ice. Amstrup et al. (2001) have also used mark-recovery methods to estimate polar bear abundance and survival rates using open population models. In many situations, these methods are ill-suited to rugged forest terrain and too costly for routine population monitoring. DNA mark-recapture methods have shown to be promising in estimating the abundance of predator populations based on sampling-resampling of animal sign, such as hair or fecal material (Mowtag and Stobeck 2000). Among game populations, yet another option is statistical population reconstruction which uses age-at-harvest data. In many states and provinces, bear and cougar harvests must be registered with local game agencies which collect a dental

sample for age determination. From this information, along with hunter effort, estimates of abundance, natural survival, recruitment, and harvest mortality can be derived.

I use statistical population reconstruction (SPR) to evaluate trends in an Oregon cougar population based on eight years of age-at-harvest data (Table 6.1). I demonstrate the analysis using 1.5-year-old and older animals. It is illegal to harvest young-of-the-year, so my inference will be to the population of older age classes.

Table 6.1. Age-at-harvest data for cougars, 1.5 to 18.5+ years of age, 1987–1994, for Zone E management units 54–64 in the state of Oregon.

| | Age class | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Yr | 1.5 | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 | 8.5 | 9.5 | 10.5 | 11.5 | 12.5 | 13.5 | 14.5 | 15.5 | 16.5 | 17.5 | 18.5 | 19.5 |
| 1987 | 0 | 9 | 22 | 12 | 6 | 7 | 5 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1988 | 2 | 13 | 18 | 11 | 8 | 3 | 2 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1989 | 0 | 6 | 21 | 8 | 2 | 4 | 6 | 3 | 4 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 1990 | 2 | 3 | 12 | 11 | 14 | 9 | 4 | 1 | 3 | 0 | 3 | 3 | 2 | 0 | 1 | 0 | 1 | 0 | 0 |
| 1991 | 0 | 2 | 16 | 8 | 11 | 12 | 4 | 5 | 2 | 4 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| 1992 | 3 | 0 | 10 | 11 | 12 | 12 | 7 | 10 | 5 | 3 | 0 | 6 | 2 | 1 | 1 | 0 | 0 | 0 | 0 |
| 1993 | 3 | 3 | 13 | 8 | 9 | 4 | 11 | 2 | 3 | 5 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1994 | 0 | 9 | 13 | 10 | 9 | 8 | 9 | 2 | 3 | 3 | 4 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |

Due to the length of hunting seasons (two months), it would be unrealistic to model hunting and natural mortality as sequential processes, as has been done in previous SPR applications (Chapters 2–5, Skalski et al. 2007, Gove 2002). Therefore, this analysis provides an example of natural and harvest mortality modeled as instantaneous and congruent processes. This analysis will also illustrate the use of the number of hunters as the sole measure of effort (Table 6.2). Number of hunters is the coarsest measure of hunter effort;

however, it can be fairly easily collected and may often be the only measure of effort available. Radiotelemetry information was provided by Oregon Department of Fish and Wildlife by age class (Table 6.2). These data were used to help estimate age-specific harvest and survival probability parameters, providing an example of SPR augmented with radiotelemetry auxiliary data.

Table 6.2. Number of cougars 1.5 years of age and older that were harvested and aged from zone E, management units 53–64, Oregon, 1987–1994, along with hunter effort experienced in terms of hunters.

| Year | Total harvest | Sampled for age | Number of hunters |
|---|---|---|---|
| 1987 | 74 | 66 | 149 |
| 1988 | 61 | 60 | 151 |
| 1989 | 60 | 59 | 142 |
| 1990 | 74 | 69 | 165 |
| 1991 | 67 | 67 | 153 |
| 1992 | 85 | 83 | 171 |
| 1993 | 71 | 66 | 173 |
| 1994 | 75 | 73 | 139 |

## 6.2 Study Area

The age-at-harvest, hunter effort, and auxiliary data all come from management units 54–63 of the Blue Mountains region of Northeastern Oregon (Figure 6.1). Hunters are required to report kills in person within 10 days of a kill. From 1987-1994, between 208 and 235 tags were sold in this management zone. The Blue Mountains comprise about 15,929 $mi^2$ of diverse terrain, 49% of which is public land. The Blue Mountains have a range of vegetation from sagebrush to alpine forests, with mixed conifer forests being most predominant. Much of the Blue Mountain region is used for cattle grazing and timber extraction. Elevations within this management zone range from 1,500 ft to over 10,000 ft.

Figure 6.1. Map of cougar management zones in Oregon, data come from zones 53-64 (shaded).

## 6.3 Methods

### 6.3.1 Model Construction

#### 6.3.1.1 Modeling Harvest Mortality

In this population reconstruction, as with most others, the years began with the hunting season that collected the age-at-harvest data, which forms the basis of the analysis. Recruitment of 1.5-year-old cougars was then net recruitment at time of the hunting season, reflecting the birth rate adjusted for survival between birth and beginning of the second fall harvest. Harvest mortality also started at the beginning of each year demarcated by the hunting season.

