

Small Game Population Reconstruction:
Model Development and Applications

Kristin Broms

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Kristin Broms

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examining committee have been made.

Committee Members:

John R. Slaski

Andre E. Punt

Joshua J. Millspaugh

Date: _____

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Abstract

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Kristin Broms

Chair of the Supervisory Committee:
Professor John R. Skalski
Quantitative Ecology & Resource Management

Managing recreational hunting is a major responsibility for state fish and wildlife agencies. For proper management, the agencies collect information from the hunters: number of days afield, estimates of the number, sex, and species hunted, and often also age-at-harvest data. These data are sometimes used for population indices to track the effect of hunting on a given population. If an animal's age can be extracted, then the age-at-harvest information may also be used to estimate abundances through population reconstruction models. Bird game species, though, are aged through wing clippings, and can generally only be aged as young-of-the-year or as adults, their actual age can not be determined. This lack of specific aging, combined with a high natural mortality, means that traditional population reconstruction methods cannot be applied to most small game species. Presented here is a new version of population reconstruction methods that gives accurate estimates of population abundances and the variances associated with the estimates. Using maximum likelihood methods, the model estimates the natural survival rates (S_i), harvest probabilities as a function of age-specific vulnerability coefficients ($H_{i,j} = 1 - e^{-c_j f_i}$), juvenile abundances ($N_{i,1}$) and adult abundance in year 1 ($N_{1,2}$). From these parameters, the other adult abundances and yearly population estimates are derived. In this thesis, I describe the

model, present results from simulations that demonstrate the model's efficiency and robustness, and provide examples of the model being applied to mourning doves at the James A. Reed Memorial Wildlife Area in Missouri and the statewide population of sage grouse in Oregon. The results are compared to common population indices and parameter estimates from the literature.

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Chapter 1

INTRODUCTION

Harvest management began in the 1800s in response to the collapsing populations of many North American game species. Previously common species such as the passenger pigeon, bison, wood duck, wild turkey, California condor, and peregrine falcon, species often noted in early natural history accounts for their plentiful abundance, were almost hunted to extinction (Bolen and Robinson 2003). After the demise of the passenger pigeon, regulations began on hunting and poaching to protect other species from the same fate.

In the beginning, harvest management consisted mainly of adding more and more restrictions to the existing hunting regulations (Bolen and Robinson 2003). In the 1930s, the work of Aldo Leopold became popular and science began to be integrated into wildlife management decisions (Bolen and Robinson 2003).

As many of the populations of concern and others have recovered or stabilized, overexploitation is no longer the main concern of their management (Strickland et al. 1994). Harvest is now managed under 3 chief objectives: conservation, to raise densities of small or declining populations; sustained yield management, to maintain stable populations while maximizing hunter yield; and control, to stabilize or reduce populations that have become a nuisance (Strickland et al. 1994).

Wildlife managers set these objectives to please hunters, to meet the public's desire to see more or less wildlife, and to maximize the benefits of hunting, which are manyfold. Economically, the sport provides a revenue boost to surrounding stores and landowners, and the license sales fund research and the habitat management (Strick-

land et al. 1994). Politically, hunting effects land use planning and habitat protection (Strickland et al. 1994). Hunting also has a huge impact on the wildlife. For example, if hunters prefer males over females, or if the young-of-the-year are more vulnerable to hunting, population sizes, sex-age ratios and reproductive capabilities are affected. Wildlife behavior can be modified; heavy hunting encourages birds to flush more readily and elk to change migration routes in response (Strickland et al. 1994).

Harvested species fall into 2 broad categories: big game and small game (Strickland et al. 1994). Big game, or large game, are the ones that often rank higher in public interest and have greater visibility. They are of the taxonomic orders Carnivora and Artiodactyla, and include bears, cats, pigs, elk, and deer. Small game covers all other animals, including small mammals (squirrel, rabbit, fox), upland birds (grouse, pheasant), and migratory birds (duck and geese) (Strickland et al. 1994). Small game are usually less visible and therefore harder to monitor. In general, they have lower survival rates and shorter life spans than big game leading to different population characteristics.

The management of these animals is set by following historical policies or through the creation of a management plan. Species that have been historically harvested at a specific level and appear to remain stable are managed by plans set through tradition (Strickland et al. 1994). Other hunting regulations, especially for species in decline, are set more proactively with specific goals. The development of such a harvest management plan includes 4 steps: (1) Determine the status of the population; (2) Define the goals and objectives of management; (3) Establish strategies to attain objectives; and (4) Determine how well the strategies achieved the objectives (Strickland et al. 1994).

The status of a population is determined through historical records and research with techniques that allow for year-to-year comparisons. One of the most popular ways to determine the status of a species is through a population index. Indices are

inexpensive, noninvasive and have a specific species focus. They are usually easy to gather, requiring little time, personnel, or strenuous work. Animals are not handled in their collection, so the animals are not harmed in any way in the creation of an index. There are many types of indices and a population index can be specifically tailored to individual species.

There are 2 general types of indices: a direct, partial count, or an indirect measurement of a trait (Skalski et al. 2005). Partial counts include call-count surveys, breeding surveys, and incomplete line transects. Indirect indices use the evidence of an animal's presence rather than direct observations (Skalski et al. 2005). Traits related to abundance include pellet counts, track counts, and scent station surveys.

The trend in an index count is assumed to track the trend in abundance. Unfortunately this assumption is often and easily violated. First and foremost, most index surveys have not been calibrated or validated (Williams et al. 2002). This lack of rigorous statistical design means that the relationship between index and absolute abundance is practically never known, nor is the relationship between index and relative abundance known. Even if an index is tracking abundance, it is not known if the index is capturing the magnitude of the abundance changes, because it is not known if the index and abundance have a linear relationship or not.

Index counts are confounded by a multitude of variables- weather, season, year, habitat, observer skill, and detection rates. A trend in an index could be the result of a change in any of the above factors and it is not possible to discern if an index trend is measuring a change in one of the above variables or if it represents a change in population abundance (Anderson 2003). Detectability may also have spatial or temporal trends, neither of which are fully quantified or mentioned in the calibration of an index.

These drawbacks on the use of an index count raise many questions on their use in harvest management. Proposed in this thesis is a different way to gain year-to-year abundance comparisons, using population reconstruction techniques. Population

reconstruction is the use of harvest data broken down into age-classes over a series of years, “to reproduce the historical trends in animal abundance” (Gove et al. 2002). This method also provides population size estimates.

Some of the merits of population reconstruction are similar to the index counts. Population reconstruction uses harvest data from hunter check stations and hunter surveys, both of which are often already collected. Therefore, it is inexpensive, as is an index survey. Also similar to an index, it provides long term trend information, allowing for year-to-year comparisons to examine a population’s status over time.

Population reconstruction also has many advantages over an index. It is rooted in statistical theory, so its properties and assumptions can be examined and critiqued theoretically. In addition to providing the long term trend information, the reconstruction outputs yearly age-class and total absolute abundance estimates. It also outputs natural survival and natural mortality estimates. Because population reconstruction uses a statistical model, it produces standard errors for each of these estimates.

Although population reconstruction has not yet been applied to small game animals, it is not a new method in harvest management. Fry 1949 applied its concepts to a lake trout fishery with what he called a virtual population analysis. In his model, natural survival was assumed to be 100% and the only source of mortality was from fishing. Each year’s harvest was broken into age-classes. After multiple years of data were collected, more years of data than the species’ life span, minimum historical abundances were estimated. The age-class information from the harvests were added as a series of years to provide minimum population estimates for a given cohort.

Since 1949, virtual population analysis has been expanded and greatly improved. Gulland (1965) used a nonlinear system of equations to more accurately estimate abundances and explicitly incorporate natural mortality. Pope (1972) simplified the calculations in Gulland’s model via approximations to make the method usable without a computer. The methods have continued to evolve, be improved upon, and specified

for different population characteristics. Modifications of the method now include natural mortality in the model, formulas to fill in incomplete cohorts and the inclusion of stochasticity to allow for standard errors for the estimates. The use of catch-at-age data (i.e. catch-at-length) is the basis of most stock assessments in fisheries and is the “state of the art” in fisheries data analyses (Hilborn and Walters 1992). Various versions of these models are called cohort analysis, statistical catch-at-age, and tuned VPA in fisheries. For terrestrial species, they are called population reconstruction.

The population reconstruction was popularized for big game by Downing (1980) when he applied the model to a population of mule deer at Oak Creek, Utah. Advancements and adaptations of population reconstruction have since been applied to populations of moose (Fryxell et al. 1988, Ferguson 1993), elk (Laake 1992), white-tailed deer (Roseberry and Woolf 1991, Novak et al. 1991), black-tailed deer (Gilbert and Raedeke 1994) and black bear (Gove et al. 2002). The most recent advancement was the introduction of a statistical version of the model so that estimates included standard errors (Gove et al. 2002, Skalski et al. 2005). The work in this thesis was inspired by her statistical population reconstruction model.

Up until this point, population reconstruction has been limited to big game species. Traditionally, reconstruction assumes that natural mortality is low, but most small game species are believed to have high natural mortality. The greater complication is that small game cannot be aged as accurately as big game; most small game species can only be identified as juvenile or adult. Once adults, the animal’s exact age, whether it is 1, 2, or 3+ years old, cannot be determined. Because the animals cannot be aged to the year, they cannot be separated into distinct age classes and independent cohorts can no longer be tracked through time. Most population reconstruction models are based on the use of independent cohorts, making traditional population reconstruction intractable for small game.

In this thesis, I introduce and evaluate a new version of population reconstruction that is applicable to harvested species with only limited aging information. In general,

this version uses the same age-at-harvest data as more traditional methods. The loss of independent cohorts does mean that the model will require more information and will have a slightly different sampling design. In addition to the age-at-harvest data, the model also must input catch-effort data and possibly a third set of auxiliary data.

In Chapter 2, I introduce the specifics of the methods used in the small game population reconstruction model. The methods are based on the concepts of traditional population reconstructions, but the limited aging information changed the model structure and processes. I describe in detail the sampling process that led to the small game population reconstruction models. The models are tested through a series of simulations to evaluate its precision and accuracy. Because of its differences from previous big game population reconstruction models, there was uncertainty surrounding the model behavior. Through the simulation work, I hope to answer questions on the practical use of the population reconstruction technique.

There was also uncertainty as to whether, after being tested, the model will actually produce realistic, reliable estimates with real data. Necessarily, real data does not match the model assumptions as well as computer-generated data, and unmet assumptions may affect the output. Therefore, two examples are provided to further examine the model's utility. The first example, in Chapter 3, is a population reconstruction of a mourning dove population in the James A Reed Memorial Wildlife Area near Kansas City, Missouri. It is a short data set, 5 years long, and is of a species with a high harvest mortality. The second example, in Chapter 4, analyzes the statewide population of sage grouse in Oregon. It is an extensive data set, 14 years long, and the species has a low harvest mortality. A comparison of the results of these two disparate examples should provide additional insight into the model's mechanisms.

Through this thesis, I hope to validate the application of population reconstruction to small game and provide recommendations on its uses. The simulations will clarify the species and harvest characteristics for which the most precise and accurate results can be expected, and for which situations the model is not applicable. The work

should be beneficial to state fish & wildlife agencies with the responsibility to manage small game populations. For species like doves, ducks or wild turkeys where wing samples are typically collected, the population reconstruction may provide a means to analyze these commonly collected but neglected data.

Chapter 2

MODEL DEVELOPMENT AND EVALUATION

2.1 Introduction

In this chapter, I introduce the processes and likelihoods that form the small game population reconstruction model. The objective is to describe model processes, equations, and assumptions. The general concepts of the model are similar to the population reconstruction used for large game species, but there are many notable differences in the structure of the model that are explained in detail.

Once the model is developed, I describe several sets of simulations to assess the model's accuracy and precision. It was unknown whether population reconstruction models could provide accurate abundance estimates for small game because of the demographic differences from large game and because of the necessity of using numerical methods for parameter estimation.

The purpose of the first set of simulations is to gain a general idea of how well the model performs and under what situations it should be applied. A variety of different data characteristics are inputted. These scenarios had altering juvenile and adult demographic parameters, levels of harvest, and assorted auxiliary information. This set constituted the bulk of the simulation work completed.

A second set of simulations rigorously tests the effect of harvest mortalities on parameter estimation. The first set of simulations concluded that the harvest mortality rate had a significant effect on the parameter estimates. This notion is further tested to learn the full range of harvest mortalities for which the model could be applied.

The third set of simulations tests the robustness of the model; I generate data under one set of assumptions, but estimate model parameters under alternative as-

sumptions. This set of simulations is important because it is often not known whether juveniles and adults are equally vulnerable to hunting, or if they have similar natural survival rates.

From the simulations, I conclude that the model can have varying degrees of success. With enough inputted data, it has the potential to be a powerful management tool.

2.2 Model Development

Small game population reconstruction uses both the age-at-harvest and catch-effort information to estimate abundances and the other demographic information. The age-at-harvest information is the basis of the age-class structure, and the catch-effort data builds on top to reconstruct the abundance sizes. The structure and constraints of the model, which includes deriving the adult abundances from the other parameters, reduces the number of parameters, allotting enough degrees of freedom to make them estimable. Estimates are obtained through maximum likelihood estimation (MLE) of binomial distributions.

The flow diagram (Figure 2.1) demonstrates the sampling process associated with the model. In each year i for which data is available, there is a population of size N_i , comprised of juveniles, $N_{i,1}$, and adults, $N_{i,2}$, so that $N_i = N_{i,1} + N_{i,2}$.

From the population, N_i , a random sample is harvested. The number harvested (h_i) is the sum of the number of juveniles ($h_{i,1}$) and adults ($h_{i,2}$) harvested. The harvest, h_i , is a random variable; the expected number harvested is the sum of the age-class specific abundances times the age-class specific harvest mortalities (Figure 2.1).

$$E[h_i] = E[h_{i,1} + h_{i,2}] = E[h_{i,1}] + E[h_{i,2}] = N_{i,1} \cdot H_{i,1} + N_{i,2} \cdot H_{i,2} \quad (2.1)$$

Harvest mortalities are based on a relationship with hunter effort. The probability

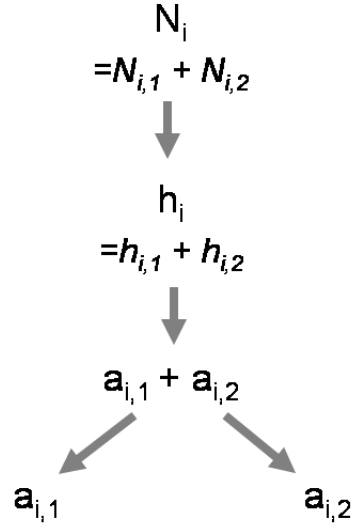


Figure 2.1: Flow diagram of the model's three stages of sampling. The symbols are described in the text and in Tables 2.1 and 2.2.

associated with the harvests for year i and age-class j is modeled as follows:

$$H_{i,j} = 1 - e^{-c_j \cdot f_i} \quad (2.2)$$

This equation says that the probability of being harvested for age class j in year i depends on c_j , the vulnerability coefficient, which is an intrinsic value of how a specific age-class is affected by hunting effort, f_i , a measure of the hunting pressure put forth in a given season. For example, effort may be measured as total hours spent hunting, number of shots fired, hunter-days, or total number of hunters. Defining harvest mortality by this relationship and having its value dependent on effort was first used by Leslie and Davis 1939 and is a basic relationship assumed in many catch-effort models (Seber 1982, pp. 296-302).

From the harvest in the i^{th} year, h_i , a sample is aged with probability p_i . The

expected number aged is the harvest times the sampling probability, where:

$$E[a_{i,1} + a_{i,2}] = h_i \cdot p_i \quad (2.3)$$

and where $a_{i,1}$ = the number of juveniles aged in year i , and where $a_{i,2}$ = the number of adults aged in year i .

From the total number aged, each animal can either be a juvenile or an adult. It is again assumed to be random as to whether each aged animal is a juvenile or an adult. The expected number aged for each age class j in year i is therefore:

$$E[a_{i,j}] = N_{i,j} \cdot H_{i,j} \cdot p_i \quad (2.4)$$

This sampling process is repeated for each year that aging data and catch-effort information is known. From the process, model specific juvenile recruitment, $N_{i,1}$, is estimated for all years, and model-specific adult abundance, $N_{1,2}$, is estimated for the first year only. Adult abundance in subsequent years is extrapolated by using the following equation:

$$\hat{N}_{i,2} = \hat{N}_{i-1,1} \cdot S_1 \cdot (1 - H_{i-1,1}) + \hat{N}_{i-1,2} \cdot S_2 \cdot (1 - H_{i-1,2}) \quad (2.5)$$

The adult population in year i is the juveniles from the previous year that survived natural causes of death and that survived the hunting season plus the adults from the previous year that survived natural causes of death and that survived the hunting season (Figure 2.2). It was assumed that all juveniles had an equal probability of surviving natural sources of mortality each year, and all adults had an equal probability of natural survival.

Year	Age Class		Population
	Juvenile	Adult	
1	$N_{1,1}$	$N_{1,2}$	N_1
2	$N_{2,1}$	$N_{2,2}$	N_2
3	$N_{3,1}$	$N_{3,2}$	N_3
4	$N_{4,1}$	$N_{4,2}$	N_4
⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮

+		=
↓		↙
+	$= N_{1,1} S_1 (1-H_{1,1}) + N_{1,2} S_2 (1-H_{1,2})$	↘
↓		↙
+	$= N_{2,1} S_1 (1-H_{2,1}) + [N_{1,1} S_1 (1-H_{1,1}) + N_{1,2} S_2 (1-H_{1,2})] S_2 (1-H_{2,2})$	↘
↓		↙
+	$= N_{3,1} S_1 (1-H_{3,1}) + \{N_{2,1} S_1 (1-H_{2,1}) + [N_{1,1} S_1 (1-H_{1,1}) + N_{1,2} S_2 (1-H_{1,2})] S_2 (1-H_{2,2})\} S_2 (1-H_{3,2})$	↘

Figure 2.2: The adult abundances in the small game reconstruction model are derived from the survival, harvest and recruitment processes.

2.2.1 Model Equations

The sampling process described in the preceding section becomes a joint likelihood of 3 binomial relationships. Each of the resulting equations and the derivation of the harvest mortalities will be discussed separately and then combined at the end of this section.

The first part of the joint likelihood incorporates the catch-effort data and the process of sampling the harvest from the population. As a binomial distribution, it is as follows:

$$L_{catch} = \prod_{i=1}^Y \binom{N_i}{h_i} \left(\frac{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}}{N_{i,1} + N_{i,2}} \right)^{h_i} \left(1 - \frac{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}}{N_{i,1} + N_{i,2}} \right)^{N_i - h_i} \quad (2.6)$$

Every year of data is considered independently forming the joint likelihood in the above equation. The total harvest probability is taken to be the total expected harvest divided by the total population for year i . All juveniles are assumed to have an equal probability of being harvested, as are all adults, in each year. The harvest mortalities are defined by Equation 2.2.