In the previous population reconstructions of Chapters 3–5, the hunting season was relatively short and natural mortality was assumed negligible during that period; therefore, harvest mortality and natural mortality were modeled as conditionally independent processes. The probability an animal died due to harvest was then parameterized as $p_H$, and the probability an animal died from natural causes was expressed as

$$1-p_H \quad 1-S_H \quad . \tag{6.1}$$

The probability an animal survived both mortality sources was modeled as

$$1-p_H \quad S_H \, , \tag{6.2}$$

where

$$p_H + 1-p_H \quad 1-S_H \quad + 1-p_H \quad S_H = 1.$$

Since the cougar hunting seasons constituted biologically significant proportions of the year, harvest and natural mortality needed to be considered concurrently. The traditional

way of doing this was to use instantaneous mortality rates where the probability of mortality from all sources $M = 1 - S$ can be written as

$$M = 1 - S = 1 - e^{-\mu_E + \mu_N} \ , \tag{6.3}$$

where

$\mu_E$ = instantaneous harvest mortality rate,

$\mu_N$ = instantaneous natural mortality rate.

In turn, survival was parameterized as

$$S = e^{-\mu_E + \mu_N} \ . \tag{6.4}$$

The quantity $\mu_E + \mu_N$ was the instantaneous total mortality rate over some fixed period. The instantaneous natural mortality rate was reexpressed as an explicit function of *t*, such that

$$S = e^{-\mu_E + \mu t} \ , \tag{6.5}$$

where the natural mortality rate was in the same units as *t* (i.e., months). The instantaneous exploitation rate was reexpressed in terms of effort (*f*) where

$$S = e^{-cf + \mu t} \ . \tag{6.6}$$

The overall survival probability *S* in Eq. (6.6) was then an explicit function of time (*t*) over which natural mortality was expressed and an explicit function of hunter effort (*f*) over that same duration *t*. The probability an animal died from natural causes based on Eq. (6.6) was then

$$\frac{\mu t}{cf + \mu t} \ 1 - e^{-cf + \mu t} \ , \tag{6.7}$$

while the probability of harvest mortality was then

$$\frac{cf}{cf+\mu t}\ 1-e^{-\ cf+\mu t} \quad . \tag{6.8}$$

For the period 1987–1994 with a two-month hunting season, the probability of harvest was modeled as

$$\left(\frac{cf_i}{cf_i+2\mu}\right) 1-e^{-\ cf_i+2\mu} \quad . \tag{6.9}$$

The probability an animal survived both natural and harvest mortality over a year was then modeled as

$$S = e^{-\ c_1 f+2\mu} \quad e^{-10\mu} \ = e^{-\ c_1 f+12\mu} \ , \tag{6.10}$$

where $\mu$ was the monthly instantaneous mortality rate and $c$ was the vulnerability coefficient.

In this analysis, the instantaneous natural mortality rate $\mu$ was assumed to be constant over the duration of the reconstruction. Harvest mortality was allowed to vary between years because of annual changes in hunter effort $f_i; i = 1,\ldots,21$ .

#### 6.3.1.2 Auxiliary Radiotelemetry Likelihood

There were three observable outcomes from the tagging data:

1. Animal survived the entire year, the hunting season $S_1$ , and the following non-hunting season $S_2$ with probability $S_1 S_2$.
2. Animal was harvested in the hunting season with probability $1-S_1\ H$ where $H$ is the conditional probability of being harvested, given the animal died in the first period.

3. Animal died due to natural causes with probability $1-S_1 \quad 1-H \quad +S_1 \quad 1-S_2$ .

Note:

$$S_1S_2 + \ 1-S_1 \ \ H + \ 1-S_1 \quad 1-H \ \ +S_1 \ \ 1-S_2 \ \ =1. \tag{6.11}$$

The likelihood was stratified by animal age classes 1.5 and 2.5 (Table 6.3).

Table 6.3 Summary of radiotelemetry results by year for juvenile (1.5 years) and adult (2.5+ years and older) age classes of cougar provided by the Oregon Department of Fish and Wildlife.

| | Juveniles (1–2 years) | | | Adults (2+ years) | | |
|---|---|---|---|---|---|---|
| Year | Alive | Natural mortality | Harvest mortality | Alive | Natural mortality | Harvest mortality |
| 1987 | 0 | 0 | 0 | 1 | 0 | 0 |
| 1988 | 2 | 0 | 0 | 2 | 0 | 0 |
| 1989 | 1 | 1 | 0 | 8 | 0 | 0 |
| 1990 | 5 | 0 | 0 | 7 | 1 | 5 |
| 1991 | 3 | 1 | 0 | 13 | 0 | 2 |
| 1992 | 2 | 1 | 0 | 16 | 2 | 1 |
| 1993 | 4 | 0 | 2 | 18 | 1 | 5 |
| 1994 | 3 | 0 | 0 | 21 | 0 | 4 |

Define:

$c_J$ = vulnerability coefficient for 1.5-year-old juveniles;

$c_A$ = vulnerability coefficient for adults $\geq 2.5$ years old;

$\mu_J$ = instantaneous natural mortality rate for 1.5-year-old juveniles;

$\mu_A$ = instantaneous natural mortality rate for subadults and adults 2.5 years and older.