The likelihood associated with the sampling probability is

$$L_{samp} = \prod_{i=1}^N \binom{h_i}{a_{i,1} + a_{i,2}} p_i^{a_{i,1} + a_{i,2}} (1 - p_i)^{h_i - (a_{i,1} + a_{i,2})} \quad (2.7)$$

Because the total harvest and total number aged are known, p_i can be estimated independently from the other parameters and L_{samp} is independent from the other likelihoods. Therefore, the sampling probability and its likelihood, although necessary in the conceptual description of the model, drop out of the equations because their derivation is independent of the other parameters and are not present in the other parts of the joint likelihood function.

The second part of the joint likelihood is then the age-at-harvest likelihood, L_{AAH} , which utilizes the aging information (juvenile or adult) to help with the parameter

estimation. It reflects how the age ratios from the harvest relate to the age ratios in the population, taking into account the fact that juveniles and adults may be harvested at different rates.

$$L_{AAH} = \prod_{i=1}^Y \binom{a_{i,1} + a_{i,2}}{a_{i,1}} \left(\frac{N_{i,1}H_{i,1}}{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}} \right)^{a_{i,1}} \left(\frac{N_{i,2}H_{i,2}}{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}} \right)^{a_{i,2}} \quad (2.8)$$

The small game population reconstruction model can therefore be written as the following joint likelihood:

$$L_{joint} = L_{catch} \cdot L_{AAH}$$

It is a combination of Equations 2.6 and 2.8. The variables and parameters are defined in Tables 2.1 and 2.2, and $H_{i,j} = 1 - e^{-c_j \cdot f_i}$. Including the derivations of the adult abundances (Equation 2.5) in likelihoods 2.6 and 2.8, the joint model can be fully expressed as follows:

$$\begin{aligned} L_{catch} = & \binom{N_1}{h_1} \left(\frac{N_{1,1}H_{1,1} + N_{1,2}H_{1,2}}{N_{1,1} + N_{1,2}} \right)^{h_1} \cdot \\ & \left(1 - \frac{N_{1,1}H_{1,1} + N_{1,2}H_{1,2}}{N_{1,1} + N_{1,2}} \right)^{N_1 - h_1} \cdot \\ & \binom{N_2}{h_2} \left(\frac{N_{2,1}H_{2,1} + [N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})] H_{2,2}}{N_{2,1} + [N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})]} \right)^{h_2} \cdot \\ & \left(1 - \frac{N_{2,1}H_{2,1} + [N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})] H_{2,2}}{N_{2,1} + [N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})]} \right)^{N_2 - h_2} \\ & \vdots \end{aligned} \quad (2.9)$$

$$\begin{aligned} L_{AAH} = & \binom{a_{1,1} + a_{1,2}}{a_{1,1}} \left(\frac{N_{1,1}H_{1,1}}{N_{1,1}H_{1,1} + N_{1,2}H_{1,2}} \right)^{a_{1,1}} \left(\frac{N_{1,2}H_{1,2}}{N_{1,1}H_{1,1} + N_{1,2}H_{1,2}} \right)^{a_{1,2}} \cdot \\ & \binom{a_{2,1} + a_{2,2}}{a_{2,1}} \left(\frac{N_{2,1}H_{2,1}}{N_{2,1}H_{2,1} + [N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})] H_{2,2}} \right)^{a_{2,1}} \cdot \\ & \left(\frac{[N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})] H_{2,2}}{N_{2,1}H_{2,1} + [N_{1,1}S_1(1 - H_{1,1}) + N_{1,2}S_2(1 - H_{1,2})] H_{2,2}} \right)^{a_{2,2}} \\ & \vdots \end{aligned} \quad (2.10)$$

Table 2.1: Symbols and descriptions of variables associated with the small game population reconstruction model.

Symbol	Description
<i>Survey and wing clipping information</i>	
$a_{i,1}$	No. of juveniles aged in year i
$a_{i,2}$	No. of adults aged in year i
f_i	Hunter effort in year i
h_i	Harvest (juveniles and adults) in year i
$h_{i,j}$	Harvest of age-class j in year i
<i>Mark-Recapture or Banding Study</i>	
T_1	No. of juveniles tagged
T_2	No. of adults tagged
$h_1^{(r)}$	No. of tagged juveniles found harvested
$h_2^{(r)}$	No. of tagged adults found harvested
<i>Index Survey</i>	
I_i	Index count in year i

For ease of notation, the model will be referred to in its simpler form, Equations 2.6 and 2.8, hereafter.

2.2.2 Adding an Auxiliary Likelihood

Two survivals, two vulnerability coefficients, one adult abundance, and Y years of recruitment (i.e. $N_{i,1}, (i = 1, \dots, Y)$), a total of $5 + Y$ parameters, are estimated through the model. From the model, we accrue two minimum sufficient statistics (MSS) for each year of data, one from L_{catch} and one from L_{AAH} . Theoretically, all parameters should be estimable with a minimum of five years of data (i.e. $5 + Y = 10$ and $MSS = 10$). On the other hand, if only one vulnerability coefficient is assumed or one natural survival rate, then only four years of data are necessary ($4 + Y = 8$ and $MSS = 8$). If only one vulnerability coefficient and only one survival are assumed, then only three years of data are theoretically necessary ($3 + Y = 6$ and $MSS = 6$) for all parameters to be estimable.

In reality, more than the minimum amount of information may be needed to obtain the parameter estimates. If the likelihood function is flat or the parameters highly

Table 2.2: Symbols and descriptions of parameters associated with the small game population reconstruction model.

Parameter	Description
$i = 1, \dots, Y$	The years of data used in the model
$N_{i,2}$	Adult abundance in each year i
$N_{i,1}$	Juvenile abundances in each year i
$N_i = N_{i,1} + N_{i,2}$	Total yearly abundance in each year i
S_1	Juvenile survival rate, assumed constant over time
S_2	Adult survival rate, assumed constant over time
c_1	Vulnerability coeff. for juveniles, assumed constant over time
c_2	Vulnerability coeff. for adults, assumed constant over times
$H_{i,1} = 1 - e^{-c_1 f_i}$	Hunting probability for juveniles in year i
$H_{i,2} = 1 - e^{-c_2 f_i}$	Hunting probability for adults in year i
<i>Auxiliary Index Likelihood</i>	
α	Index to abundance proportion
σ^2	Variance associated with the index- abundance relationship

correlated, the parameters may be imprecise and inaccurate. Excessive variability in the available data may also have a negative effect on model calculability.

There are a couple ways to improve the model estimates. Having more years of data allows for more degrees of freedom and more precise parameter estimates. Including additional information from other data sources, in the form of a third auxiliary likelihood, is another way to augment the estimation. I investigate both methods of model improvement in the simulations in Section 2.3. I describe the theory behind the auxiliary likelihoods in the following two subsections.

Radiotelemetry Studies

A variety of techniques and a large body of literature exist involving mark-recapture methods. This type of information can lead to the estimation of most demographic parameters, including abundance, density, natural mortality, and harvest mortality (Seber 1982).

A particular type of mark-recapture data that can readily lead to estimates of harvest mortality rates is radiotelemetry. By putting radio transmitters on the species

under study, one can continuously track movements and gain detailed, timely information on mortality. Because telemetry work can locate animals soon after death, has high recovery rates, and can identify causes of mortality, radiotelemetry is a mark-recapture technique likely to be used to estimate harvest mortalities for hunted species (Bookhout 1994, pg. 403). For the work discussed here, it is assumed that this type of study was conducted.

The likelihood associated with radiotelemetry is binomial, as in the previous model likelihoods. Here, the sample size is the number of tagged animals, the sampling probability is the harvest mortality, and the random variable is the number of tagged animals that were harvested. Broken into two age-classes, the likelihood for a telemetry study is:

$$L_{radio} = \binom{T_1}{h_1} H_{i,1}^{h_1} (1 - H_{i,1})^{T_1 - h_1} \binom{T_2}{h_2} H_{i,2}^{h_2} (1 - H_{i,2})^{T_2 - h_2} \quad (2.11)$$

The symbols are described in Table 2.1, and the harvest rates are assumed to follow the relationship of Equation 2.2.

The radiotelemetry likelihood provides a separate means to estimate the vulnerability coefficients. Because of the potentially high correlations between model parameters, independently estimating the vulnerability coefficients from a separate source can greatly help in the estimation of the other parameters as well.

Population Index

Population indices are measures of relative abundance assumed to be proportional to the true abundance of a populations. They can be used to monitor the trend of wildlife populations without interfering or disrupting the animals (Skalski et al. 2005). Indices can be either incomplete counts of animal numbers or a measurable trait that is related to abundance. Some examples of common indices include call-count surveys, scat counts, catch-per-unit-effort, and track counts.

Although indices have many shortcomings, they are a convenient way to obtain

information on a population and its trends. It is assumed that the index is proportional to the true abundance, this proportionality determined by the probability of detection, percentage counted, and area covered. For our purposes, it is assumed here that the index count (I_i) and true abundance (N_i) have a direct relationship so that $E[I_i] = \alpha \cdot N_i$ (Skalski et al. 2005). It is further assumed that the index is normally distributed about that mean with a variance of σ^2 . In likelihood form, the index information is:

$$L_{index} = \prod_{i=1}^Y \frac{1}{\sqrt{2\pi}\sigma} \exp \left[\frac{-(I_i - \alpha N_i)^2}{2\sigma^2} \right] \quad (2.12)$$

On its own, the index count is not enough information to estimate abundance because α and σ^2 are not known. The information can be incorporated with the other population reconstruction likelihoods and the additional information of population trend may help with the estimation of the total abundances, and therefore the juvenile and adult abundances. The likelihood requires the estimation of two additional parameters- α and σ^2 , but also adds one degree of freedom for each year of data. Therefore, after two years of data, its inclusion should be helpful in the population reconstruction.

Using 2 Auxiliaries

If both radiotelemetry and index data are available, it may be beneficial to include likelihoods from both studies. The model would become:

$$\begin{aligned}
 L_{joint} &= L_{catch} \cdot L_{AAH} \cdot L_{radio} \cdot L_{index} \\
 L_{catch} &= \prod_{year=i=1}^Y \binom{N_i}{h_i} \left(\frac{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}}{N_{i,1} + N_{i,2}} \right)^{h_i} \left(1 - \frac{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}}{N_{i,1} + N_{i,2}} \right)^{N_i - h_i} \\
 L_{AAH} &= \prod_{year=i=1}^Y \binom{a_{i,1} + a_{i,2}}{a_{i,1}} \left(\frac{N_{i,1}H_{i,1}}{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}} \right)^{a_{i,1}} \left(\frac{N_{i,2}H_{i,2}}{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}} \right)^{a_{i,2}} \\
 L_{radio} &= \binom{T_1}{h_1} H_{i,1}^{h_1} (1 - H_{i,1})^{T_1 - h_1} \binom{T_2}{h_2} H_{i,2}^{h_2} (1 - H_{i,2})^{T_2 - h_2} \\
 L_{index} &= \prod_{i=1}^Y \frac{1}{\sqrt{2\pi}\sigma} \exp \left[-\frac{(I_i - \alpha N_i)^2}{2\sigma^2} \right] \tag{2.13}
 \end{aligned}$$

2.2.3 Model Assumptions

As with any ecological model, some assumptions must be made in its construction. The following assumptions are associated with the small game population reconstruction:

1. The fate of every animal is independent of all other animals. The fates of the juveniles are identically distributed; and the fates of the adults are identically distributed.
2. Juvenile survival is constant across all years; adult survival is constant across all years.
3. The harvest process is correctly modeled as a function of hunter effort.
4. There is no net migration.

5. All input data is correct: the total harvest is known without error, the effort is known without error and all animals are aged correctly.
6. Tagging does not affect an animal's harvest or natural mortality (necessary when a radiotelemetry study is included in the model).
7. Index data is normally distributed with expected values defined by $E[I_i] = \alpha N_i$ (necessary when an index is included in the model).

2.3 Monte Carlo Simulations

I performed simulation work to investigate whether and when the model produces accurate estimates. The joint likelihood must be solved numerically, therefore estimates and associated standard errors may not be stable or calculable. As mentioned in Section 2.2.2, there may be enough degrees of freedom to theoretically estimate the parameters but the likelihood may be flat or the parameters may be too highly correlated for consistent maximum likelihood estimation.

The model was tested in 3 ways. In the first set of simulations, I tested how variations in the incoming data affected the model's performance. One of the results from these simulations was that average harvest mortality significantly affected the model outputs, leading to the second set of simulations. In this second set, I tested how extremes in average harvest mortality affected the model's performance and examined the optimal levels of harvest mortality for population reconstruction use.

The third set of simulations was a sensitivity analysis. I generated data with 2 survivals and 2 vulnerability coefficients and then ran the model assuming 1 survival and/or 1 vulnerability coefficient. The purpose was to gain insight into model performance when assumptions were not met.

For all tests, 600 simulations were run for each scenario. The primary purpose of the simulations was to test if the parameter estimates were bias, the standard error values were secondary. The standard errors would have required 10,000 runs in order

to approach their asymptotic values and know their biases. Instead, the simulations in this thesis were used as a starting point to learn the behavior of the standard errors.

2.3.1 Simulations to Investigate Precision and Study Design

As each species and each state have different hunting regulations, different qualities of data may result which can affect the population reconstruction precision. I conducted simulations on a variety of scenarios to evaluate how the inputted data affects the outputs. A scenario was defined by a given recruitment trend, effort variability, average harvest mortality, number of years of available data, number of vulnerability coefficients, and auxiliary study.

Through these simulations, I determined whether estimates were obtainable, whether patterns of bias in the abundance estimates exist, and whether parameter estimates were precise for the population reconstruction model.

Range of factors considered

A range of factors were considered to determine the optimal performance of the reconstruction model. All input data were chosen to be a realistic characterization of typical small game species. The sources of variation (listed in Table 2.3) are described below in detail.

Abundance trends were investigated as one source of variation related to the population characteristics. Hunting regulations may change depending on whether a population is increasing or decreasing. Therefore, it is important to know if the model can detect trends in abundance. Trends in abundance were simulated through trends in recruitment, i.e. trends in juvenile abundances. Three situations were considered: steady recruitment with a 5% CV associated with mean recruitment, noisy recruitment with a 20% CV associated with mean recruitment, and a decreasing trend where recruitment decreased by 3% each year with a 10% CV.

Table 2.3: Different levels of data variation incorporated in each simulation scenario.

Source of Variation	Levels	No. of Levels
Yearly recruitment trend	steady, not noisy steady, noisy decreasing	3
Harvest Mortalities	low high	2
Hunter Effort	low variation high variation	2
Juvenile versus Adult hunting vulnerability	2 vulnerability coefficients 1 vulnerability coefficient	2
No. of years of data	5 yrs 10 yrs	2
Type of auxiliary study	no auxiliary telemetry auxiliary population index auxiliary telemetry plus index auxiliaries	4
Total No. of Scenarios to Simulate:		192

The second population characteristic considered was harvest mortality because species experience varying levels of hunting pressure. For example, sage grouse experience a harvest rate of $< 5\%$ in Oregon, while some populations of mourning doves are harvested at rates above 50% (Willis et al. 1993). The dramatic differences between harvest mortality levels may or may not have an impact on the model's estimation. In this set of simulations, two levels of mortality were tested: low harvest mortality, where an average of 9% of the population is taken every year, and high harvest mortality, where an average of 40% of the population size is taken each year.

Another characteristic of the hunting season that interacts with the harvest mortality and may affect the model's estimation was the range of variation in the hunter effort. A wider range in effort values leads to a wider range in harvest mortalities and easier regression estimation of the vulnerability coefficients (Hilborn and Walters 1992). Models with a 10% CV and a 30% CV in effort variation were tested.

Another difference between species is that for some, juveniles and adults are equally vulnerable to hunting and therefore only one vulnerability coefficient need

be estimated. For these models, the likelihoods collapsed:

$$\begin{aligned}
 L_{joint} &= L_{catch} \cdot L_{AAH} \\
 L_{catch} &= \prod_{year=i=1}^Y \binom{N_i}{h_i} (H_i)^{h_i} (1 - H_i)^{N_i - h_i} \\
 L_{AAH} &= \prod_{year=i=1}^Y \binom{a_{i,1} + a_{i,2}}{a_{i,1}} \left(\frac{N_{i,1}}{N_{i,1} + N_{i,2}} \right)^{a_{i,2}} \left(\frac{N_{i,2}}{N_{i,1} + N_{i,2}} \right)^{a_{i,1}} \quad (2.14)
 \end{aligned}$$

Conversely, it may be previously determined that juveniles have a decidedly different harvest rate, implying two vulnerability coefficients must be incorporated into the model. This situation was described in the previous sections (Equations 2.6 and 2.8).

Differences in the data structure were also considered. Models were tested with 5 years and 10 years of available data. Because of the increase in degrees of freedom, models with 10 years of data were expected to perform better than the same model with only 5 years of data. Comparisons of models with 10 years of data to models with 5 years of data helped in determining how much there is to gain with more years of data. Testing models with only 5 years of data also determined if the model could produce stable results with the minimum number of sufficient statistics.

Another major difference between data sets was whether or not auxiliary data were available. Four situations were considered: a population where no auxiliary data were available, a population with index data, a population in which a radiotelemetry study on harvest mortalities had been completed, and a population with both the index and radiotelemetry data. The importance of a radiotelemetry study or index survey to population reconstruction can help managers decide whether they should allocate resources to such studies.

Altogether, accounting for all possible combinations of the above sources of variation, 192 different scenarios were simulated.

Model formulation

In this section, I describe how the data were generated. For each simulation, the parameters were set to simulate a specific data scenario. From these parameters, the adult abundances, the age-at-harvests, and the total harvests (Table 2.1) were generated from binomial distributions. This input data was then used in the model, and the results were compared to the originating parameters.

Constant parameters. The survivals and harvest mortalities did not vary between runs although the harvest mortalities varied between scenarios. For all models, juvenile survival was set at 0.45 and adult survival was set at 0.65. Harvest mortalities varied between scenarios in three ways. The first difference was in hunter effort. Half of the models had low variability in hunter effort, so that the range of harvest mortalities was small, and half of the models had high variability in hunter effort so that the range of harvest mortalities was greater. Models with low variation in effort used the following set of effort values: (0.140, 0.122, 0.147, 0.175, 0.157, 0.115, 0.176, 0.151, 0.133, 0.130). Models with high variation in effort used this set of effort values: (0.166, 0.116, 0.240, 0.187, 0.137, 0.187, 0.147, 0.144, 0.183, 0.144). Both sets of effort had a mean of 0.150, only the spread around this mean changed.

The second difference was in the number of vulnerability coefficients. Harvest mortalities also varied because half of the models were generated and tested under the assumption of one common harvest mortality for both juveniles and adults (Equations 2.14). The other models were generated and tested under the assumption of separate harvest vulnerabilities for juveniles and adults (Equations 2.6 and 2.8).