It was assumed natural mortality rates were constant over years but differed between juvenile and adult age classes. Harvest mortality was affected by age class and hunter effort. The above probabilities were then defined for juveniles as:

$$S_{J1} = e^{-\ c_J f_i + t\mu_J}\ , \quad S_{J2} = 1 - e^{-(12-t)\mu_J}, \quad H_J = \left( \frac{c_J f_i}{c_J f_i + t\mu_J} \right)$$

and for adults as:

$$S_{A1} = e^{-\ c_A f_i + t\mu_A}\ , \quad S_{A2} = 1 - e^{-(12-t)\mu_J}, \quad H_A = \left( \frac{c_A f_i}{c_A f_i + t\mu_J} \right).$$

The auxiliary likelihood had four different contributions, age-class-specific mortality coefficients $\mu_J, \mu_A$ and age-class-specific vulnerability coefficients (i.e., $c_J$, $c_A$ ).

For juveniles that were 1.5-year-olds,

$$L = \prod_{i=1}^{8} \left[ \begin{pmatrix} J_i \\ a_i, h_i, n_i \end{pmatrix} e^{-\ c_J f_i + 12\mu_J}{}^{a_i} \left( \left( \frac{c_J f_i}{c_J f_i + 2\mu_J} \right) 1 - e^{-\ c_J f_i + 2\mu_J} \right)^{h_i} \right.$$
$$\left. \cdot \left( \left( \frac{2\mu_J}{c_J f_i + 2\mu_J} \right) 1 - e^{-\ c_J f_i + 2\mu_J} + e^{-\ c_J f_i + 2\mu_J} \quad 1 - e^{-10\mu_J} \right)^{n_i} \right]; \tag{6.12}$$

For the adults 2.5 years and older,

$$L = \prod_{i=1}^{8} \left[ \begin{pmatrix} A_i \\ a_i, h_i, n_i \end{pmatrix} e^{-\ c_A f_i + 12\mu_J}{}^{a_i} \left( \left( \frac{c_A f_i}{c_A f_i + 2\mu_A} \right) 1 - e^{-\ c_A f_i + 2\mu_A} \right)^{h_i} \right.$$
$$\left. \cdot \left( \left( \frac{2\mu_A}{c_A f_i + 2\mu_A} \right) 1 - e^{-\ c_A f_i + 2\mu_A} + e^{-\ c_A f_i + 2\mu_A} \quad 1 - e^{-10\mu_A} \right)^{n_i} \right]; \tag{6.13}$$

where

$J_i$ = number of juvenile cougars (i.e., 1.5) that had tags in year *i*,

$A_i$ = number of adult cougars (i.e., 2.5+) that had tags in year *i*,

and where

$a_i$ = number of animals that survived in year *i*,

$h_i$ = number of animals harvested in year *i*,

$n_i$ = number of natural mortalities in year *i*.

Note, age-class notations associated with $a_i$, $h_i$, and $n_i$, were omitted only for the convenience of expressing the likelihoods. Note, too, annual natural survival probability for juveniles is estimated as

$$S_J = e^{-12\mu_J}$$

and, similarly, for adults,

$$S_A = e^{-12\mu_A} .$$

#### 6.3.1.3 Catch-Effort Likelihood

The harvest numbers were modeled as a function of harvest numbers, total abundance, effort, and vulnerability coefficients (Table 6.2). The likelihood was parameterized to differentiate juvenile and adult harvest rates. Also, the catch-effort models must account for those animals that are both aged and harvested. The model was constructed as follows.

For age class 1.5 individuals,

$$L = \prod_{i=1}^{8} \binom{N_{i1}}{h_{i1}} \left( \left( \frac{c_J f_i}{c_J f_i + 2\mu_J} \right) 1 - e^{-c_J f_i + 2\mu_J} \quad r_i \right)^{h_{i1}}$$
$$\cdot \left( 1 - \left( \left( \frac{c_J f_i}{c_J f_i + 2\mu_J} \right) 1 - e^{-c_J f_i + 2\mu_J} \quad r_i \right) \right)^{N_{i1} - h_{i1}} . \tag{6.14}$$

where

$r_i$ = sampling fraction for aging in year $i$,

$f_i$ = hunter effect in year $i$,

$N_{i1}$ = abundance in age class 1 in year $i$,

$h_{i1}$ = number of animals aged in age class 1 in year $i$.

For age classes 2.5+,

$$L = \prod_{i=1}^{8} \binom{N_{i,2+}}{h_{i,2+}} \left( \left( \frac{c_A f_i}{c_A f_i + 2\mu_A} \right) 1 - e^{-c_A f_i + 2\mu_A} \quad r_i \right)^{h_{i,2+}}$$
$$\cdot \left( 1 - \left( \left( \frac{c_A f_i}{c_A f_i + 2\mu_A} \right) 1 - e^{-c_A f_i + 2\mu_A} \quad r_i \right) \right)^{N_{i,2+} - h_{i,2+}} . \tag{6.15}$$

where

$N_{i,2+}$ = abundance of age classes 2.5+ in year $i$,

$h_{i,2+}$ = number of animals aged in age classes 2.5+ in year $i$.