The third difference affecting harvest mortality values was the average harvest mortality rate. Harvest mortality had a low level, where models all had harvest mortalities between 3% and 11%, and a high level, where models all had harvest mortalities between 25% and 57%. Models with 2 vulnerability coefficients and high variability in hunter effort covered these full ranges. Models with 1 vulnerability

Table 2.4: Ranges of harvest mortalities used in data generation; the same set of harvest rates were used for each simulation.

Effort Variation	Harvest Mortality	Harvest Probabilities	
		Min	Max
Low	Low	0.034	0.084
High	Low	0.034	0.113
Low	High	0.250	0.460
High	High	0.252	0.568

coefficient and/or low variability in hunter effort had smaller ranges for the harvest mortalities.

The 2 levels of harvest mortality (low and high) were set through the vulnerability coefficients. For low harvest mortality situations, the juvenile vulnerability coefficient was 0.5 and the adult vulnerability coefficient was 0.3. For models with one vulnerability coefficient, 0.45 was used. High harvest mortalities used a juvenile vulnerability coefficient of 3.5, an adult vulnerability coefficient 2.5, and the one-coefficient models used a value of 3.0. Combined with the effort values, this led to several possibly harvest rates. The range of harvest rates that resulted from the effort and vulnerability coefficient combinations are in Table 2.4.

Adult abundances in year 1 (i.e. $N_{1,2}$) were set to 20,000 for models with low harvest mortality, and 8,000 for models with high harvest mortality. These values were chosen so that the total abundance would be stable, given the survival and harvest rates, if recruitment was constant.

Varying parameters. Recruitment values were generated from Normal distributions and changed for each simulation. The steady juvenile abundances were generated from a Normal($\mu=18,000$, $\sigma=900$) distribution. The noisy recruitments were generated from a Normal($\mu=18,000$, $\sigma=2,700$) distribution. For the declining recruitments, year 1 was generated from a Normal($\mu=18,000$, $\sigma=900$) distribution. Each year thereafter was generated with a mean of 0.97 times the previous year's juvenile

abundance, a Normal($\mu=0.97N_{i-1,1}$, $\sigma=900$) distribution.

Adult abundances were derived from binomial distributions in combination with the numbers harvested, $h_{i,j}$, and aged for each year. For each year and age-class, the harvest came from a Binomial($n=N_{i,j}$, $p=H_{i,j}$) distribution. The juveniles harvested and adults harvested were generated separately and then summed to obtain the total harvest, h_i .

The sampling probability for aging animals was set to 0.30 for all years and all data sets. The number aged, $a_{i,j}$, was estimated from Binomial($n=h_{i,j}$, $p=0.30$) distributions.

To obtain the adult abundances, the juvenile and adult survivors from the previous year were calculated and then added separately following Equation 2.5. These survivors were considered random variables and were generated from Binomial($n=N_{i-1,j}-h_{i-1,j}$, $p=S_j$) distributions.

The harvest, juveniles aged, and adults aged were all obtained for year 1, then the adult abundance was obtained for year 2, and the process was repeated for 10 years' worth of data. Similar procedures were used to generate the data for the scenarios of 5 years of data.

Auxiliary data generation. For the radiotelemetry data, the number of juveniles tagged, T_1 , was fixed at 500, and the number of adults tagged, T_2 , was fixed at 200. The radiotelemetry harvests were generated from a Binomial($n=T_j$, $p=H_{5,j}$) distribution. These large numbers were assumed to simulate the best possible situation. Most studies tag fewer animals, which would lead to higher standard errors associated with the harvest mortalities.

To generate the index data, I assumed that the index count represented 0.3 of the abundance and that the correlation between the index and abundance averaged 0.7. A high correlation was assumed to test the addition of the index under the best possible circumstances. The index data was generated from a Normal distribution, with a

mean of 0.3 times the total abundance. The standard deviations for the index were based on the correlation with abundances and averaged 300 for the steady recruitment scenarios, 1,000 for the noisy recruitments and 700 for the decreasing recruitments. The standard deviations of the index data reflected the variability in the abundance trends.

Even though the index data was assumed to have a high correlation with abundance, its inclusion is not completely comparable to the telemetry data. The telemetry data assumed very high sample sizes (500, 200 tagged) and a comparable index would have had a higher correlation (i.e. 0.95) to emulate the same precision. Still, the index data included in these simulations will provide insight on the usefulness of including such data in the population reconstruction.

Failure to find MLEs. For each model specification, 600 simulations were run. With 192 scenarios, a total of 115,200 simulations were run with AD Model Builder. For some of the simulations, AD Model Builder ended with the error message “Hessian does not appear to be positive definite” and parameter values were not estimated. For models with 1 vulnerability coefficient, errors occurred in 5,200 out of 57,600 runs; for models with 2 vulnerability coefficients, errors occurred in 7,715 out of 57,600 runs. It was unknown whether the model failures could be rectified with different initialization values, parameter ranges, error penalties, or other coding techniques, or whether the errors were due to in calculability of specific data sets.

Performance measures evaluated

I compiled several statistics to compare model performance between scenarios. The estimated survivals and vulnerability coefficients from the simulations were averaged to test for bias. In the results’ tables, the averaged estimated survivals were represented by \hat{S}_1 and \hat{S}_2 , for the juveniles and adults, respectively. The true juvenile and adult survival rates were represented by the headers S_1 and S_2 . The averaged

estimated vulnerability coefficients were \hat{c} , \hat{c}_1 , and \hat{c}_2 , representing the 1 coefficient model, the juvenile coefficient, and adult coefficient, respectively. The true values were c , or c_1 and c_2 .

The standard errors recorded from the AD Model Builder output, the asymptotic standard errors, \widehat{SE} , were averaged and compared to the empirical standard errors, $SE(Est)$, of the replicate parameter estimates. Through this comparison, I evaluated whether the estimated standard errors were unbiased compared to the empirical variance estimations. The averaged asymptotic standard errors for the survival rates were represented by $\overline{\widehat{SE}}_{\hat{S}_1}$ and $\overline{\widehat{SE}}_{\hat{S}_2}$. The empirical standard errors, calculated as the standard deviation associated with the survival estimates, were represented by $SE(\hat{S}_1)$ and $SE(\hat{S}_2)$. The averaged asymptotic standard errors for the vulnerability coefficients were labeled $\overline{\widehat{SE}}_{\hat{c}}$, $\overline{\widehat{SE}}_{\hat{c}_1}$, and $\overline{\widehat{SE}}_{\hat{c}_2}$, and the empirical standard errors were labeled $SE(\hat{c})$, $SE(\hat{c}_1)$, and $SE(\hat{c}_2)$.

Abundances varied with each year of data and with each data set, rendering overall averages ineffective. Separate averages for each year and age-class would be too numerous and difficult to interpret, so the following statistics were calculated for easier comparisons. The “mean standardized deviation” was reported to examine the results for bias:

$$MSD_{est,j} = \frac{\sum_{i=1}^Y \frac{(\hat{N}_{i,j} - \bar{N}_{i,j})}{\bar{N}_{i,j}}}{Y} \times 100\% \quad (2.15)$$

where $\hat{N}_{i,j}$ was the average abundance estimate from the simulations of age class j in year i , $\bar{N}_{i,j}$ was the true average abundance estimate of age class j in year i , and Y was the number of years, either 5 or 10. In the results table, the juvenile standardized mean deviation was labeled $JvMSD_{est}$ and the adult standardized mean deviation was labeled $AdMSD_{est}$.

To evaluate model precision and the accuracy of the standard errors, the mean

standardized deviation in the estimated standard error was reported:

$$MSD_{SE,j} = \frac{\sum_{i=1}^Y \left(\frac{\sqrt{\widehat{Var}(\hat{N}|N)_{i,j}} - \sqrt{s_{\hat{N},i,j}^2 - s_{N,i,j}^2}}{\sqrt{s_{\hat{N},i,j}^2 - s_{N,i,j}^2}} \right)}{Y} \times 100\% \quad (2.16)$$

The standard errors reported by the software, the asymptotic standard errors, were averaged and represented by $\sqrt{\widehat{Var}(\hat{N} | N)}$, and were the expected measurement errors. The empirical variances of the estimated abundances were $s_{\hat{\theta}}^2$, and they included both the measurement errors and the variances associated with the true abundances. The true variances of the true abundances were s_{θ}^2 . The square root of their difference, $\sqrt{s_{\hat{N}}^2 - s_N^2}$, was the observed measurement error. Ideally, this value and the software's standard error, $\sqrt{\widehat{Var}(\hat{N} | N)}$, would be equal, making the fraction equal to 0, and concluding the reported asymptotic standard errors were accurately measuring the error associated with the estimation.

In the results table, the juvenile mean standardized deviation in standard error was $JvMSD_{SE}$ and the adult version was $AdMSD_{SE}$. Because only 600 simulations were run for each scenario, the mean standardized deviations in standard error should be used as guidance rather than conclusive numbers on the models' standard errors performance.

Another point of note concerning the standard errors is the binomial distribution assumptions, which often leads to overdispersion. Assuming binomial distributions in the data generation matches the processes and likelihoods of the population reconstruction model, but if individuals are not independent, the count data will not conform to the implied variance assumptions associated with the binomial distribution. The MLEs will still be consistent, but there will be overdispersion and the empirical variance will be greater than the theoretical variance. Therefore, the MSD_{SE} may often be positively biased.

Model Evaluation When Population Correctly Modeled

The simulation results demonstrated that the small game population reconstruction model is capable of correctly producing all parameter estimates. Management implications are highlighted by a few direct comparisons in the following subsections. With 192 scenarios, all results could not reasonably be included. In the comparisons below, I tried to cover the full range of scenarios, trying to include each source of data variation in at least two tables. The other criteria used when picking the combinations was to find the model scenarios that provided the best contrast and clearest example of the results' conclusions.

Best Scenario. The most precise and accurate abundance estimates were obtained when radiotelemetry data was available (Table 2.5). The number of years of data, abundance trend, average harvest mortality, and effort variability did not have an effect on these conclusions.

The models with high harvest mortalities did have large mean standardized deviations for the standard errors. This was because the true measurement errors of these abundances were very low. The reported asymptotic standard errors were also small, but they still overestimated the true measurement error of the abundances. It is not known if this large bias was inherent to the model, or if it was due to the low number of simulations.

Still, the estimates and their precision associated with these models were much better than any other, suggesting that even with fewer tagged animals in the radiotelemetry study, this conclusion would not change. These results could be compared to the models with 2 vulnerability coefficients and no auxiliary likelihood (Table 2.6). The models with the telemetry data consistently had much more precise and accurate survival and vulnerability coefficient estimates and less biased abundance estimates.

Most Likely Scenario. A likely scenario was to have 10 years of aging and catch-effort data but no auxiliary data, and a species with separate juvenile and adult vulnerability coefficients and survivals. This model tended to overestimate the natural survival probabilities and the vulnerability coefficients (Table 2.6). The abundances were negatively biased and had high standard errors. Better results were obtained with high variability in the hunter effort, and much better results were obtained with high harvest mortalities. These models had unbiased abundance estimates.

Many of the models with no auxiliary study and 2 vulnerability coefficients had small MSD_{SE} but imprecise abundance estimates. For these models, the errors were unbiased, but the reported asymptotic errors and the observed measurement errors were both high.

Harvest Mortality. High harvest mortalities consistently led to more precise and more accurate estimates for all parameters and under all data scenarios (Tables 2.5 and 2.6). This may have been because high harvest mortalities led to a greater harvest and age-at-harvest numbers, creating larger sample sizes which leads to better estimates. The dramatic difference between the abundance estimations with high and low harvest mortalities led to further simulations on the effect of harvest mortality levels (Section 2.3.1).

Variation in Hunter Effort. Variable hunter effort, which led to larger ranges in the harvest mortalities, had a small, but significant, effect on the estimates, yielding both slightly more accuracy and better precision (Table 2.7).

Inclusion of Auxiliary Likelihood. Including harvest radiotelemetry data led to improved accuracy and precision for all parameter estimates and under all scenarios. I believe the telemetry data was advantageous because it separately estimated two of the parameters of the model, the vulnerability coefficients. Because of the high cor-

relation between all the parameters, the separate estimation of these two parameters coerced the abundance and survival estimation into their correct ranges.

Without the radiotelemetry, low harvest mortalities led to unstable abundance estimates with extremely high standard errors (Table 2.6). Without the radiotelemetry data, high harvest mortalities led to accurate abundance estimates, but survivals and vulnerability coefficients were overestimated (Table 2.8).

Including population index data slightly improved parameter estimates and standard errors. The inclusion of index data was more helpful for models with low harvest mortalities or low effort variability. The results with the index data were better than no auxiliary study, but did not lead to accurate and reliable abundance estimates as with the telemetry data. I believe the index data were less effectual because abundance trends were already incorporated into the model through the effort and harvest numbers.

Including both the index and telemetry data did not improve any estimates over the model with only the telemetry data.

Abundance Trend. Trend in recruitment did not have an effect on parameter estimation (Table 2.9).

Years of Data. Including more years of data did not affect those studies that included a radiotelemetry auxiliary, but did have a significant benefit on abundance estimation in models without the radiotelemetry data (Table 2.10). The accuracy of the estimates improved slightly, and the precision was much higher with more years of data.

Vulnerability Coefficients. The population reconstruction model was able to estimate all parameters when 2 vulnerability coefficients were included, but often with less accuracy than a similar model with only 1 vulnerability coefficient (Table 2.11).

Models without the telemetry data tended to overestimate the survivals and the adult vulnerability coefficients.

Table 2.5: Results of Monte Carlo simulations to examine the effect of the level of harvest mortality and year-to-year variation in hunter effort on estimates from population reconstruction. Models include radiotelemetry data, 1 vulnerability coefficient, separate juvenile and adult natural survivals, 10 years of data, and noisy recruitment.

Harvest Mort.	Effort Variation	S_1	\hat{S}_1	$\overline{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\overline{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
Harvest Mort.	Effort Variation	c	\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$				
Low	constant	0.45	0.447	0.091	0.108	0.65	0.653	0.084	0.100
Low	variable	0.45	0.451	0.084	0.092	0.65	0.650	0.079	0.086
High	constant	0.45	0.449	0.038	0.040	0.65	0.658	0.077	0.079
High	variable	0.45	0.451	0.036	0.039	0.65	0.656	0.079	0.086
Harvest Mort.	Effort Variation	c	\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$				
Low	constant	0.45	0.453	0.065	0.064				
Low	variable	0.45	0.451	0.069	0.071				
High	constant	3.00	3.026	0.183	0.192				
High	variable	3.00	3.028	0.182	0.185				
Harvest Mort.	Effort Variation	$J_{0}MSD_{est}(\%)$	$J_{0}MSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
Low	constant	1.3	-7.2	1.4	-3.0				
Low	variable	2.0	-10.7	2.2	-7.4				
High	constant	-0.1	49.5	-0.2	2.2				
High	variable	-0.4	85.7	-0.3	37.0				

Table 2.6: Results of Monte Carlo simulations to examine the effect of harvest mortality and effort variation on population reconstruction models without an auxiliary likelihood. Models include 2 vulnerability coefficients, 2 natural survival rates, 10 years of data, and noisy recruitment.

Harvest Mort.	Effort Variation	S_1	\hat{S}_1	$\overline{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\overline{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
Low	constant	0.45	0.737	0.698	0.241	0.65	0.789	0.142	0.173
Low	variable	0.45	0.646	0.632	0.285	0.65	0.727	0.132	0.160
High	constant	0.45	0.619	0.320	0.254	0.65	0.714	0.142	0.153
High	variable	0.45	0.539	0.220	0.203	0.65	0.702	0.126	0.133
Harvest Mort.	Effort Variation	c_1	\hat{c}_1	$\overline{SE}_{\hat{c}_1}$	$SE(\hat{c}_1)$	c_2	\hat{c}_2	$\overline{SE}_{\hat{c}_2}$	$SE(\hat{c}_2)$
Low	constant	0.5	3.203	2.305	1.947	0.3	1.597	1.070	1.015
Low	variable	0.5	1.919	2.579	1.805	0.3	0.955	0.725	0.727
High	constant	3.5	4.620	1.625	1.664	2.5	2.844	1.008	0.917
High	variable	3.5	4.092	1.063	1.113	2.5	2.716	0.713	0.707
Harvest Mort.	Effort Variation	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
Low	constant	-43.9	15.8	-34.3	-25.0				
Low	variable	-9.4	22.3	-0.3	-5.0				
High	constant	-6.8	-12.3	2.9	-34.2				
High	variable	-5.3	-1.8	-0.6	-7.9				

Table 2.7: Results of Monte Carlo simulations to examine the effect of effort variation on demographic estimates from the population reconstruction. Models include 1 vulnerability coefficient, 10 years of data, steady recruitment, high harvest mortality, and index auxiliary.

Effort Variability	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
Constant	0.45	0.450	0.094	0.108	0.65	0.725	0.207	0.262
Variable	0.45	0.451	0.072	0.081	0.65	0.682	0.184	0.210
Effort	c	\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$				
Variability								
Constant	3.00	3.283	0.658	0.704				
Variable	3.00	3.101	0.432	0.466				
Effort Variability	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
Constant	-2.3	-22.5	-2.3	-22.0				
Variable	-0.6	-13.7	-0.6	-13.3				

Table 2.8: Results of Monte Carlo simulations to examine the effect of auxiliary likelihood inclusion in the population reconstruction model. Models include 1 vulnerability coefficient, 10 years of data, variable hunter effort, noisy recruitment, and high harvest mortality.

Auxiliary Type	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$	
No Aux	0.45	0.466	0.048	0.053	0.65	0.692	0.107	0.118	
Index	0.45	0.465	0.048	0.053	0.65	0.691	0.106	0.119	
Radio	0.45	0.451	0.036	0.039	0.65	0.656	0.079	0.086	
Radio+Index	0.45	0.451	0.035	0.039	0.65	0.655	0.079	0.085	
Auxiliary Type	c	\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$					
No Aux	3.00	3.256	0.500	0.512					
Index	3.00	3.244	0.495	0.514					
Radio	3.00	3.028	0.182	0.185					
Radio+Index	3.00	3.026	0.181	0.186					
Auxiliary Type	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$					
No Aux	-3.9	0.9	-3.9	-2.5					
Index	-3.8	0.6	-3.8	-2.8					
Radio	-0.4	85.7	-0.3	37.0					
Radio+Index	-0.5	43.6	-0.4	29.9					

Table 2.9: Results of Monte Carlo simulations to examine the effect of recruitment trend on demographic estimates from the population reconstruction. Models include with 2 vulnerability coefficients, 10 years of data, low hunter effort variability, low harvest mortality, and the radiotelemetry auxiliary.

Recruitment	S_1	\hat{S}_1	$\overline{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\overline{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
Trend								
Steady	0.45	0.457	0.234	0.350	0.65	0.641	0.193	0.313
Noisy	0.45	0.483	0.202	0.217	0.65	0.650	0.104	0.120
Decr	0.45	0.474	0.248	0.330	0.65	0.639	0.176	0.262
Recruitment								
Trend	c_1	\hat{c}_1	$\overline{SE}_{\hat{c}_1}$	$SE(\hat{c}_1)$	c_2	\hat{c}_2	$\overline{SE}_{\hat{c}_2}$	$SE(\hat{c}_2)$
Steady	0.5	0.497	0.080	0.081	0.3	0.308	0.096	0.095
Noisy	0.5	0.507	0.081	0.085	0.3	0.311	0.098	0.093
Decr	0.5	0.501	0.081	0.080	0.3	0.306	0.096	0.100
Recruitment								
Trend	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
Steady	3.5	-5.0			9.1	-22.8		
Noisy	1.2	-6.1			6.4	-6.4		
Decr	2.2	4.4			10.2	-8.6		

Table 2.10: Results of Monte Carlo simulations to examine how the number of years of available data affects the demographic estimates from the population reconstruction. Models include 2 vulnerability coefficients, steady recruitment, low effort variation, high harvest mortality, and an index auxiliary.

No. of Years	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
5	0.45	0.598	0.232	0.330	0.65	0.728	0.184	0.332
10	0.45	0.499	0.213	0.241	0.65	0.746	0.191	0.257
No. of Years	c_1	\hat{c}_1	$\widehat{SE}_{\hat{c}_1}$	$SE(\hat{c}_1)$	c_2	\hat{c}_2	$\widehat{SE}_{\hat{c}_2}$	$SE(\hat{c}_2)$
5	3.5	4.414	1.736	2.259	2.5	2.717	1.025	1.114
10	3.5	4.055	1.199	1.381	2.5	2.869	0.915	0.938
No. of Years	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
5	15.4	-36.8	19.5	-34.3				
10	0.2	-31.1	0.4	-17.2				

Table 2.11: Results of Monte Carlo simulations to examine how the number of vulnerability coefficients affects the demographic estimates from the population reconstruction. Models include 10 years of data, high harvest mortality, variable hunter effort, steady recruitment, and no auxiliary study.

No. of Vulner. Coefficients	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
1	0.45	0.451	0.072	0.082	0.65	0.699	0.192	0.224
2	0.45	0.550	0.218	0.214	0.65	0.755	0.177	0.204
No. of Vulner. Coefficients	c	\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$				
1	3.00	3.159	0.534	0.560				
No. of Vulner. Coefficients	c_1	\hat{c}_1	$\widehat{SE}_{\hat{c}_1}$	$SE(\hat{c}_1)$	c_2	\hat{c}_2	$\widehat{SE}_{\hat{c}_2}$	$SE(\hat{c}_2)$
2	3.5	4.480	1.365	1.479	2.5	2.736	0.682	0.626
No. of Vulner. Coefficients	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
1	-1.1	-12.4	-1.1	-12.1				
2	-8.6	-8.7	-2.3	-4.5				

2.3.2 Simulations to Investigate Effects of Harvest Levels on Model Performance

For models without radiotelemetry data, the preceding simulations demonstrated that predictive capabilities were dependent upon the harvest mortality rate (e.g. Table 2.6). Because it is likely that a telemetry study would not be available, it is important to know under what circumstances population reconstruction can be applied. These simulations were run to determine the best harvest levels for optimal model performance, and at what harvest mortality levels the model breaks down without the telemetry data.

Range of factors considered

The harvest mortality simulations were based on the previous simulation conditions described in Section 1.2.1. Juvenile survival was fixed at 0.45, adult survival was fixed at 0.65, and the same set of variable effort was applied (Section 2.3.1). Stable recruitment was generated from a Normal($\mu=18000$, $\sigma=900$) distribution and noisy recruitment was generated from a Normal($\mu=18000$, $\sigma=3600$) distribution. Decreasing abundances were not tested. 10 years of data were used, without an auxiliary study. Both the 1 vulnerability coefficient and the 2 vulnerability coefficient models were tested.

Seven levels of harvest mortality were tested, with average mortalities equal to 0.05, 0.10, 0.20, 0.30, 0.40, 0.50, and 0.60. Using the harvest effort relationship from Equation 2.2, these harvest mortalities combined with the effort values and led to the vulnerability coefficients and mortality ranges listed in Table 2.12. To match the harvest levels and have stable abundances, adult abundance in year 1 changed with each level (Table 2.12).

Numbers harvested, aged, and adult abundances were derived with the same process of using binomial distributions as the previous simulations described in Section 2.3.1.

Table 2.12: Each harvest mortality level is defined by the average harvest mortality over the years and age classes. Associated with each level, the range of harvest mortalities, vulnerability coefficients and adult abundances for year 1 are also listed.

\bar{H}	H_{min}	H_{max}	c	c_j	c_a	$N_{1,2}$
0.05	0.034	0.11	0.45	0.50	0.30	20,000
0.1	0.061	0.17	0.70	0.80	0.55	17,000
0.2	0.13	0.32	1.40	1.60	1.20	14,000
0.3	0.20	0.48	2.30	2.70	1.90	11,000
0.4	0.28	0.60	3.30	3.80	2.80	8,000
0.5	0.35	0.71	4.50	5.10	3.80	6,000
0.6	0.44	0.80	6.00	6.80	5.10	4,000

In this section, 56 scenarios were looked at, and 600 simulations were run for each scenario. Less than 10 errors occurred for each scenario when average harvest mortality was below 0.50. When the harvest mortality was 0.50, 228 errors occurred during the 4,800 simulations; when the average harvest mortality was 0.60, 672 errors occurred during the 4,800 simulations.

Results

The 1 vulnerability coefficient and 2 vulnerability coefficient models exhibited the same precision and accuracy patterns (Tables 2.13 and 2.14). The models were unable to estimate the model parameters, especially the abundances, when average harvest mortality was 0.05 to 0.10. For hunting levels below 0.50, the survivals and vulnerability coefficients were positively biased. At the high mortality rates of 0.50 and 0.60, survivals and vulnerability coefficients were negatively biased.

Estimates for abundance were accurate when harvest levels were between 0.20 and 0.50. As mortality increased from 0.05, the variance decreased and the accuracy improved considerably. When the harvest mortality reached 0.50, estimates became less accurate again and the asymptotic errors significantly underestimated the true measurement error.

Table 2.13: Results of harvest mortality simulations to examine how the level of harvest mortality impacts parameter estimates for populations with one common vulnerability coefficient for juveniles and adults. Models include 10 years of data, noisy recruitment, variable hunter effort, and no auxiliary study.

Harvest Mortality	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
0.05	0.45	0.494	0.108	0.126	0.65	0.711	0.115	0.138
0.1	0.45	0.474	0.090	0.098	0.65	0.692	0.106	0.115
0.2	0.45	0.464	0.065	0.071	0.65	0.688	0.098	0.104
0.3	0.45	0.461	0.052	0.055	0.65	0.678	0.097	0.112
0.4	0.45	0.461	0.045	0.049	0.65	0.691	0.110	0.128
0.5	0.45	0.441	0.034	0.051	0.65	0.675	0.097	0.143
0.6	0.45	0.385	0.019	0.048	0.65	0.595	0.076	0.187

Harvest Mortality	c	\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$
0.05	0.45	0.953	0.600	0.664
0.1	0.70	1.021	0.553	0.575
0.2	1.40	1.634	0.528	0.541
0.3	2.30	2.467	0.508	0.522
0.4	3.30	3.507	0.483	0.534
0.5	4.50	4.431	0.340	0.639
0.6	6.00	4.899	0.139	0.755

Harvest Mortality	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$
0.05	12.0	107.6	12.0	109.1
0.1	16.3	76.3	16.2	78.4
0.2	-0.7	43.2	-0.5	43.3
0.3	-1.3	2.9	-1.3	1.8
0.4	-2.4	-2.0	-2.5	-3.0
0.5	2.7	-43.5	3.4	-41.5
0.6	14.6	-83.1	21.0	-82.0

Table 2.14: Results of harvest mortality simulations to examine how the level of harvest mortality impacts parameter estimates for populations with separate juvenile and adult vulnerability coefficients. Models include 10 years of data, noisy recruitment, variable hunter effort, and no auxiliary study.

Harvest Mortality	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$
0.05	0.45	0.661	0.638	0.283	0.65	0.744	0.135	0.162
0.1	0.45	0.654	0.545	0.292	0.65	0.712	0.117	0.136
0.2	0.45	0.581	0.348	0.294	0.65	0.694	0.113	0.116
0.3	0.45	0.558	0.265	0.245	0.65	0.688	0.115	0.128
0.4	0.45	0.523	0.195	0.188	0.65	0.698	0.123	0.138
0.5	0.45	0.511	0.129	0.191	0.65	0.689	0.124	0.162
0.6	0.45	0.512	0.101	0.227	0.65	0.541	0.108	0.228
Harvest Mortality	c_1	\hat{c}_1	$\widehat{SE}_{\hat{c}_1}$	$SE(\hat{c}_1)$	c_2	\hat{c}_2	$\widehat{SE}_{\hat{c}_2}$	$SE(\hat{c}_2)$
0.05	0.50	2.072	1.686	1.529	0.30	1.065	0.756	0.814
0.1	0.80	1.749	1.341	1.289	0.55	0.979	0.648	0.662
0.2	1.60	2.196	1.179	1.101	1.20	1.490	0.643	0.581
0.3	2.70	3.253	1.127	1.171	1.90	2.114	0.666	0.646
0.4	3.80	4.263	1.002	1.086	2.80	2.954	0.709	0.736
0.5	5.10	5.287	0.724	0.984	3.80	3.724	0.697	1.055
0.6	6.80	5.884	0.486	1.145	5.10	4.017	0.677	1.681
Harvest Mortality	$J^0MSD_{est}(\%)$	$J^0MSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$				
0.05	-27.6	20.6	-20.6	8.6				
0.1	-1.6	24.0	18.2	6.2				
0.2	2.7	5.6	-0.2	-13.0				
0.3	-1.9	-5.6	0.3	1.4				
0.4	-3.0	-7.0	2.0	-32.5				
0.5	0.2	-27.2	9.7	-54.4				
0.6	11.6	-71.4	40.0	-75.8				

2.3.3 Robustness Studies: Sensitivity of Abundance Estimates

The previous simulations used models whose assumptions matched the generated data. Because the demographics of hunted species are not always established, it is important to understand how the model works if some assumptions are not met. For example, it may be assumed in the model that juveniles and adults are harvested at the same rate, but in reality juveniles are more vulnerable to hunting. In this set of simulations, the robustness of the model to such misspecifications was examined.

Data was generated with 2 survivals and 2 vulnerability coefficients. Four different likelihoods were run on these data: one that incorporated the true 2 survival-2 vulnerability coefficient scenario, one that incorporated 1 survival or 1 vulnerability coefficient, and one that assumed only 1 survival and 1 vulnerability coefficient. The purpose of this section was to gain insight on the bias and precision to be expected if the model does not match the biological reality of the full model.

Range of factors considered

For these simulations, data was generated using separate juvenile and adult survivals, juvenile and adult vulnerability coefficients, 3 levels of hunting mortalities, 10 years of data, high effort variability, steady recruitment, and no auxiliary study.

The survival parameters used were the same as in the previous studies, 0.45 and 0.65 for juveniles and adults, respectively. The effort values were also the same as in the previous studies (see Section 2.3.1). Juvenile abundances were generated from a $N(\mu=25,000, \sigma=1,200)$ distribution. Adult abundance for year 1 was set at 10,000. Numbers harvested, aged, and additional years of adult abundance were generated from the Binomial distributions described in Section 2.3.1.

Three sets of vulnerability coefficients were used to generate the harvest mortalities. In each set, juveniles were increasingly more vulnerable to hunting in order to determine if the magnitude of the difference in juvenile and adult harvest vulnerabil-

Table 2.15: Vulnerability coefficients and harvest rates used in robustness study.

Scenario	Juvenile				Adult			
	c_1	$H_{1,min}$	$H_{1,max}$	\bar{H}_1	c_2	$H_{2,min}$	$H_{2,max}$	\bar{H}_2
10%	3.2	0.31	0.54	0.41	2.8	0.27	0.49	0.37
20%	3.5	0.33	0.57	0.44	2.7	0.29	0.48	0.36
50%	3.8	0.36	0.60	0.46	2.2	0.23	0.41	0.30

ities affected the results. Each set had the same combined and averaged juvenile and adult harvest mortality of 39%. The first set had the juvenile harvest mortality 10% greater than the adult harvest mortality. The second set made the juvenile harvest mortality 20% greater and the third set had them 50% greater than the adult harvest mortality. The vulnerability coefficients and associated harvest mortality ranges that arose from these restrictions are listed in Table 2.15.

For the sensitivity analysis, only 3 scenarios were tested— the 3 levels of juvenile to adult vulnerability. For each scenario, 4 models were run: one that assumed 2 vulnerability coefficients and 2 survivals (the true model), one that assumed 2 vulnerability coefficients and 1 survival, one that assumed 1 vulnerability coefficient and 2 survivals, and one that assumed 1 vulnerability coefficient and 1 survival.

For each model-data scenario combination, 600 simulations were run, for a total of 7,200 simulations, 196 of these simulations resulted in error.

Results

As the juvenile age class became more vulnerable to hunting, the parameter estimates became less accurate for all models (Tables 2.16, 2.17 and 2.18).

Both the survival and vulnerability coefficient estimates were often biased for all models, but the abundance estimates remained accurate (Tables 2.16, 2.17). These parameters were positively correlated. If a vulnerability coefficient increases, the harvest mortality increases. If a survival rate increases, the natural mortality decreases. The proportion of deaths from hunting and natural causes changes, but total mortality

does not. Therefore, abundance estimates could still be accurate even if the other parameters were not, which was the case for these models.

The best abundance estimates came from the true model with 2 vulnerabilities and 2 survivals (Table 2.18). The 2c1s and 1c2s models were less accurate. The 2c1s model consistently underestimated the juvenile abundances and overestimated the adult abundances. The 1c2s model did the opposite, it overestimated the juvenile abundances and underestimated the adult abundances. The 1c1s model had inaccurate juvenile abundance estimates. For all models, the standard errors reported with the abundance estimates underestimated the true measurement error.

Discussion of the Survival Parameter

The abundance estimates in this sensitivity analysis were robust to some model misspecifications. The 2c1s and 1c2s models both produced reasonable abundance estimates, albeit less accurate than the full 2c2s model. When the difference between the juvenile and adult harvest mortalities was greater, estimates became less accurate and less precise.

These results are suggestive of what would happen if the constant survival assumption was not met. Nonconstant survival would still lead to reasonably accurate abundance estimates; as survivals become more variable, the abundances estimates would be less accurate.

Table 2.16: Results from the sensitivity analysis simulations to examine how model misspecification and difference between juvenile and adult harvest vulnerabilities impact survival estimates. All models were generated with 2 survivals and 2 vulnerability coefficients, and included 10 years of data, high effort variability, steady recruitment, and no auxiliary study.

Model	Scenario	S_1	\hat{S}_1	$\widehat{SE}_{\hat{S}_1}$	$SE(\hat{S}_1)$	S_2	\hat{S}_2	$\widehat{SE}_{\hat{S}_2}$	$SE(\hat{S}_2)$	
2c2s	10%	0.45	0.515	0.186	0.169	0.65	0.710	0.169	0.186	
2c2s	20%	0.45	0.519	0.190	0.169	0.65	0.717	0.172	0.187	
2c2s	50%	0.45	0.531	0.211	0.209	0.65	0.748	0.168	0.186	
\hat{S} $\widehat{SE}_{\hat{S}}$ $SE(\hat{S})$										
2c1s	10%		0.618	0.114	0.147					
2c1s	20%		0.628	0.118	0.148					
2c1s	50%		0.664	0.132	0.181					
S_1 \hat{S}_1 $\widehat{SE}_{\hat{S}_1}$ $SE(\hat{S}_1)$ S_2 \hat{S}_2 $\widehat{SE}_{\hat{S}_2}$ $SE(\hat{S}_2)$										
1c2s	10%	0.45	0.391	0.054	0.059	0.65	0.722	0.166	0.192	
1c2s	20%	0.45	0.342	0.049	0.053	0.65	0.733	0.174	0.198	
1c2s	50%	0.45	0.256	0.041	0.041	0.65	0.742	0.177	0.211	
\hat{S} $\widehat{SE}_{\hat{S}}$ $SE(\hat{S})$										
1c1s	10%		0.455	0.033	0.036					
1c1s	20%		0.406	0.031	0.034					
1c1s	50%		0.318	0.027	0.031					

Table 2.17: Results from the sensitivity analysis simulations to examine how model misspecification and difference between juvenile and adult harvest vulnerabilities impact vulnerability coefficient estimates. All models were generated with 2 survivals and 2 vulnerability coefficients, and included 10 years of data, high effort variability, steady recruitment, and no auxiliary study.

Model	Scenario	c_1	\hat{c}_1	\widehat{SE}_{c_1}	$SE(\hat{c}_1)$	c_2	\hat{c}_2	\widehat{SE}_{c_2}	$SE(\hat{c}_2)$
2c2s	10%	3.2	3.695	0.965	1.027	2.8	2.904	0.609	0.587
2c2s	20%	3.5	4.069	1.081	1.092	2.7	2.805	0.620	0.580
2c2s	50%	3.8	4.724	1.429	1.583	2.2	2.426	0.616	0.578
		c_1	\hat{c}_1	\widehat{SE}_{c_1}	$SE(\hat{c}_1)$	c_2	\hat{c}_2	\widehat{SE}_{c_2}	$SE(\hat{c}_2)$
2c1s	10%	3.2	3.937	0.932	1.193	2.8	2.626	0.414	0.445
2c1s	20%	3.5	4.341	1.055	1.291	2.7	2.498	0.401	0.419
2c1s	50%	3.8	5.123	1.364	1.899	2.2	2.087	0.385	0.400
		\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$					
1c2s	10%		3.136	0.478	0.503				
1c2s	20%		3.172	0.505	0.513				
1c2s	50%		2.931	0.553	0.631				
		\hat{c}	$\widehat{SE}_{\hat{c}}$	$SE(\hat{c})$					
1c1s	10%		2.752	0.438	0.475				
1c1s	20%		2.649	0.461	0.497				
1c1s	50%		2.139	0.504	0.586				

Table 2.18: Results from the sensitivity analysis simulations to examine how model misspecification and difference between juvenile and adult harvest vulnerabilities impact abundance estimates. All models were generated with 2 survivals and 2 vulnerability coefficients, and included 10 years of data, high effort variability, steady recruitment, and no auxiliary study.