#### 6.3.1.4 Reporting Likelihood

The proportion of the total harvest that was aged was modeled as a function of total annual harvest, the number of aged animals, and a year-specific aging proportion (Table 6.2). The likelihood was modeled as follows

$$L_{\text{Aging}} = \prod_{i=1}^{8} \binom{H_i}{E_i} r_i^{\;E_i} \; 1 - r_i^{\;H_i - E_i} \tag{6.16}$$

for

$H_i$ = number of animals harvested,

$E_i$ = number of animals examined for age,

$r_i$ = year-specific sampling fraction.

#### 6.3.1.5 Age-at-Harvest Likelihood

The parameterization of the age-at-harvest likelihood was based on juvenile and adult natural survival parameters $\mu_J, \mu_A$ and vulnerability coefficients that were age-class specific ($c_J$, $c_A$). Consider the cohort represented by abundance $N_{11}$ (i.e., age class 1 in 1987). The age-at-harvest likelihood modeled the expected number of animals harvested in consecutive years as follows:

$$\begin{aligned}
E\;\; h_{11} &= N_{11}\left(\frac{c_J f_1}{c_J f_1 + 2\mu_J}\right) 1 - e^{-\,c_J f_1 + 2\mu_J} \quad r_1 = N_{11}\theta_{11} \\
E\;\; h_{22} &= N_{11}\;\; e^{-\,c_J f_1 + 12\mu_J} \;\; \left(\frac{c_A f_2}{c_A f_2 + 2\mu_A}\right) 1 - e^{-\,c_A f_2 + 2\mu_A} \quad r_2 = N_{11}\theta_{22} \\
E\;\; h_{33} &= N_{11}\;\; e^{-\,c_J f_1 + 12\mu_J} \;\; e^{-\,c_A f_2 + 12\mu_A} \;\; \left(\frac{c_A f_3}{c_A f_3 + 2\mu_A}\right) 1 - e^{-\,c_A f_2 + 2\mu_A} \quad r_3 = N_{11}\theta_{33} \\
&\vdots
\end{aligned}$$

The likelihood for this cohort was then

$$L = \binom{N_{11}}{\underset{\sim}{h}_{ij}} \prod_{i=0}^{Y-1} \theta_{1+i,1+i}^{\,h_{1+i,1+i}} \left(1 - \sum_{i=0}^{Y-1} \theta_{1+i,1+i}\right)^{N_{11} - \sum_{i=0}^{Y-1} h_{1+i,1+i}} . \tag{6.17}$$

I used Program USER to construct and optimize the age-at-harvest likelihood, along with the likelihoods for catch-effort, reporting, and the auxiliary radiotelemetry data. I

examined four alternative models for the cougar population; these included $McS$, $McS_{1.5,2.5+}$, $Mc_{1.5,2.5+}S$, and $Mc_{1.5,2.5+}S_{1.5,2.5+}$, where:

Model $McS$: A single instantaneous mortality coefficient ($\mu$) constant over time and across age classes, and one vulnerability coefficient ($c$) constant across age classes and time.

Model $McS_{1.5,2.5+}$: Two age-specific instantaneous mortality coefficients ($\mu_{1.5}, \mu_{2.5+}$) constant over time and one vulnerability coefficient ($c$) constant across age classes and time.

Model $Mc_{1.5,2.5+}S$: A single instantaneous mortality coefficient ($\mu$) constant over time and across age classes, and two age specific vulnerability coefficients $c_{1.5}, c_{2.5+}$ constant across time.

Model $Mc_{1.5,2.5+}S_{1.5,2.5+}$: Two age-specific instantaneous mortality coefficients ($\mu_{1.5}$, $\mu_{2.5+}$) constant over time two age specific vulnerability coefficients ($c_{1.5}$, $c_{2.5+}$) constant across time.

I based model selection on likelihood ratio tests (LRTs), Akaike's Information Criterion (AIC) (Burnham and Anderson 2002), and residual analysis to find the most appropriate model. The reported standard errors were expanded by the scale parameter based on a goodness-of-fit to the age-at-harvest matrix where:

$$\text{Scale parameter} = \sqrt{\frac{\chi^2_{\text{df}}}{\text{df}}}, \qquad \chi^2_{\text{df}} = \sum\left(\frac{\text{Observed}_i - \text{Expected}_i}{\sqrt{\text{Expected}_i}}\right)^2,$$

df = number of cells in the age-at-harvest matrix – number of parameters estimated.

The models were unable to estimate juvenile abundance in the final year of the study (i.e., $N_{8,1}$) because no juveniles were harvested in the final year of the study (1994). Average historic recruitment levels were used to estimate juvenile abundance in 1994.

## 6.4 Results

The best population reconstruction model based on AIC was model $Mc_{1.5,2.5+}S_{1.5,2.5+}$ (Table 6.4). An LRT showed that the best model ($Mc_{1.5,2.5+}S_{1.5,2.5+}$) was significantly different from all other models tested (Table 6.5). The Anscombe residuals for the $Mc_{1.5,2.5+}S_{1.5,2.5+}$ model did not indicate a lack of fit (Figure 6.2) to the age-at-harvest data. Model $Mc_{1.5,2.5+}S_{1.5,2.5+}$ was selected for the cougar population reconstruction.