Model	Scenario	$JvMSD_{est}(\%)$	$JvMSD_{SE}(\%)$	$AdMSD_{est}(\%)$	$AdMSD_{SE}(\%)$
2c2s	10%	-4.4	-9.3	0.5	6.5
2c2s	20%	-5.0	-6.8	0.9	-4.9
2c2s	50%	-6.2	-14.1	-2.5	-3.4
<i>JvMSD_{est}(%)</i>					
2c1s	10%	-8.2	-19.4	7.8	-9.8
2c1s	20%	-8.7	-15.2	8.9	-4.5
2c1s	50%	-9.5	-29.8	7.8	-5.7
<i>JvMSD_{SE}(%)</i>					
1c2s	10%	3.8	-8.5	-6.2	-7.7
1c2s	20%	10.5	-20.4	-9.3	-19.7
1c2s	50%	28.2	-36.4	-16.1	-35.4
<i>JvMSD_{est}(%)</i>					
1c1s	10%	15.4	-12.8	4.2	-12.6
1c1s	20%	28.0	-14.1	5.0	-13.8
1c1s	50%	68.8	-18.5	10.4	-18.2
<i>JvMSD_{SE}(%)</i>					
<i>AdMSD_{est}(%)</i>					
<i>AdMSD_{SE}(%)</i>					

2.4 Conclusions

2.4.1 Factors Affecting Model Performance

Under most scenarios, precise and accurate estimates are calculable. Concerning incoming data, the following was concluded:

- The model worked best with harvest mortalities in the range of 0.20-0.50.
- A minimum of 5 years of data was necessary to calculate all parameters, with more years preferable.
- More variable effort led to better accuracy and precision for the estimates.
- Trends in recruitment did not affect the precision or accuracy of abundance estimates.
- Applying the model to a species where age-classes shared a common harvest vulnerability or a common natural survival yielded better results. If such an assumption was not known to be true, more accurate estimates were obtained by assuming a full model of 2 vulnerability coefficients and 2 survivals.
- Abundance estimates could be accurate even if the survival and vulnerability coefficient estimates were inaccurate (Table 2.6).

Other conclusions were drawn on the addition of auxiliary data:

- Including harvest radiotelemetry data led to vastly improved accuracy and precision for all scenarios.
- Including index data improved model results over similar models without an auxiliary study, but its inclusion did not necessarily lead to accurate parameter estimates.

- If no telemetry data was available, precise results were obtained only if harvest mortalities were greater than > 0.20 .

2.4.2 Recommendations on the Design of Small Game Population Reconstruction Studies

From these findings, the following recommendations are made concerning the use of population reconstruction on small game:

- It is highly recommended to obtain radiotelemetry data on natural or harvest mortality.
- If no telemetry data is available, only apply the model to species with harvest mortalities in the range of 0.20-0.50. Lower or higher harvest mortalities may lead to unstable abundance estimates with extremely high standard errors.
- More years of data is preferable, and a minimum of 5 years is necessary.
- Do not assume common vulnerability coefficients or common survivals between age-classes unless there is good evidence to assume that the different age-classes are homogeneous with regard to natural or harvest mortality.

Chapter 3

MOURNING DOVE POPULATION RECONSTRUCTION AT JAMES A. REED WILDLIFE AREA, MISSOURI

3.1 Introduction

In this chapter, the population reconstruction models presented in Chapter 2 are applied to a population of mourning doves (*Zenaidura macroura*) in Missouri, for years 2002-2006. Mourning doves are the most popular game bird in North America so there is much interest in their abundance trends and management techniques. I provide background on the mourning dove season and detailed information on the current methods to monitor the populations. The population model is reintroduced with the specific versions applied to this data set. The results are presented and they are compared and contrasted to a deterministic model, the simulations from Chapter 2, a dove survey index, and previous parameter estimates from other publications.

3.1.1 Background

Mourning dove hunting is a popular recreational activity in Missouri. Every year, over 35,000 people participate in this hunting season, harvesting more than 700,000 birds (Schulz 2007). Nationwide, almost 70 million birds are shot annually (Mirarchi and Baskett 1994). Mourning dove hunting is prevalent for several reasons: they reside in areas close to urban centers, shooting fields can be as small as 5 acres, the hunt does not require dogs, and the dove season is the first hunt of the year in Missouri (Schulz 2007). All of these factors of convenience add to the sport's enthusiasm and popularity.

The Missouri Department of Conservation monitors and regulates the dove hunting

season to assure healthy, abundant hunting populations for future generations on all wildlife conservation areas on which hunting occurs (Missouri Dept. of Conservation 2008). In Missouri, the season has been 70 days with a 12-bird/day bag limit since 2001 (Schulz 2007). In order to determine whether this is an optimal level of harvest and to coordinate with national efforts, several surveys, a banding program, and other studies are conducted every year. The purpose of this work is to gain information on population and demographic trends.

3.1.2 Current Monitoring Efforts

“With respect to abundance, management may be directed at: (1) reducing population size in areas experiencing undesirable economic problems, such as crop depredation; (2) increasing numbers in areas where a species is declining or persisting at low levels; and (3) maintaining sizes of populations judged to be at desirable levels. For a game species, these abundant-oriented goals must be considered in the context of creating or maintaining a harvest level consistent with recreational interests. (Dolton (1993), page ?)”

In Missouri, these goals are currently achieved by comparing a variety of index surveys each year: a Mourning dove Call Count Survey of doves heard (CCS_h), a Call Count Survey of doves seen (CCS_o), the North American Breeding Bird Survey (BBS), and a state Roadside Dove Survey (RDS) (Schulz and Jump 2005).

The CCS_h and CCS_o are nationwide surveys that have been in place since 1966. These surveys are conducted concurrently, with the primary purpose of recording the number of perch coos heard, CCS_h . The number of doves seen, CCS_o , is recorded as a supplement to the birds heard. In Missouri, there are 20 standard routes on lightly traveled secondary roads. The total number of calls heard is recorded and the average number of calls per mile is used to build the index. On each route, listening

stations are at 1.0-mile intervals. Three minutes are spent at each stop with a 3-minute drive between listening locations. Doves heard are recorded at the listening stations; doves seen are recorded both at the listening station and during the drive. The season, time of day, limits for weather and habitat have been standardized to rid the survey of their confounding influences (Baskett 1993). An adjustment for observers is included in the analysis because it was found to significantly affect the call count results (Dolton 1993).

While nationally the rigorous design of this survey may lead to reliable trends, the number of routes in Missouri, 20, is too small to have statistical significance or local value. The small sample size also means that we cannot compare trends between counties or physiographic regions within the state.

The North American Breeding Bird Survey (BBS) is administered by the U.S. Fish and Wildlife Service and annually monitors more than 2,000 routes in the United States and Canada. It tracks all birds seen and heard along these routes, and has no mourning dove-specific focus (Dolton 1993). An advantage of this survey is its large sample size which lends itself to smaller standard errors. A disadvantage is its focus on all bird species; since the mourning dove is not a priority, its counts are not given as much attention and are considered less reliable (Dolton 1993).

The Roadside Dove Survey (RDS) has been in place since 1948. This index records the average number of doves seen and is conducted by the state and not nationally. This survey includes 111 routes traveled in June, each 20 miles long (Baskett 1993). The state and mourning dove focus of this survey is appealing, but it still produces an index and therefore has all of the shortcomings described below and previously in Chapter 2.

3.1.3 Critique of Indices

A problem with relying on indices is they often contradict each other (Figure 3.1). A comparison of the CCS_h and BBS surveys from 1966-88 demonstrates significant

differences in trends for 11 of the 48 contiguous states (Dolton 1993). Some of the surveys show similar trends (Figure 3.2), but year-to-year variation was still considerable.

Another chief criticism is that these surveys have never been experimentally tested to determine whether they actually reflect real changes in populations (Schulz and Jump 2005). Survey trends may not represent population trends but rather changes in the timing of the breeding season, detectability rates, observer skill, or habitat growth, all variables that display time trends themselves (Anderson 2001). These factors are confounded with the population changes, and it cannot be determined what is affecting the index. For example, the CCS_h survey records the perch coo, a call uttered primarily by unmated males. This survey could be indexing the proportion of unmated males in the population, and not the total population size. As Anderson (2003) argues, without knowing detection probabilities and the relationship of detection probabilities to vegetation changes or observer variables, indices are fundamentally flawed.

Indices are built from subjective sampling. Consequently, there is no basis for assessing the precision or accuracy of the estimated trend (Mourning Dove Council 2005). In addition to being unreliable, indices provide little information beyond long-term trends. A veritable function does not exist to convert the surveys into abundance or density estimates, so population sizes are still unknown (Mourning Dove Council 2005). Nor does an index contribute to survival, harvest rates, or other parametric estimation.

Index data is easy and inexpensive to collect, but its functionality is limited.

3.1.4 Utility of Population Reconstruction

The intensive harvests of mourning doves prove the importance of this North American game bird. As other small game populations decline and as more grasslands get developed, doves may receive greater hunting pressure. Over time, it will become

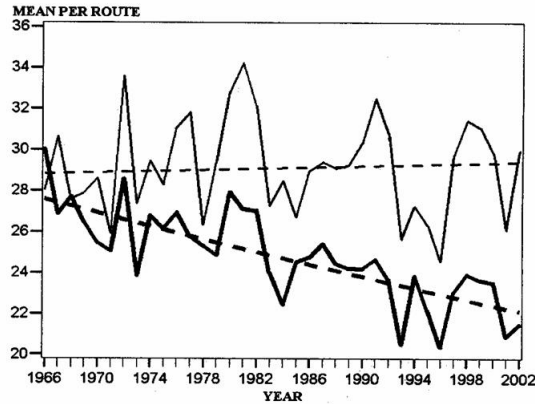


Figure 3.1: Contradicting index trends of CCS_h and CCS_o surveys from the mourning dove Central Management Unit, 1966-2002. The Central Management Unit covers 14 states: Montana, Colorado, Wyoming, New Mexico, Texas, Kansas, Oklahoma, Nebraska, Iowa, South Dakota, North Dakota, Minnesota, Missouri and Arkansas. CCS_h is the darker, bottom line, and CCS_o is the lighter, upper line (Schulz and Jump 2005).

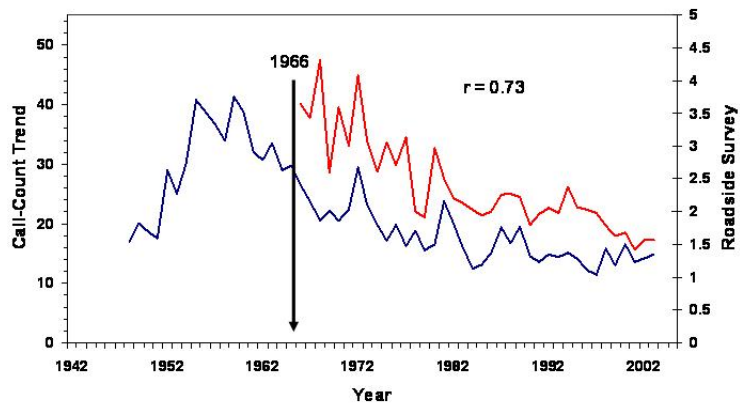


Figure 3.2: Similar index trends of RDS and CCS_h surveys in Missouri, 1966-2002. The RDS is the lower line, and CCS_h is the upper line (Schulz and Jump 2005).

more important to learn how harvests impact dove populations, and to have better measures of abundance trends (Schulz and Jump 2005). Population reconstruction models are a means of doing that.

Here, the model was applied to a population of mourning doves at the James A. Reed Memorial Wildlife Area (referred to as JARMWA hereafter) in Missouri. The model used the following data from 2002-2006: age-at-harvest from wing clippings; catch-effort from hunter surveys, and tagging results from an auxiliary, radiotelemetry study conducted in 2005 and 2006. Survivals, harvest mortalities, juvenile (hatching year) abundances and adult (after hatching year) abundances were estimated with this information. The estimated abundances were for the end of August, just prior to the hunting season.

3.2 Area of Study

JARMWA covers 2,603 acres, with 12 man-made lakes covering 250 of those acres. It is managed through the Dingall-Johnson Sport Fish Restoration Act for year-round vegetations available as wildlife food to encourage hunted populations to reside there. This hunting area is unique and of interest because of its proximity to a large urban area: it is located within 70 miles of Kansas City, resulting in greater hunting pressure than many other areas within Missouri (Missouri Dept of Conservation 2007).

Many sources of data are collected at JARMWA to gain a better understanding of the hunting season and hunter-harvest relationship. In 1998, the Missouri Department of Conservation began surveying hunters to gather information on the dove hunting season. At 8 wildlife areas, hunters check out at the end of the day and fill out a survey card. Through their responses, the number of hunters, total harvest, number of shots fired, hours hunted, and recently, birds shot but not retrieved are totaled. The data for JARMWA is in Table 3.1. It may be noted that the effort and harvest numbers from 2002 are significantly lower than other years; the reason behind this anomaly is unknown.

Table 3.1: Survey data of check stations and wing clippings for mourning doves in JARMWA, 2002-2006.

Variable	Symbol	Year				
		2002	2003	2004	2005	2006
No. of hunters		666	1,323	1,384	1,425	1,712
Doves harvested	H_i	1,153	6,187	4,682	7,418	7,875
Shots fired		4,879	30,303	24,387	39,599	43,752
Hours hunted	f_i	1,378	2,683	4,042	2,618	4,916
Juveniles aged	$a_{i,1}$	491	1,010	1,428 [†]	1,845	2,298
Adults aged	$a_{i,2}$	138	384	415 [†]	446	587

^bWing clippings were not collected in 2004. The missing data was filled in by averaging wing counts from years 2003 and 2005.

In 2002, Missouri Department of Conservation began to collect wing clippings and use their molting patterns to age a percentage of the harvested birds as juveniles or adults (Table 3.1). In 2004, aging information was not collected. To fill in the missing data, the number of wing clippings from each age-class in the preceding year, 2003, and the following year, 2005, were averaged.

The aging information excluded unclassifiable wings. Some wings were too badly damaged to examine their feathers, leading to one type of unclassifiable wings. The other type of unclassifiable wing was one that was too far along in its molting to be aged. Birds were aged by examining the molting, primary feathers on its wings. If a bird had been recently hatched, its wing coverts had a white tip. If a bird had previously gone through a molting season, then the buffy-tipped wing coverts were absent (Schulz et al. 1995). There were 10 primary molting feathers and if a bird was on the 9th, 10th, or sometimes 8th molting feather, then the progression of the primary molt was too far along to age the bird. The percentage of the unclassifiable wings that were expected to be adults versus juveniles was not known (personal comm. with J. Schulz). Unfortunately, this lack of knowledge led to a loss of information that could not be included in this analysis.

In 2005, a 10-year banding study of the doves was begun with the objective to

Table 3.2: Radiotelemetry data from mourning dove banding study in JARMWA, 2005-2006.

Variable	Symbol	Year	
		2005	2006
No. of tagged juveniles	$T_1^{(r)}$	30	52
No. of tagged & harvested juveniles	$h_1^{(r)}$	20	30
No. of tagged adults	$T_2^{(r)}$	23	47
No. of tagged & harvested adults	$h_2^{(r)}$	9	27

learn how locally intensive harvests, like that which occurs at JARMWA, impacts populations (Schulz 2007). Every summer approximately 200 doves were implanted with radiotelemetry transmitters. Many of these radio transmitters were lost for various reasons: the battery died, the equipment malfunctioned, or the bird left the range of the transmitter. For the study, data was recorded daily from June to mid-September. For the population reconstruction, only a subset of this information was used. In our model, the tagged birds that were located within the 2 weeks before the start of the hunting season were counted as “Tagged” birds, and any radio signal that was lost before then was censored. Of these birds, the ones harvested by hunters were counted as “Tagged & Harvested” birds (Table 3.2).

Birds that were crippled but not killed by the hunters were censored. Although wounded birds soon die, cripples were excluded from the harvest mortality estimates because crippling information was not recorded in the hunter surveys for years 2002, 2003. Including cripples as harvest would change the relationship between effort and harvest rates, creating a discrepancy between years when cripples were included, and years when that information was not available. In the future, when more information is available, crippling rates may be incorporated as another type of mortality. For this analysis, deaths resulting from cripples were absorbed into the natural mortality.

3.3 Methods

Population estimates were based on a joint likelihood model in the form:

$$L_{joint} = L_{catch} \cdot L_{AAH} \cdot L_{radio} \quad (3.1)$$

The auxiliary likelihood, L_{radio} , used the data from the multi-year radiotelemetry study to supplement the estimation of harvest mortalities as a function of hunter effort, measured as hours hunted. The catch-effort and age-at-harvest likelihoods combined the harvest numbers, effort information, and age composition to estimate annual recruitment, natural survival, harvest mortalities, and in turn, total yearly abundances.

Harvest mortality was modeled as a function of hunter effort of the form:

$$H_{i,j} = 1 - e^{-c_j \cdot f_i} \quad (3.2)$$

where f_i was the effort exerted in year i , c_j was the vulnerability coefficient of age-class j , and $H_{i,j}$ was the harvest mortality for age-class j in year i (Seber 1982). The vulnerability coefficient was the parameter that defined how effort exerted related to harvest mortality. At JARMWA, 3 measures of effort were recorded: number of hunters, hours hunted, and shots fired. These data were collected in 8 wildlife areas, including JARMWA, in Missouri from 1998-present (Fig. 3.3). The number of hours spent hunting was chosen as the effort measurement. Number of shots fired may be highly correlated with harvest sizes, but it did not adequately describe the effort exerted. For example, a hunter may spend 8 hours in the field, but never see a single dove. He has exerted considerable effort, but measuring the number of shots fired does not record it.

I applied 4 versions of the population reconstruction presented in Chapter 2 to the mourning doves. Versions 1 and 2, referred to as model 2c2S and model 2c1S,

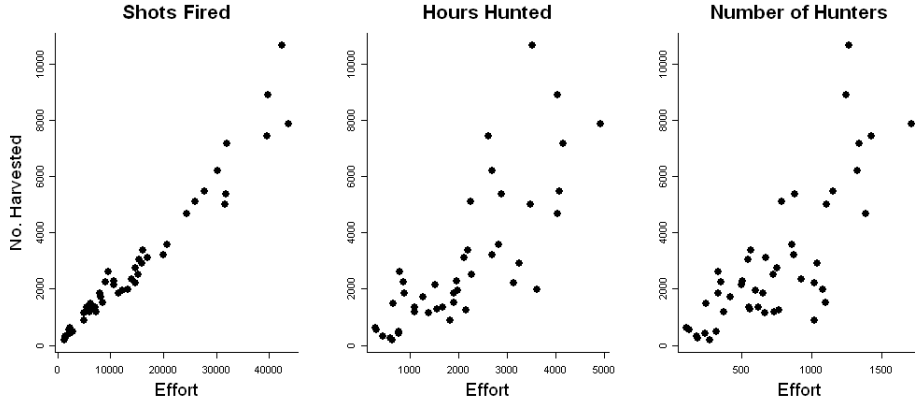


Figure 3.3: Harvest versus three measurements of effort from the mourning dove hunting season. Data points were taken from 8 conservation areas in Missouri, years 1998-2006. The 8 conservation areas were: August A Busch CA, Bois D’Arc CA, Columbia Bottoms CA, Otter Slough CA, Pony Express CA, James A Reed Memorial WA, Talbot CA, and Ten Mile Pond CA.

respectively, assumed that juveniles and adults had different vulnerability coefficients.