Cougar annual abundance estimates remained stable during the course of the study (1987–1994), with a maximum estimate of 611 cougars (SE = 115.55) in 1986 and a minimum estimate of 577 cougars (SE = 125.02) in 1988 (Figure 6.2, Table 6.7). Harvest probability estimates ranged from 0.126 (SE = 0.026) to 0.154 (SE = 0.032) for adults (age 2.5+) and from 0.014 (SE = 0.0078) to 0.017 (SE = 0.0063) for juveniles (age 1.5) with no discernable trends (Figure 6.4). Annual recruitment estimates declined from 145 cougars (SE = 34.15) in 1987 to 71 cougars (SE = 0.26.37) in 1988, and rebounded to 122 cougars (SE = 57.26) in 1990 (Figure 6.5). The chosen model (i.e., $Mc_{1.5,2.5+}S_{1.5,2.5+}$) estimated age specific harvest vulnerability and natural survival coefficients (Table 6.6). Juvenile (age 1.5) cougar natural survival probability was estimated to be 0.887 (SE = 0.117), slightly lower than the adult (age 2.5+) cougar natural survival probability estimate of 0.979 (SE = 0.019).

Table 6.4. Likelihood and Akaike information criterion (AIC) values for alternative population reconstruction models for cougars in North East Oregon.

| Model | ln $L$ | No. of model parameters | AIC |
|---|---|---|---|
| $McS$ | –416.549 | 28 | 889.098 |
| $McS_{1.5,2.5+}$ | –416.5387 | 29 | 891.077 |
| $Mc_{1.5,2.5+}S$ | –333.1027 | 29 | 724.21 |
| $Mc_{1.5,2.5+}S_{1.5,2.5+}$ | –330.9958 | 30 | 721.99 |

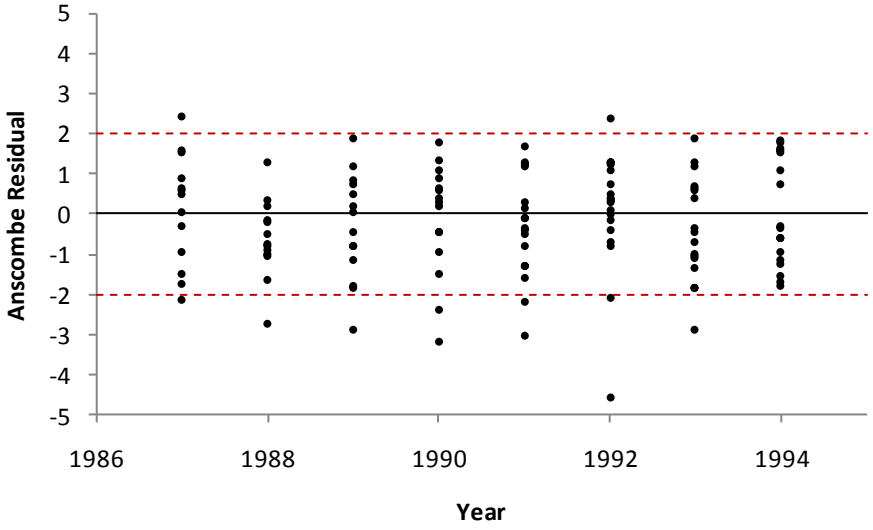
Table 6.5. Likelihood ratio tests (LRTs) comparing alternative nested population reconstruction models for cougars in Northeast Oregon.

| Full–reduced | Chi-square | df | $P$ |
|---|---|---|---|
| $McS_{1.5,2.5+}$ vs. $McS$ | 0.021 | 1 | 0.886 |
| $Mc_{1.5,2.5+}S$ vs. $McS$ | 166.893 | 1 | 0.000 |
| $Mc_{1.5,2.5+}S_{1.5,2.5+}$ vs. $McS_{1.5,2.5+}$ | 171.086 | 1 | 0.000 |
| $Mc_{1.5,2.5+}S_{1.5,2.5+}$ vs. $Mc_{1.5,2.5+}S$ | 4.214 | 1 | 0.040 |

Table 6.6. Maximum likelihood estimates of vulnerability and natural mortality coefficients from model $Mc_{1.5,2.5+}S_{1.5,2.5+}$, for a cougar population in Oregon.

| Parameter | Estimate | SE |
|---|---|---|
| $c_{1.5}$ | 0.103 | 0.046 |
| $c_{2.5+}$ | 0.974 | 0.216 |
| $\mu_{1.5}$ | 0.0099 | 0.0105 |
| $\mu_{2.5+}$ | 0.0018 | 0.0016 |

a)




b)