The structure of these likelihoods was as follows:

$$L_{joint} = L_{catch} \cdot L_{AAH} \cdot L_{radio} \quad (3.3)$$

$$L_{catch} = \prod_{year=i=2002}^{2006} \binom{N_i}{h_i} \left(\frac{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}}{N_{i,1} + N_{i,2}} \right)^{h_i} \left(1 - \frac{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}}{N_{i,1} + N_{i,2}} \right)^{N_i - h_i} \quad (3.4)$$

$$L_{AAH} = \prod_{year=i=2002}^{2006} \binom{a_{i,1} + a_{i,2}}{a_{i,1}} \left(\frac{N_{i,1}H_{i,1}}{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}} \right)^{a_{i,1}} \left(\frac{N_{i,2}H_{i,2}}{N_{i,1}H_{i,1} + N_{i,2}H_{i,2}} \right)^{a_{i,2}} \quad (3.5)$$

$$L_{radio} = \prod_{r=2005}^{2006} \prod_{j=1}^2 \binom{T_j^{(r)}}{h_j^{(r)}} H_{r,j}^{h_j^{(r)}} (1 - H_{r,j})^{T_j^{(r)} - h_j^{(r)}} \quad (3.6)$$

Table 3.3: Data symbols used in mourning dove population reconstruction models.

Symbol	Description
$a_{i,1}$	No. of juveniles aged in year i
$a_{i,2}$	No. of adults aged in year i
f_i	Hunter effort, measured as no. of shots fired, in year i
h_i	Harvest (juveniles and adults) in year i
<i>Radiotelemetry study</i>	
$T_j^{(r)}$	No. of animals in age-class j tagged in year r
$h_j^{(r)}$	No. of tagged animals in age-class j found harvested in year r

The definitions of the symbols and parameters are found in Tables 3.3 and 3.4. In model 2c2s, separate survivals for juveniles and adults were assumed, and adult abundances (for every year except 2002) were derived iteratively from the other parameters following the equation:

$$\hat{N}_{i,2} = \hat{N}_{i-1,1}(1 - H_{i-1,1})\hat{S}_1 + \hat{N}_{i-1,2}(1 - H_{i-1,2})\hat{S}_2 \quad (3.7)$$

Model 2c1s assumed juveniles and adults had the same survival, and adult abundances were estimated as follows:

$$\hat{N}_{i,2} = [\hat{N}_{i-1,1}(1 - H_{i-1,1}) + \hat{N}_{i-1,2}(1 - H_{i-1,2})]\hat{S} \quad (3.8)$$

Versions 3 and 4 of the population reconstruction, called model 1c2S and model 1c1S, included a common vulnerability coefficient for juveniles and adults. In these cases, the joint likelihood simplified as follows:

Table 3.4: Parameters used in mourning dove population reconstruction models.

Parameter	Description
$i = 1, \dots, Y$	The years of data used in the model
$N_{i,2}$	Adult abundance in each year i
$N_{i,1}$	Juvenile abundances in each year i
$N_i = N_{i,1} + N_{i,2}$	Total yearly abundance in each year i
\hat{S}_1	Juvenile survival rate, assumed constant over time
\hat{S}_2	Adult survival rate, assumed constant over time
c_1	Vulnerability coeff. for juveniles, assumed constant over time
c_2	Vulnerability coeff. for adults, assumed constant over times
$H_{i,1} = 1 - e^{-c_1 f_i}$	Hunting probability for juveniles in year i
$H_{i,2} = 1 - e^{-c_2 f_i}$	Hunting probability for adults in year i
<i>Auxiliary Index Likelihood</i>	
α	Index to abundance proportion
σ^2	Variance associated with the index- abundance relationship

$$L_{joint} = L_{catch} \cdot L_{AAH} \cdot L_{radio} \quad (3.9)$$

$$L_{catch} = \prod_{year=i=2002}^{2006} \binom{N_i}{h_i} (H_i)^{h_i} (1 - H_i)^{N_i - h_i} \quad (3.10)$$

$$L_{AAH} = \prod_{year=i=2002}^{2006} \binom{a_{i,1} + a_{i,2}}{a_{i,1}} \left(\frac{N_{i,j}}{N_{i,1} + N_{i,2}} \right)^{a_{i,1}} \left(\frac{N_{i,2}}{N_{i,1} + N_{i,2}} \right)^{a_{i,2}} \quad (3.11)$$

$$L_{radio} = \prod_{year=r=2005}^{2006} \prod_{j=1}^2 \binom{T_j^{(r)}}{h_j^{(r)}} H_{r,j}^{h_j^{(r)}} (1 - H_{r,j})^{T_j - h_j^{(r)}} \quad (3.12)$$

Version 3 of the model, version 1c2S, assumed separate survivals for juveniles and adults, and adult abundances (for every year except 2002) were derived iteratively from the other parameters following the equation:

$$\hat{N}_{i,2} = [\hat{N}_{i-1,1} \hat{S}_1 + \hat{N}_{i-1,2} \hat{S}_2] (1 - H_{i-1}) \quad (3.13)$$

Model 1c1S, assumed that juveniles and adults have the same survival, and adult

abundances were derived from:

$$\hat{N}_{i,2} = [\hat{N}_{i-1,1} + \hat{N}_{i-1,2}](1 - H_{i-1})\hat{S} \quad (3.14)$$

The model assumptions were described and justified in chapter 2.

The model shown above, combined with the data presented earlier, was used to estimate the desired parameters- natural survival rate, harvest mortality, recruitment, and population abundances, along with their standard errors. The model used maximum likelihood methods, and the associated invariance property of MLEs to obtain these estimates. Because of the nature of the model, the estimates could not be found analytically, but instead were obtained through numerical methods. The computer software program AD Model Builder (Otter Research Ltd. 2004) was used to find the estimates and standard errors. All analyses thereafter were conducted in the statistical software R (R Development Core Team 2007).

3.4 Results

The 4 versions of the model resulted in similar abundance trends, but with a range of population sizes (see Appendix 3.7 for parameter estimates). In 2002, populations were lowest, with an up and down pattern for the following years, and in 2005, population sizes were the highest. All models suggested a slightly increasing trend over the 5 years. Only the 1c1S model was able to estimate all parameters; the other models were unable to estimate the survival rates (see Appendix 3.7). Model versions with separate juvenile and adult survivals were unable to estimate the adult survival rate; the 2c1S model was unable to estimate the common survival. When survival was incalculable, the computer software set the parameter at 1.0, the maximum of its allowable range.

Using Akaike information criterion (AIC) and likelihood ratio tests (LRTs) (Table 3.5), model 2c2S was the best fitting model. The model selection tool AIC_c was

not used because of the difficulty in determining sample size for this data set. Model selection was discussed further at the end of the Methods section of Chapter 3.

Model 2c2s estimated juvenile survival at 0.23 (SE = 0.051), and was unable to successfully estimate the adult survival. The juvenile vulnerability coefficient was 2.20 (SE = 0.331), and the adult vulnerability coefficient was 0.51 (SE = 0.086); combined with the effort values, the average juvenile harvest mortality was 47.9% and the average adult mortality was 14.6% (Figure 3.4). The 5-year abundance trend (Figure 3.5) indicated that the population size fluctuated between 10,189 and 21,476 and increased at an average rate of 1.24 per year.

3.4.1 Goodness of Fit

To test for goodness-of-fit, χ^2 values were calculated:

$$\chi^2 = \sum_{i=2002}^{2006} \sum_{j=1}^2 \frac{(a_{i,j} - \hat{a}_{i,j})^2}{\hat{a}_{i,j}} \quad (3.15)$$

where $\hat{a}_{i,j} = \hat{N}_{i,j} \hat{h}_{i,j} \hat{p}_{smp,i}$. The values obtained are in Table 3.5. There were other values that could have been compared for this model, such as the total observed versus expected harvests. The total harvests were not compared because the age-at-harvests were seen as more detailed portrayals of the model estimates.

A graph of the observed versus expected age-at-harvest values for the 2c2s model

Table 3.5: Log-likelihood, AIC, and chi-squared goodness-of-fit values associated with the 4 model versions. $AIC = 2k - 2\ln(L)$, where k = the number of parameters, and $\ln(L)$ was the log-Likelihood value. The chi-squared values were for the observed versus expected age-at-harvests from the wing clipping data.

Model	$\ln[L(\hat{\theta})]$	k	AIC	AIC _c	χ^2 Values
1c1S	-531.3	7	1076.6	1132.6	2006
1c2S	-320.7	8	657.4	801.4	1894
2c1S	-322.7	7	659.4	715.4	410
2c2S	-301.3	8	618.6	762.6	2126

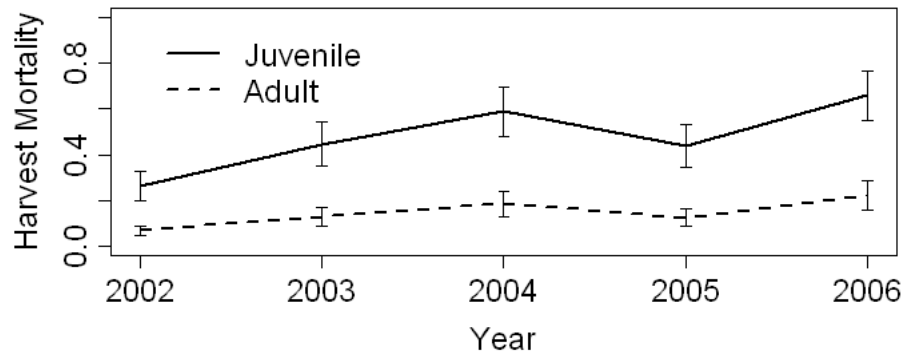


Figure 3.4: Model 2c2s estimates of the harvest mortalities at JARMWA, 2002-2006.

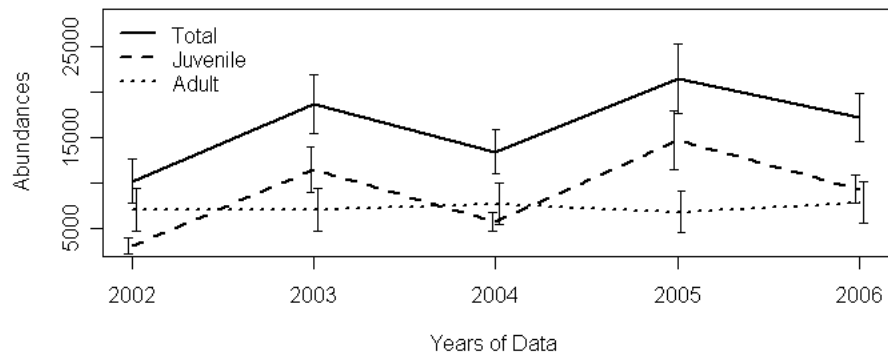


Figure 3.5: Model 2c2s estimates of abundances at JARMWA during the beginning of the hunting season, 2002-2006.

Table 3.6: Mourning dove abundance estimates with standard errors of each model. The estimates are for mourning dove population sizes at JARMWA, 2002-2006.

2002	\hat{SE}	2003	\hat{SE}	2004	\hat{SE}	2005	\hat{SE}	2006	\hat{SE}
<i>Juvenile Abundances</i>									
3,143	423	11,512	1,274	5,745	551	14,669	1,629	9,326	789
<i>Adult Abundances</i>									
7,046	1,202	7,109	1,187	7,687	1,163	6,807	1,162	7,878	1,165
<i>Total Abundances</i>									
10,189	1,242	18,621	1,663	13,433	1,257	21,476	1,934	17,204	1,366

Table 3.7: Mourning dove parameters: estimated survival rates, vulnerability coefficients, and average harvest mortalities of mourning doves at JARMWA, 2002-2006.

	\hat{x}_j	\hat{SE}	\hat{x}_a	\hat{SE}
Survival	0.23	0.051	1.0	0.0
Vulnerability Coefficients	2.20	0.331	0.51	0.086
Average Hunting Mortalities	0.479	0.048	0.146	0.022

showed two years where the expected number of juveniles harvested was much lower than the observed values (Figure 3.6). The lack of fit was attributed to the inappropriate use of χ^2 for this model. Only 5 years of data were available; without a larger sample size, the χ^2 approximations did not hold and did not accurately assess the model fit (Williams et al. 2002). Another problem was that the chi-square assumed that each expected value is independent, but the model derived adult abundances from the previous year. In addition, there were no replicates, each observation came from a different age-class and year.

In this case, AIC was a more robust model selection tool and the 2c2S model was chosen as best fitting.

3.5 Discussion

The population reconstruction model applied to the mourning doves had two deficiencies. The first was the missing wing data in 2004 (Table 3.1). The model would not work without aging information so the age-class information from 2003 and 2005

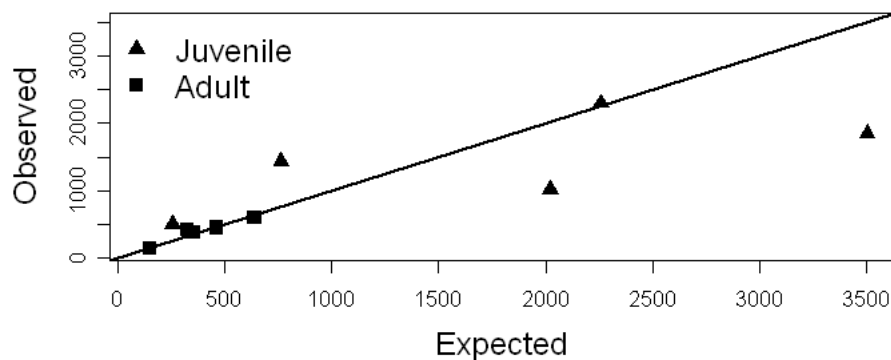


Figure 3.6: The observed and estimated mourning dove age-at-harvests for JARMWA, 2002-2006. Expected values were equal to the abundance estimate times the harvest rate times the sampling probability for a given year. The observed value was the observed number of wing clippings for each age class and year. Estimates were taken from the 2c2S model.

were averaged. With only 5 years of collected data, any missing information had the potential for a huge impact; it remains unknown how the replacement numbers affected these results.

The second issue was the inability of the model to provide estimates for the adult survival parameter, which brought the other estimates into question and also meant that the variances associated with these parameters were incorrect. The inability to estimate survival may have arisen from the small harvest and effort numbers from 2002 compared to 2003 (Table 3.1). Because the data set consisted of only 5 years, the 2002 data could not be dropped. If the model was run without bounds on the survival parameter, it was estimated above 1.0 and abundance estimates similarly did not make sense. Another option was to set the survival rates at the values found within the literature and see if the abundance estimates were robust to this change. This option was completed in the section below.

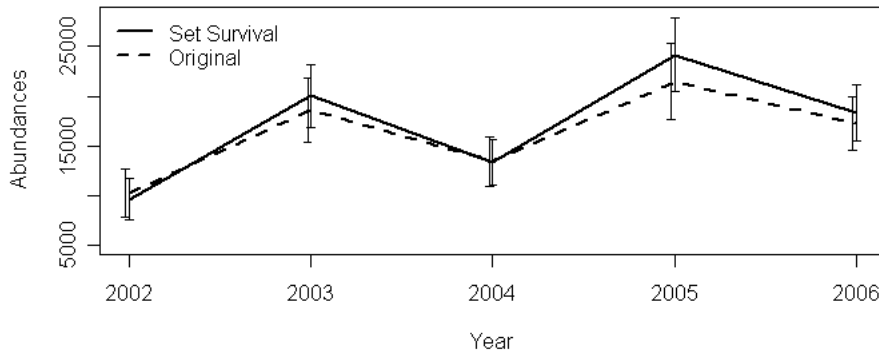


Figure 3.7: A Comparison of total abundances estimates from the best-fitting model, model 2c2s, and a similar model that used preset survival rates. The preset survival rates were an average of the values found in the literature.

3.5.1 Sensitivity to Survival Parameter

The model was rerun using preset survival estimates based on the literature values found in Tomlinson and Dunks (1993). The estimates for the eastern CMU were used, and juvenile survival was set at 36.7% and adult survival was set at 46.9%. The model with preset survival rates had larger juvenile abundance estimates and smaller adult abundance estimates (Table 3.8). The total abundances that this model obtained were very similar to the original model, model 2c2s, results (Fig. 3.7).

The similarity between the two model estimates suggest that the original abundance estimates were accurate and robust against the survival rate values.

3.5.2 Method-of-Moments Values

For this data set, alternative abundance estimates were obtained using method-of-moments techniques to directly estimate the abundances using the following formula:

$$\hat{N}_{i,j} = \hat{h}_{i,j} / \hat{H}_{i,j} \quad (3.16)$$

Table 3.8: A Comparison of the best-fitting model, model 2c2s, with a similar model that used preset survival rates. The preset survival rates were an average of the values found in the literature.

Juvenile Abundances										
Model	2002	\hat{SE}	2003	SE	2004	\hat{SE}	2005	SE	2006	\hat{SE}
Preset Survival	5,241	432	16,596	1,162	7,892	531	20,664	1,428	11,764	715
Original	3,143	423	11,512	1,274	5,745	551	14,669	1,629	9,326	789
Adult Abundances										
Model	2002	\hat{SE}	2003	SE	2004	\hat{SE}	2005	SE	2006	\hat{SE}
Preset Survival	4,383	724	3,432	456	5,456	629	3,511	483	6,555	748
Original	7,046	1,202	7,109	1,187	7,687	1,163	6,807	1,162	7,878	1,165
Total Abundances										
Model	2002	\hat{SE}	2003	SE	2004	\hat{SE}	2005	SE	2006	\hat{SE}
Preset Survival	9,624	1,062	20,028	1,595	13,347	1,150	24,175	1,906	18,319	1,455
Original	10,189	1,242	18,621	1,663	13,433	1,257	21,476	1,934	17,204	1,366

The radiotelemetry results were directly used to estimate the harvest mortalities and the wing clippings combined with the total harvests to estimate the age-at-harvests using method-of-moments techniques.

Estimating harvest mortality directly

This method estimated abundances for 2005 and 2006 only, the years in which the telemetry data were collected. The harvest rates, $\hat{H}_{i,j}$, were set as the numbers harvested divided by the numbers tagged (Table 3.9). Multiplying the total harvest by the age ratios from the wing clippings estimated the age-at-harvests:

$$\hat{h}_{i,j} = h_i \cdot \frac{a_{i,j}}{a_{i,1} + a_{i,2}} \quad (3.17)$$

Equation 3.16 then led to the abundance values in Table 3.9.

The difference in abundance values between this model and the 2c2s model were attributed to a lack of biological restraints and inattention to data variability in the method-of-moments values, as discussed in the subsection below.

Using telemetry to estimate vulnerability coefficients directly

The other set of simple method-of-moments formulas used the radiotelemetry to find the vulnerability coefficients by rearranging the harvest process formula (Equation 3.2):

$$c_{i,j} = -\frac{\log(1 - H_{i,j})}{f_i} \quad (3.18)$$

I applied Equation 3.18 to the telemetry data, averaged the vulnerability coefficients for years 2005 and 2006, then used Equation 3.2 to find harvest rates for all years, 2002-2006. I estimated juvenile and adult harvests using Equation 3.17, and age-class abundances using Equation 3.16.

The abundances obtained from this method-of-moments method led to the esti-

Table 3.9: Method-of-moments abundance estimates, using harvest rates directly from radiotelemetry work, compared to the population reconstruction model.

<i>Deterministic harvest rates</i>				
	2005	SE	2006	SE
Juvenile	0.67	0.086	0.58	0.068
Adult	0.39	0.102	0.57	0.072
<i>Abundance Estimates</i>				
		2005		
	Deterministic	\widehat{SE}	2c2S	\widehat{SE}
Juvenile	8,961	1,159	14,669	1,629
Adult	3,690	963	6,807	1,162
Total	12,651	1,507	21,476	1,934
		2006		
	Deterministic	\widehat{SE}	2c2S	\widehat{SE}
Juvenile	10,873	1,294	9,326	789
Adult	3,383	353	7,878	1,165
Total	14,255	1,342	17,204	1,366

mates in Table 3.10. On the outset, these estimates did not look much different from those obtained with the population reconstruction. But upon closer inspection, these abundances were not realistic, nor were they possible. The adult abundance in one year cannot be greater than the abundance from the year before, yet this was the case from 2002-2003 (Table 3.10). Also, the juvenile to adult ratio for the method-of-moments model is 2.53, meaning that if every dove were to produce offspring, each couple must produce over 5 fledglings on average. Since every dove will not reproduce, the reproductive rate must necessarily be higher. Previous studies have estimated this rate much lower, at 3.37 and 3.8 (see Section on clutch information below).

The method-of-moments models demonstrate the need to connect the years of data and to put biological restraints on the model. The method-of-moments models did not lead to logical answers, did not account for the necessary variation in the parameters, and put too much faith into the radiotelemetry work. There is natural variability in both the data and the parameters which the statistical model is able to

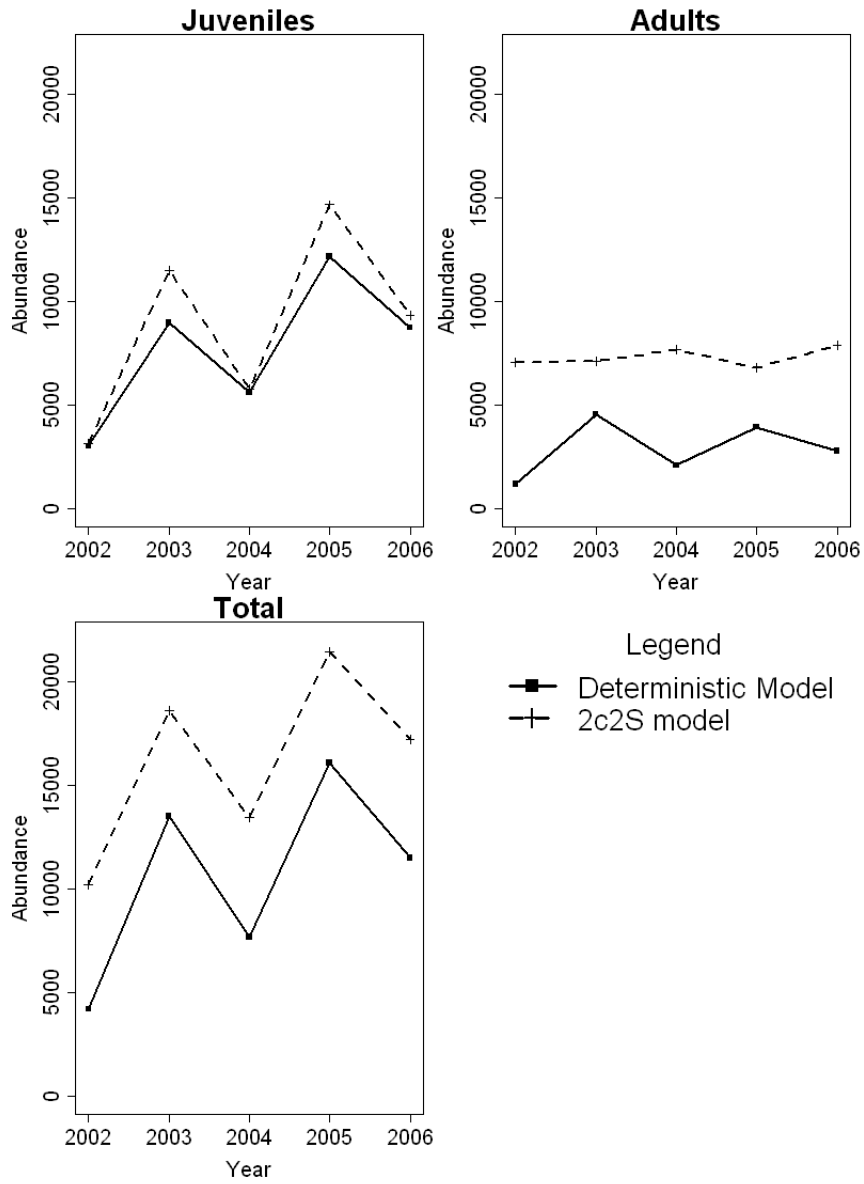


Figure 3.8: A comparison of the method-of-moments and reconstructive abundance estimates. The method-of-moments estimates were those from Table 3.10.

Table 3.10: Parameter estimates from the method-of-moments model that estimated the vulnerability coefficients of mourning doves at JARMWA, 2002-2006.

	2002	2003	2004	2005	2006
<i>Harvest Rates</i>					
Juvenile	0.299	0.500	0.648	0.491	0.719
Adult	0.214	0.375	0.507	0.368	0.577
<i>Abundances</i>					
Juvenile	3,007	8,971	5,601	12,161	8,726
Adult	1,180	4,547	2,079	3,928	2,776
Total	4,187	13,518	7,679	16,089	11,502

overcome and incorporate.

3.5.3 Index surveys

The national index counts, BBS and CCS, have inadequate sample sizes within Missouri to be compared to the population reconstruction. The statewide RDS does survey multiple routes within each county of Missouri, and this data may be compared to the reconstruction estimates. JARMWA is in Jackson County. Index data is not available for this county, but was collected in 5 of its surrounding counties: Platte, Ray, Lafayette, Johnson and Cass. Each county suggests a slightly different abundance trend (Fig. 3.9), but all suggest a stable or slightly declining population.

When the counties are combined to create an average index for the area, the trend is still slightly decreasing, which is in contrast to the population reconstruction estimates (Fig. 3.10). Considering the doubt and mistrust surrounding index surveys, it is not surprising that the trends do not agree.

3.5.4 Simulations

The dove results were compared to the simulations of models with radiotelemetry data, 5 years of data, and 2 vulnerability coefficients. For the simulated models, the standard errors associated with the survivals were high, partially explaining the mourning dove model's inability to fully estimate survivals. The abundance estimates

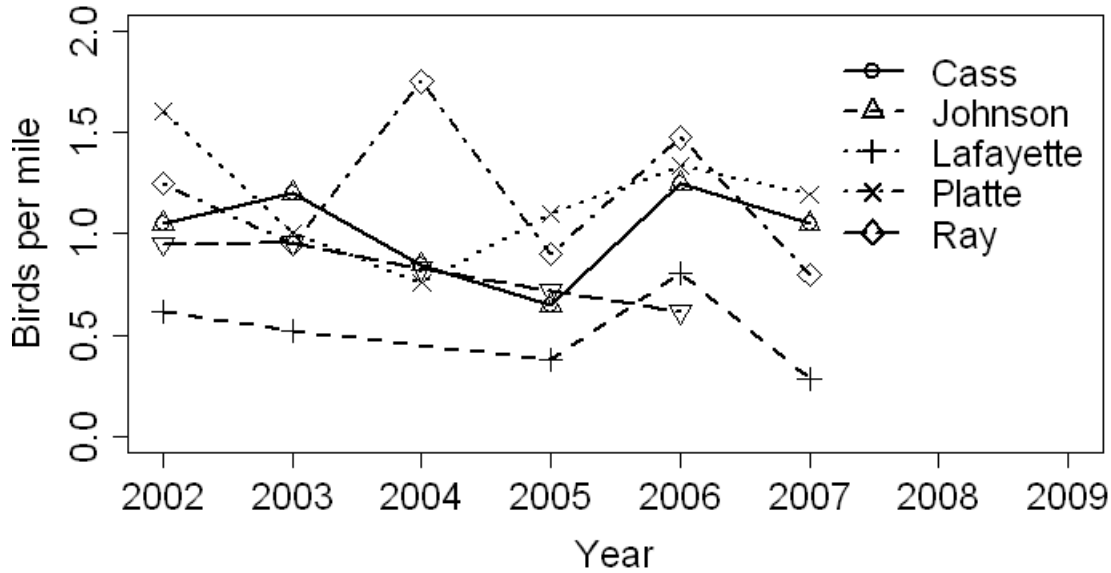


Figure 3.9: A comparison of the index roadside counts for the 5 counties adjacent to JARMWA: Platte, Ray, Lafayette, Johnson, and Cass counties, 2002-2006.

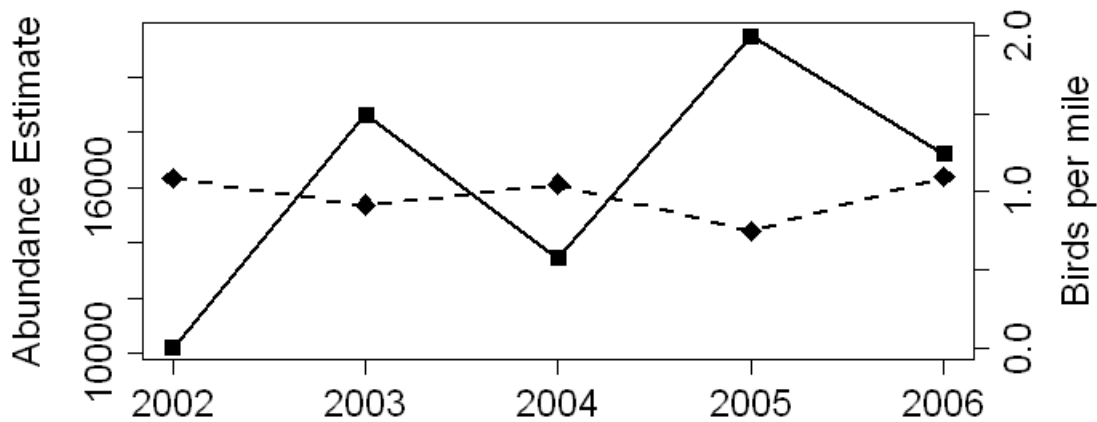


Figure 3.10: A comparison of the estimated abundances and the averaged index counts revealed discrepancies between trends. The straight line represented the population reconstruction estimates and the dotted line was the averaged index trend.

under these specifications were unbiased, with low and possibly underestimated standard errors. These results provided backing for the dove estimates, and reason for the small standard errors.

The mourning dove results matched the expectations developed from the sensitivity analysis simulations; the doves were a real-life comparison of the 4 different model combinations of 1 or 2 vulnerability coefficients and 1 or 2 survivals. As expected from the previous results, the 2c1S model produced juvenile abundances that were lower than the 2c2S abundances, and adult abundances that were higher than the 2c2S model. The 1c2S model produced juvenile abundances that were higher and adult abundances that were lower than the 2c2S model. The vulnerability coefficients followed the same pattern: the 2c1S model had a higher juvenile vulnerability coefficient and a lower adult vulnerability coefficient than the 2c2S model, and the 1c2S model had a vulnerability coefficient that fell between the juvenile and adults estimates from 2c2S.

3.5.5 Demographic parameter estimates compared to previous studies

Tomlinson and Dunks (1993) estimated survival rates for mourning doves in the Central Management Unit (CMU), the 14 states of the U.S. that Missouri is grouped with in determining national dove management strategies. For the whole unit, they estimated adult survival at 52.1% and juvenile survival at 43.8%. For the eastern CMU, where Missouri is located, they estimated adult survival at 46.9% and juvenile survival at 36.7%.

Unfortunately, the best-fitting models were unable to provide full survival estimates, so these parameters cannot be compared. Once more years of harvest data becomes available, and in turn, survival becomes easier to estimate, the model output could be compared to these previous survival rates.

Using the results from a nationwide banding program administered by the U.S. Fish and Wildlife Service in 1967-74, Tomlinson and Dunks (1993) concluded that

juveniles are 1.3 times more vulnerable than adults to hunting in the CMU. The population reconstruction concluded that this ratio is greater: for the 2c2S model, juveniles were 3.3 times more vulnerable than adults. This difference could be due to the differences in study regions between the entire CMU and the small region of the JARMWA, or it could be related to the correlation between harvest and natural mortalities in the population reconstruction.

3.5.6 Clutch and Fledging Information

The population reconstruction results match with known clutch information. Mourning dove clutch size is 2 eggs, and in Missouri, an average of 4-5 nesting attempts occur each year (Mirarchi and Baskett 1994). Incorporating nest and fledging mortality, Sayre and Silvy (1993) estimated 3.8 fledglings per pair of mourning doves; Otis (2003) estimated this ratio to be 3.37 (CI: 1.93, 4.81) for doves in the southern Central Management Unit (CMU); and for the entire contiguous United States, the estimated reproductive rates ranged from 3.37 to 6.37.

For the 2c2S model, the average ratio of juveniles to pair of adults was 2.46. Because all adults will not successfully mate, these ratios are negatively biased reproduction rates; incorporating mating rates is likely to push the ratios into the same range as previous studies.

3.5.7 Varying the Telemetry Data

The telemetry data affected the precision of the abundance estimates. The necessary number of doves to be tagged for the desired coefficient of variation (CV) of the abundance estimates may be of interest to wildlife managers designing such studies. The ideal number of tags depends on the harvest mortality of the species and the desired CV for the abundance estimates.

For the JARMWA mourning doves, the model was rerun changing the number of doves tagged but keeping the age ratios and harvest proportions constant. As

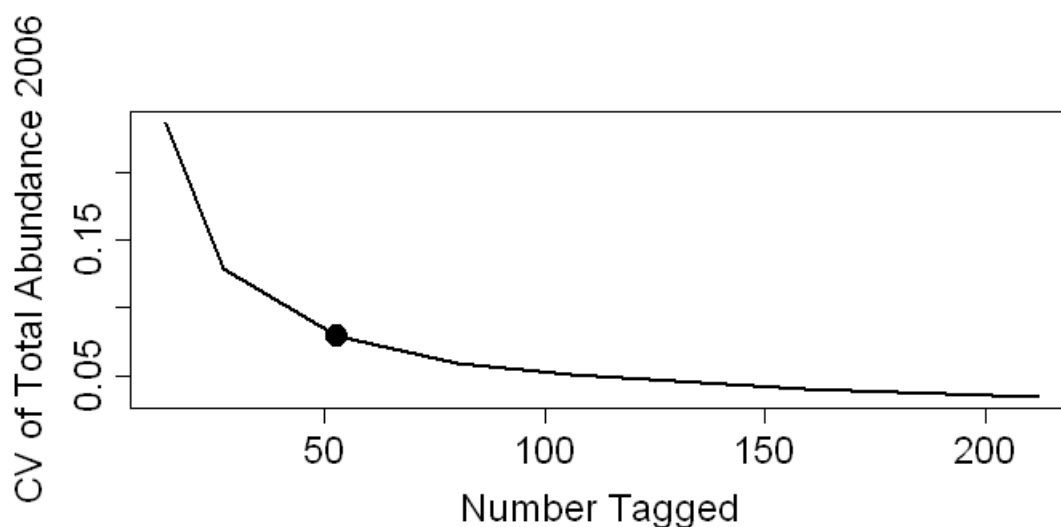


Figure 3.11: CV of total abundance versus the number tagged in the radiotelemetry study. In the true study, 53 doves were tagged in 2005 and the CV was 8%.

the number tagged decreased, the CV of total abundance increased exponentially (Figure 3.5.7). The model that used the true number tagged had a CV of 8%. For this data set, the CV of abundance approaches zero as the number of doves tagged approaches 1,000.

3.6 Management Implications

Mourning doves are one of the most harvested game birds in North America. As their popularity continues, the management of the species remains of interest. Current management plans are often based on historical records or the population index surveys. Relying on historical regulations does not lend any insight into the population dynamics or how hunting may be affecting the population. The population indices for mourning doves have often been criticized for their deficiencies, as mentioned in the Introduction.

The population reconstruction model provided a valid abundance trend. This

trend is a good supplement to the index surveys. A comparison of the index counts to the population reconstruction results hopefully provides insight into the behavior of both models.

In addition, the population reconstruction produced robust abundance estimates and vulnerability coefficients, both broken down by age-class. I believe that as more years of data are incorporated into the model, the results will stabilize further. Tagging more birds in the telemetry study would reduce the CV of the abundance estimates, leading to better precision.

The model's inability to estimate adult survival should not result in distrust in the abundance estimates. As mentioned in the Discussion, survivals were often estimated at 1.0 in the simulations. Also, when survival values from the literature were used, the abundance estimates were robust to the new survivals.

In the late 1990s, a National Strategic Harvest Management Plan was formed to improve nationwide mourning dove harvest management strategies. Under this plan, a 26+ state bird banding study was begun in 2003 with tens of thousands of birds banded each spring. The recovery of the bands gives migration route information and mortality rate data. Pilot wing clippings studies have also been started, and the collected aging information gives further insight on mortality rates as well as age ratios and harvest ratios.

Once enough years of wing data are collected, this data could be used for population reconstructions for many other mourning dove populations across the nation.

Population reconstruction is a good choice for management plans that call for specific abundance information. Its estimates for juvenile and adult abundances are robust, and the model provides the additional demographic parameters of harvest vulnerabilities and natural survival rates.

3.7 Alternate Model Results

Table 3.11: Tables of parameters, excluding abundances, estimated from 4 alternative models. Estimated survival rates of mourning doves at JARMWA, 2002-2006.

Model	\hat{S}	\hat{SE}		
1c1S	0.48	0.042		
2c1S	1.0	0.0		
	\hat{S}_j	\hat{SE}	\hat{S}_a	\hat{SE}
1c2S	0.08	0.011	1.0	0.0
2c2S	0.23	0.051	1.0	0.0

Table 3.12: Estimated vulnerability coefficients of mourning doves.

Model	\hat{c}	\hat{SE}		
1c1S	3.07	0.276		
1c2S	0.93	0.099		
	\hat{c}_j	\hat{SE}	\hat{c}_a	\hat{SE}
2c1S	4.87	0.26	0.42	0.08
2c2S	2.20	0.331	0.51	0.086

Table 3.13: Average harvest mortalities, derived from the vulnerability coefficients, of mourning doves at JARMWA, 2002-2006.

Model	\hat{H}	\hat{SE}		
1c1S	0.590	0.030		
1c2S	0.248	0.022		
	\hat{H}_j	\hat{SE}	\hat{H}_a	\hat{SE}
2c1S	0.742	0.017	0.121	0.022
2c2S	0.479	0.048	0.146	0.022

Table 3.14: Alternative model abundance estimates with standard errors. The estimates are for mourning dove population sizes at JARMWA, 2002-2006.