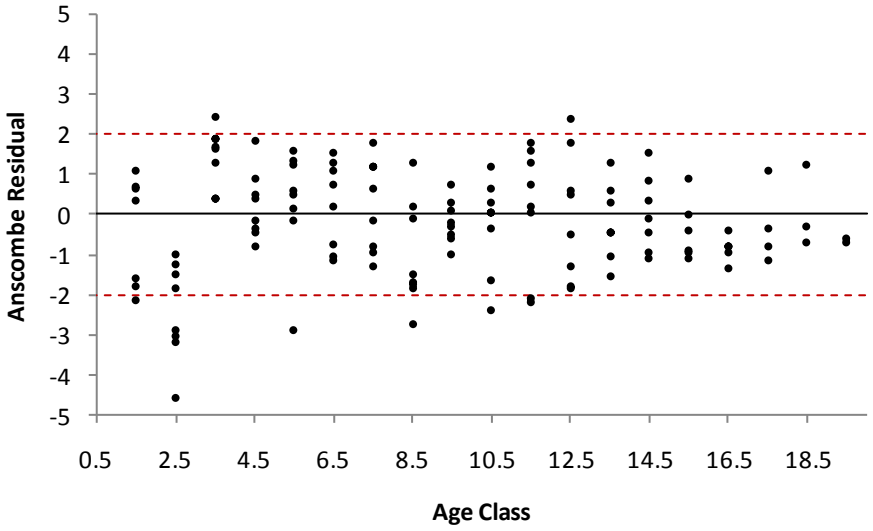



Figure 6.2. Anscombe residuals based on the best available population reconstruction model (i.e., $Mc_{1.5,2.5+}S_{1.5,2.5+}$) by year (a) and age class (b) for cougars in Oregon 1987-2007.

Table 6.7. Estimates of cougar abundance by age class and year, for management zone E (management units 53–64), Oregon, 1987–2007, based on a statistical population reconstruction.

| Yr | Age class | | | | | | | | | | | | | | | | | | | Annual abundance | SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1.5 | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 | 8.5 | 9.5 | 10.5 | 11.5 | 12.5 | 13.5 | 14.5 | 15.5 | 16.5 | 17.5 | 18.5 | 19.5 | | |
| 1987 | 145.1 | 115.5 | 101.2 | 74.2 | 39.2 | 29.7 | 29.7 | 10.6 | 10.6 | 15.4 | 1.0 | 4.2 | 0.0 | 3.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 579.7 | 97.77 |
| 1988 | 105.2 | 126.8 | 97.8 | 85.7 | 62.8 | 33.2 | 25.1 | 25.1 | 9.0 | 9.0 | 13.0 | 0.9 | 3.6 | 0.0 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 599.8 | 106.48 |
| 1989 | 101.7 | 91.9 | 107.1 | 82.6 | 72.4 | 53.1 | 28.1 | 21.2 | 21.2 | 7.6 | 7.6 | 11.0 | 0.7 | 3.0 | 0.0 | 2.3 | 0.0 | 0.0 | 0.0 | 611.5 | 115.55 |
| 1990 | 80.3 | 89.0 | 78.3 | 91.3 | 70.4 | 61.7 | 45.2 | 23.9 | 18.1 | 18.1 | 6.5 | 6.5 | 9.4 | 0.6 | 2.6 | 0.0 | 1.9 | 0.0 | 0.0 | 603.6 | 121.09 |
| 1991 | 71.0 | 70.0 | 74.1 | 65.3 | 76.1 | 58.7 | 51.4 | 37.7 | 19.9 | 15.1 | 15.1 | 5.4 | 5.4 | 7.8 | 0.5 | 2.2 | 0.0 | 1.6 | 0.0 | 577.2 | 125.05 |
| 1992 | 88.9 | 62.0 | 59.0 | 62.5 | 55.0 | 64.1 | 49.5 | 43.3 | 31.8 | 16.8 | 12.7 | 12.7 | 4.5 | 4.5 | 6.6 | 0.4 | 1.8 | 0.0 | 1.3 | 577.7 | 133.75 |
| 1993 | 122.2 | 77.5 | 51.4 | 48.9 | 51.8 | 45.6 | 53.1 | 41.0 | 35.9 | 26.3 | 13.9 | 10.5 | 10.5 | 3.8 | 3.8 | 5.5 | 0.4 | 1.5 | 0.0 | 603.6 | 149.04 |
| 1994 | 102.1 | 106.6 | 64.1 | 42.5 | 40.4 | 42.8 | 37.7 | 43.9 | 33.9 | 29.7 | 21.8 | 11.5 | 8.7 | 8.7 | 3.1 | 3.1 | 4.5 | 0.3 | 1.2 | 606.6 | 136.09 |

Figure 6.3. Annual trend in abundance of cougars in Oregon 1987-2007, based the best available population reconstruction model (i.e., $Mc_{1.5,2.5+}S_{1.5,2.5+}$), and associated 95% confidence intervals (dashed lines).

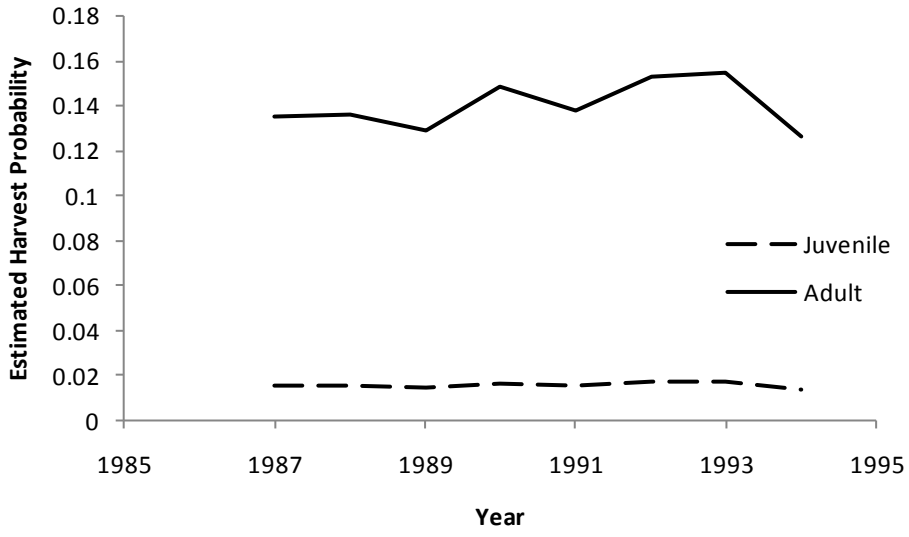



Figure 6.4. Annual trend in harvest probability of cougars in Oregon 1987-2007, based the best available population reconstruction model (i.e., $Mc_{1.5,2.5+}S_{1.5,2.5+}$)

Figure 6.5. Annual trend in recruitment (age class 1.5) of cougars in Oregon 1987-2007, based the best available population reconstruction model (i.e., $Mc_{1.5,2.5+}S_{1.5,2.5+}$), and associated 95% confidence intervals (dashed lines).

## 6.5 Discussion

The SPR presented here suggests that cougar abundances in a portion of the Blue Mountains management zone of NE Oregon have remained fairly constant from 1987–1994.

The SPR presented here is an example of modeling natural survival and harvest as concurrent processes. Modeling harvest and survival simultaneously removes the assumption that natural mortality is negligible during the harvest season, which was assumed in previous SPR models (Skalski et al 2007, Chapters 3–5). When the hunting season is of significant length, as it is here with the cougar analysis, it would be unrealistic to assume that no natural mortality occurs during the harvest season. In addition, this model structure accommodates a change in the length of the hunting season. The natural survival estimate encompasses all mortality that is not reported harvest, including but not limited to non-

recovered kills and illegal harvest, sources of mortality not likely to be negligible during the hunting season. While mathematically more complicated, the harvest and natural survival processes as modeled here are the most appropriate for many population reconstruction situations.

Using the number of hunters as the measure of effort did not seem to hinder model performance in this analysis. Although a very coarse measure of effort, the number of hunters in a season seemed to adequately capture the catch-effort relationship. However, a more refined measure of effort (e.g., hunter-days) might provide a better model fit. Auxiliary information has been recommended to augment and stabilize SPR models (Broms et. al. 2010, Chapter 5). This chapter illustrates the use of radiotelemetry auxiliary information to augment an SPR model. The radiotelemetry auxiliary data used here was extensive, spanning eight years, including both juvenile (1.5) and adult (2.5+) cougars for a total of 132 cougar-years of monitoring. The extent of the data allowed for the independent estimation of vulnerability and mortality coefficients for both juvenile and adults.

### 6.6 Management Implications

I recommend the use of SPR for harvested predator populations, given its successful application here. Also, given the successful application of SPR to the cougar population in a portion of the Blue Mountains of Oregon, I recommend expanding the use of SPR throughout the state of Oregon to model each management area, in order to assess the statewide cougar population. Age-at-harvest and catch effort data are clearly quite useful and should continue to be collected. Given that the unit of hunting effort currently being recorded works adequately, I recommend the continued collection of effort in terms of the number of hunters.

# Chapter 7: Conclusion

Statistical population reconstruction (SPR) has previously been shown to be a powerful and versatile tool to estimate multiple demographic parameters simultaneously and their associated variances, allowing for maximum information extraction with minimal resource expense (Gove et. al. 2002, Skalski et al 2007, Broms et al. 2010). Population reconstruction is an effective tool for the management of harvested species in almost any situation where age-at-harvest data is available. Statistical population reconstruction can accommodate age-at- harvest data in a myriad of situations, including data from almost any harvested species, with pooled or unpooled adult age-class data, allowing for the accommodation of a diverse range of effort measurements, across multiple management regimes, and data with or without auxiliary information.

Statistical population reconstruction has been applied to a range of harvested species, such as large ungulates (Skalski et al 2007, Chapter 3), fur bearers (Chapter 4), large predators (Chapter 6), and birds (Broms et al. 2010). The only routinely harvested class that SPR has not been applied to yet is medium-sized predators, such as coyote or bobcat. However, there is no reason why SPR could not be applied to all types of harvested animals.

Statistical population reconstruction can be used with pooled age-class information. I have shown the application of SPR to as few as three age classes (0.5, 1.5, 2.5+), with and without auxiliary data (Chapters 5 and 3). Broms et al. (2010) found that SPR could be performed with data pooled to only two age classes; however, to do so required auxiliary data. The application of SPR to pooled age-class data represents a tremendous reduction in data requirements and potential costs. In addition, this allows for SPR to be used when aging animals to adult age classes is cost prohibitive or animals cannot be aged beyond two or three

age classes accurately (Kelly 1975). The use of SPR with pooled age-class data also allows for SPR to be applied to many more data sets, thus making the method tremendously more useful and appealing to managers.

Catch-effort data is required to perform SPR; however, hunter effort can be measured in many ways. Effort can be known, which is clearly the best option, or it can be estimated (Chapters 3 and 4). Chapter 4 provides an example of estimated effort with estimation error propagated throughout the model structure. In SPR models, effort can be measured on a very fine scale, such as with trap-nights or hunter-days as in Chapters 3 and 4, or effort can be measured on a coarser scale, such as with trap-days or number of hunters as in Chapters 4 and 6. The flexibility of effort input allows for the application of SPR again across a broad range of data sources.

Traditional model evaluation methods, such as chi-square goodness-of-fit, AIC, LRT, and residual analysis, provide useful information about SPR models. AIC and likelihood ratio testing were very helpful in model selection. Chi-square goodness-of-fit tests and residual analyses were helpful in assessing the fit of the model to the data, and performing sensitivity analysis on unrealistic parameter values. However, these traditional model evaluation methods may not detect model instability. I found point deletion techniques analogous to those used in regression analysis (Neter et. al. 1983) to be very useful in evaluating the stability of population estimates derived from SPR. The point deletion techniques have also been shown to be useful in identifying the types and nature of auxiliary data that are useful in stabilizing SPR models.

Statistical population reconstruction models without auxiliary information, beyond age-at-harvest and catch-effort, often produce flat likelihoods that are difficult to optimize, can produce poor estimates of precision, and may have highly correlated parameter estimates (Chapters 4 and 5). In contrast, when SPR models are augmented with auxiliary data that independently estimate one or more model parameters, the model results are more robust to point deletion sensitivity analyses (PDSA) (Chapter 5). The addition of auxiliary data in SPR also reduces the correlations between parameters, allowing for easier optimization and increased model stability (Chapter 5). Furthermore, models with auxiliary data generally seem to have increased model fitness and improved estimates of precision (Chapters 4 and 6). I found population reconstructions based on pooled and unpooled age-class data to be stabilized equally well by auxiliary data.

Statistical population reconstruction allows for the inclusion of many types of auxiliary data. Population reconstruction has been used with auxiliary data from indices (Skalski et. al. 2007), mark-recapture studies (Chapter 5), mark-harvest studies (Chapter 5), and radiotelemetry studies (Broms et al. 2010, Chapter 6). The use of indices as auxiliary studies may be less effective than other forms of auxiliary information because they do not typically provide independent estimates of model parameters. Mark-recapture studies are good for independently estimating an abundance parameter; however, they can be labor intensive. Chapter 5 showed that it is typically better, all things being equal, to estimate a vulnerability coefficient rather than an annual abundance. Radiotelemetry studies can be used to estimate both natural survival and harvest probabilities, making them an ideal form of auxiliary information to augment SPR models.

## 7.1 Management Implications

Managing wildlife populations will become increasingly difficult with shrinking budgets and increased demands on wildlife managers to produce quality management plans that are defensible to the public, state legislators, and in court. Statistical population reconstruction can help managers fulfill these daunting tasks by making use of data that is relatively inexpensive to collect and, in many cases, already being collected. Statistical population reconstruction provides more than just an index or population trend, precise estimates of abundance, or recruitment and survival parameters. Population reconstruction provides a long-term framework for adaptive management that can be easily updated and refined through time. Furthermore, SPR can help identify future study needs and prioritization through the identification of data gaps.

I recommend the use of SPR for managers who have existing age-at-harvest and catch-effort data. An assessment of the available data should be performed using the procedures laid out in Chapter 5 to assess deficiencies in data and produce preliminary population estimates. I recommend augmenting any SPR models with auxiliary data, in order to stabilize the model and produce better estimates of precision. Point deletion techniques should be used to determine the robustness of model projections and the value of auxiliary studies. However, SPR is not only for managers with existing data.

Statistical population reconstruction is recommended for managers with no previous source of data as well. Since population reconstruction requires several years of data, collection of age-at-harvest information should begin in the next available harvest season. Collection of such data is often inexpensive and takes comparatively little logistical planning. When prioritizing funding, I recommend employing cost-saving measures in collecting age-

at-harvest data in order to afford an auxiliary study. Appropriate cost-saving measures include; pooling adult age-classes, aging only a proportion of the harvest, and the collection of a coarse measure of hunter effort. When considering to include auxiliary studies, even low precision auxiliary studies (i.e., CV = 0.50) are still tremendously useful, and much better than nothing at all. Auxiliary studies that allow for the estimation of multiple parameters are ideal, such as radiotelemetry, which allows for independent estimation of both natural survival and harvest mortality parameters.

While SPR is not a panacea for all of the challenges facing wildlife populations and their managers, it is a powerful inventory tool that can be used, in conjunction with demographic analyses, to better inform management decisions.

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