Juvenile Abundances											
Model	2002	\hat{SE}	2003	\hat{SE}	2004	\hat{SE}	2005	\hat{SE}	2006	\hat{SE}	
1c1S	2,997	252	9,408	553	4,597	243	12,021	659	7,404	292	
1c2S	6,932	726	23,207	2,167	10,853	984	29,649	2,772	16,731	1,444	
2c1S	1,713	95	7,083	209	3,915	99	8,899	227	6,685	95	
2c2S	3,143	423	11,512	1,274	5,745	551	14,669	1,629	9,326	789	
Adult Abundances											
Model	2002	\hat{SE}	2003	\hat{SE}	2004	\hat{SE}	2005	\hat{SE}	2006	\hat{SE}	
1c1S	842	93	1,206	52	2,233	110	946	75	2,783	134	
1c2S	3,939	448	3,966	427	4,574	407	3,752	411	4,849	417	
2c1S	7,883	1,518	8,270	1,546	9,309	1,645	8,408	1,692	10,021	1,829	
2c2S	7,046	1,202	7,109	1,187	7,687	1,163	6,807	1,162	7,878	1,165	
Total Abundances											
Model	2002	\hat{SE}	2003	\hat{SE}	2004	\hat{SE}	2005	\hat{SE}	2006	\hat{SE}	
1c1S	3,840	313	10,614	590	6,829	337	12,967	730	10,187	407	
1c2S	10,871	1,119	27,173	2,565	15,427	1,373	33,401	3,171	21,580	1,827	
2c1S	9,546	1,547	15,353	1,638	13,223	1,699	17,307	1,825	16,706	1,886	
2c2S	10,189	1,242	18,621	1,663	13,433	1,257	21,476	1,934	17,204	1,366	

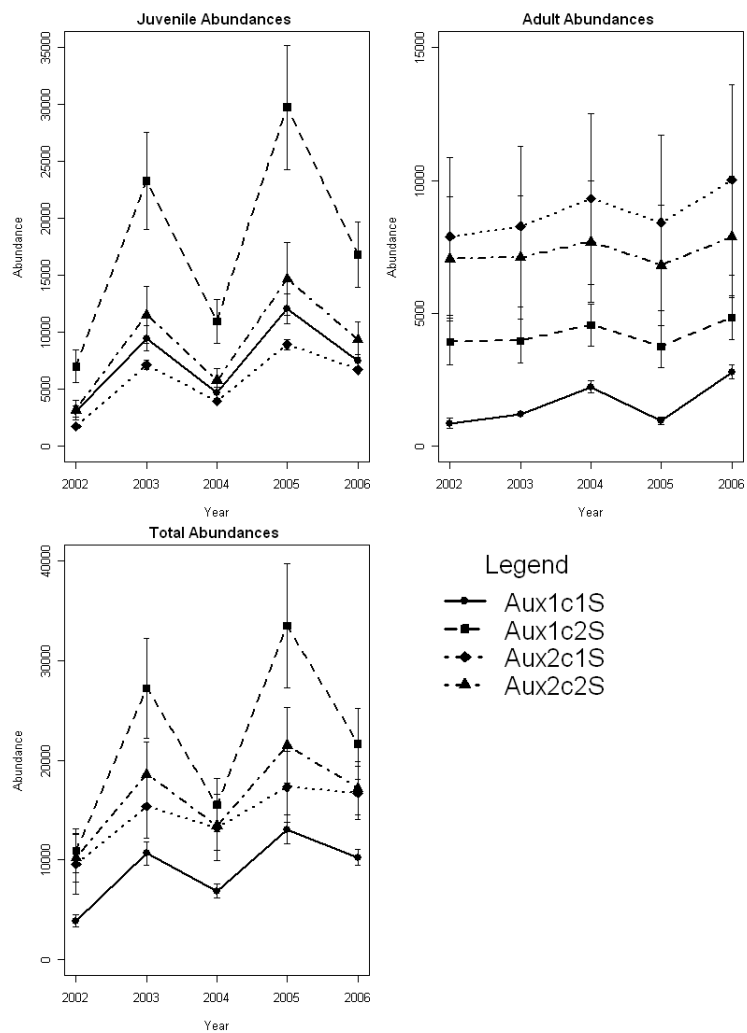


Figure 3.12: Alternative model estimates of yearly abundances at JARMWA during the beginning of the hunting season, 2002-2006. Each line represents a different model.

Chapter 4

SAGE GROUSE POPULATION RECONSTRUCTION IN OREGON

4.1 *Introduction*

In this chapter, I applied the population reconstruction models presented in Chapter 2 to the statewide population of greater sage grouse (*Centrocercus urophasianus*) in Oregon, for years 1993-2006. The state population may be broken up into seven subpopulations based on the different geographic regions, but for the work presented here, the entire state was considered as one population with common demographics.

Sage grouse are a species of concern because they have been extirpated, are endangered, or threatened throughout most of their historic range. A lek is a spring mating ground where males compete and attract females for breeding. Lek counts currently provide the abundance trend information for the species, and attempts have been made to estimate abundances from these counts using the average number of males found per lek and sex ratios from wing clippings (Willis et al. 1993, Braun 1998, Hagen 2005). While these deterministic estimates are plausible, the true relationship between the leks and total population is unknown and hence the estimates arising from the lek counts have unknown accuracy. Population reconstruction can provide valuable, unbiased abundance estimates for the entire population and for each sex and age-class. Through age-at-harvest information from wing clippings, catch-effort from hunter surveys, and a radiotelemetry study, the model produced estimates and standard errors for natural mortality, harvest mortality, and age-class abundances.

Below, I provided more background on sage grouse, reintroduced the population reconstruction model specific to the grouse, and then compared and contrasted it

to the results from the lek counts and other demographic estimates from previous publications.

4.1.1 Background & Motivation

Sagebrush habitat historically covered 220 million acres, making it one of the most widespread habitats in the country (Hagen 2005). Early European settlers reported that wherever there was sagebrush, there were sage-grouse (Mitchell and Maxfield 2001). The habitat loss, fragmentation, and degradation resulting from the settlers' agriculture, livestock, and town-building led to depleted sage grouse populations (Mitchell and Maxfield 2001). Today, sage grouse are extirpated from 5 states: Arizona, New Mexico, Oklahoma, Kansas, Nebraska, and Canada's British Columbia . In many other states: Washington, California, Utah, Colorado, North Dakota, South Dakota, and the Canadian provinces Alberta and Saskatchewan, sage grouse are 'at risk' (Hagen 2005).

Relatively stable populations exist in only 5 states: Oregon, Nevada, Idaho, Wyoming, and Montana (Braun 1998). Even within these more stable states, a 17-47% decline in breeding populations was observed through the lek count surveys, from 1984 to 1993 compared to long-term averages (Connelly and Braun 1997). As the quality and quantity of the sagebrush habitats has continued to decline over the past 50 years, the conservation of sage grouse remains a management goal (Connelly et al. 2000b).

In Oregon, one of the remaining states with relatively stable grouse populations, management plans are in place to help the survival of this species. Most focus is on conserving sagebrush habitat, which is seen as the greatest limiting factor to sage grouse abundance (Connelly et al. 2000a). Coupled with habitat protection is the need to monitor the populations to ensure that they remain healthy and respond positively to any habitat changes.

4.1.2 Current Monitoring

Several types of data are collected to monitor sage grouse populations. The most extensive information comes from a systematic monitoring of leks since 1941 (Crawford and Lutz 1985). The leks were surveyed in two complimentary ways. Through the cooperation of the Oregon Department of Fish and Wildlife (ODFW) and the Bureau of Land Management, lek searches systematically covered all inhabitable areas, usually via aircraft, to uncover new leks and to determine if old leks had become inactive. A sample of the accessible leks were selected as trend leks and male attendance at these leks was recorded. The leks were visited at sunrise, at least 3 times during the breeding season and all displaying males were censused (Hagen 2005). The visit with the highest count was the one recorded for that site.

The ODFW gathered other sources of data to measure productivity. Brood production surveys were completed in the late spring to gauge fecundity and reproductive success. Routes were traveled by vehicle between July 15 and August 10. All birds that were observed were counted and classified as juvenile, adult, male, female, or unknown (Hagen 2005). Another productivity measurement was the wing clippings from the fall harvest, collected and examined for sex and age information. The hunters themselves were also surveyed to get feedback on hunting success and total harvest.

4.1.3 Utility of Population Reconstruction

While the current data collections are helpful, they lack in rigor and full utility. The lek counts and wing-data sex ratios are used to obtain a conservative estimate of a minimum population size. While it is helpful to have a minimum population estimate, the formula used is not statistically rigorous, and the relationship between the estimate and the true abundance is not known (Beck et al. 2003). No studies have been completed that evaluate the relationship between lek counts and total population size, and statistical designs are not incorporated into the lek count surveys. While

it is believed that the leks generally capture the population trend, they may not capture the magnitude of a population change and the accuracy of the lek counts is poorly understood (Beck et al. 2003). Similarly, the relationship between the brood production survey and actual juvenile production is not known.

In addition to providing abundance and mortality estimates, the population reconstruction model can be a useful augment to current monitoring efforts. The model's results can be compared the lek surveys and used to help define the relationship between the lek counts and abundance, factors that are highly correlated, but whose relationships are not known.

Here, the population reconstruction was applied to the sage grouse population of Oregon. All subpopulations were grouped together, and it was assumed that the sage grouse in Oregon act as one population. The model used the following data from 1993-2006: age-at-harvest from wing clippings, catch-effort from hunter surveys, and tagging results from an auxiliary, radiotelemetry study conducted in 1998-2001. Natural mortalities, harvest mortalities, and juvenile (hatching year) male, juvenile female, adult male, and adult female abundances were estimated with this information. The estimated abundances were taken to be the population sizes at the end of August, just prior to the hunting season.

4.2 Area of Study

Sage grouse inhabit the Southeastern quarter of Oregon (Figure 4.2). This entire range was the area of study. The data acquired through the ODFW sage grouse monitoring efforts, described above as the wing collections, harvest surveys, and lek counts, were part of the population reconstruction inputs.

Grouse wings were collected by giving hunters bags with return envelopes that the hunters used to mail in wings clipped from their harvest. Biologists used the molt patterns on the wings to determine the sex and age of the bird. Male versus female, and juvenile versus adult wings were easily identifiable. Biologists were also

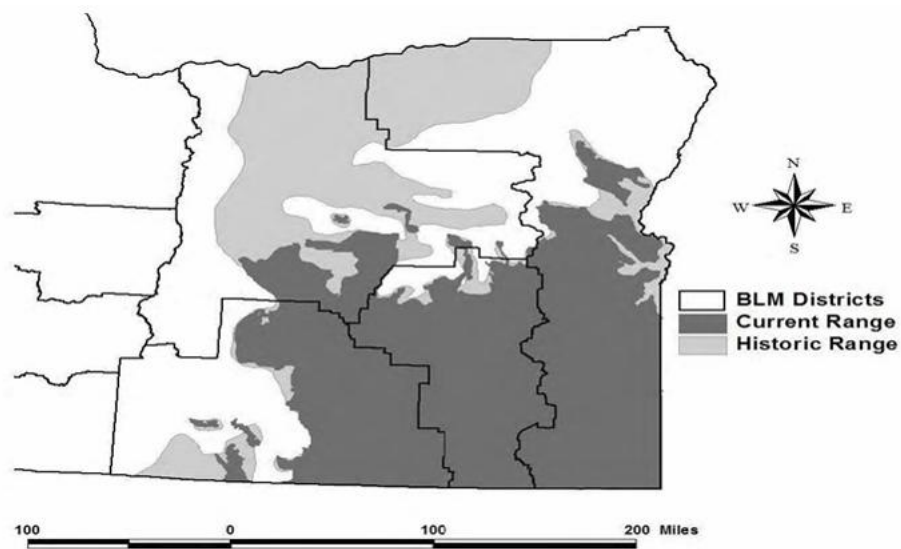


Figure 4.1: The current range of sage grouse is roughly half of its historical range. The land is managed to keep current populations stable. Taken from Hagen (2005).

able to separate the adult wings into yearlings and 2+year-old birds. This separation was less distinct and it was believed that many yearlings were misclassified as adults (Rowland and Wisdom 2002). Because of this lack of clarity, the yearlings were not given a separate age-class, and were instead grouped with the rest of the adults (Table 4.1).

A random sampling of the hunters were called each year by the ODFW to provide additional information about the hunting season. These telephone surveys provided estimates of total harvest and total number of hunters, used as a proxy for effort (Table 4.1).

The lek counts were included as an auxiliary index to adult male abundance to potentially enhance the model's estimates. Because a different number and selection of leks were counted each year, the index auxiliary used was the average number of males per lek, calculated as the total number of males seen divided by the number of active leks assessed (Table 4.1). The methods used to obtain this index were those followed by the ODFW (Hagen 2005). Although the lek counts are usually assumed to be an index to total abundance, it was more accurate to use the data to index the adult males only, because that was the sex-age class being counted.

Another auxiliary likelihood was built from a radiotelemetry study conducted in 1998-2001 in the Beatty's Management Unit (Crawford and Carver 2000). Separate from the information collected from the hunters themselves, this study used radio tags for the estimation of harvest rates of the grouse (Table 4.2). The tagged birds were not separated by sex and age because it is believed that all sex and age classes have similar harvest vulnerabilities.

4.3 Methods

Several likelihood models were run on this data set by varying the number of parameters and varying the amounts and types of auxiliary information included. Models were run: 1) without any auxiliary studies, 2) with auxiliary lek count index data, 3)

Table 4.1: Grouse telephone survey, wing collection, and lek data. Collected by the Oregon Department of Fish and Wildlife, from 1993 to the present. Index data compiled by Hagen 2005.

Variable	Symbol	Year													
		1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
No. of hunters	f_i	628	860	784	806	804	843	867	875	867	881	834	949	956	891
(Hunter Effort)															
Doves harvested	H_i	548	976	716	808	839	681	1,015	857	1,015	973	979	1,228	1,222	1,089
Juv. Males aged	$a_{M,1,i}$	103	145	68	105	147	110	173	120	181	192	145	178	169	147
Juv. Females aged	$a_{F,1,i}$	99	168	93	148	169	119	201	139	179	181	171	222	187	169
Adult Males aged	$a_{M,2,i}$	85	122	87	69	95	87	113	142	118	110	146	134	172	167
Adult Females aged	$a_{F,2,i}$	139	298	205	171	175	150	184	183	189	165	192	242	260	186
Males per Lek Index	I_i	18.05	16.47	12.95	11.04	11.88	14.82	14.61	16.97	15.67	18.06	20.11	19.18	29.27	26.12

Table 4.2: Radiotelemetry field work from University of Oregon graduate students in the Beaty's Management Unit in the Southeastern corner of Oregon.

Variable	Symbol	Year			
		1998	1999	2000	2001
No. tagged	$T^{(r)}$	50	34	19	19
No. tagged & harvested	$h^{(R)}$	2	1	0	1

with auxiliary radiotelemetry data, or 4) including both types of auxiliary information. The other source of distinction between models involved the number of survival parameters and vulnerability coefficients included in the model. Different likelihoods were built by assuming 1 survival rate, 2 survival rates differing by age class, 2 survival rates differing by sex, or 4 survivals differing by both sex and age. Similarly, different likelihoods were built by varying the number of vulnerability coefficients. For models with no auxiliary or with the lek counts as the auxiliary, models were built assuming 1 vulnerability coefficients, 2 vulnerability coefficients differing by age class, 2 vulnerability coefficients differing by sex, or 4 vulnerability coefficients, one for each age-sex class. Likelihoods that included the radiotelemetry data only incorporated 1 common vulnerability coefficient because the tagging data was not broken down by sex or age.

In theory, there were enough years of data to provide the necessary number of minimum sufficient statistics for all models described above to be estimable. In practice, only models that included the telemetry data provided parameter estimates; for the other models, estimates would not converge and the function was never minimized. Therefore, only the models that included telemetry data, and consequently, only a common vulnerability coefficient are discussed further.

The following sets of equations were used when 1 vulnerability coefficient and 4 survivals were assumed. If fewer survivals were assumed, then the derivations of the adult abundances (Equations 4.7 and 4.7) would be condensed accordingly. Models were run including and excluding the index likelihood.

$$L_{joint} = L_{catch} \cdot L_{AAH} \cdot L_{radio} \cdot L_{index}$$

$$L_{catch} = \prod_{year=i=1993}^{2005} \binom{N_i}{h_i} (H_i)^{h_i} (1 - H_i)^{N_i - h_i} \quad (4.1)$$

$$L_{AAH} = \prod_{year=i=1993}^{2005} \left(\begin{array}{c} a_{i,\cdot} \\ a_{M,1,i}, a_{F,1,i}, a_{M,2,i}, a_{F,2,i} \end{array} \right) \cdot \left(\frac{N_{M,1,i}}{N_i} \right)^{a_{M,1,i}} \left(\frac{N_{F,1,i}}{N_i} \right)^{a_{F,1,i}} \left(\frac{N_{M,2,i}}{N_i} \right)^{a_{M,2,i}} \left(\frac{N_{F,2,i}}{N_i} \right)^{a_{F,2,i}} \quad (4.2)$$

$$L_{radio} = \prod_{year=i=1998}^{2001} \binom{T^{(i)}}{h^{(i)}} H_i^{h^{(i)}} (1 - H_i)^{T^{(i)} - h^{(i)}} \quad (4.3)$$

$$L_{index} = \prod_{year=i=1993}^{2005} \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(I_i - \alpha N_{M,2,i})^2}{2\sigma^2}} \quad (4.4)$$

Descriptions of model parameters and symbols are in Tables 4.1, 4.2, and 4.3. Yearly abundances were obtained by summing the age and sex class abundances:

$$N_i = N_{M,1,i} + N_{F,1,i} + N_{M,2,i} + N_{F,2,i} \quad (4.5)$$

The adult male populations and adult female populations (excluding year 1993) were derived from the previous year's populations:

$$N_{M,2,i} = (N_{M,1,i-1} \cdot S_{M,1} + N_{M,2,i-1} \cdot S_{M,2}) (1 - H_{i-1}) \quad (4.6)$$

$$N_{F,2,i} = (N_{F,1,i-1} \cdot S_{F,1} + N_{F,2,i-1} \cdot S_{F,2}) (1 - H_{i-1}) \quad (4.7)$$

As in previous work, maximizations were obtained with AD Model Builder (Otter Research Ltd. 2004) and all other analyses were completed in R (R Development Core Team 2007).

Table 4.3: Parameters used in sage grouse population reconstruction model.

Parameter	Description
$N_{M,1,i}$	Juvenile male abundance in each year i
$N_{F,1,i}$	Juvenile female abundance in each year i
$N_{M,2,i}$	Adult male abundance in each year i
$N_{F,2,i}$	Adult female abundance in each year i
N_i	Total yearly abundance in each year i
$S_{M,1}$	Juvenile male survival rate, assumed constant over time
$S_{F,1}$	Juvenile female survival rate, assumed constant over time
$S_{M,2}$	Adult male survival rate, assumed constant over time
$S_{F,2}$	Adult female survival rate, assumed constant over time
c	Vulnerability coefficient, assumed to be constant
$H_i = 1 - e^{-c \cdot f_i}$	Harvest probability in year i
α	Proportion of the total population that the index counts
σ^2	Variance associated with the $I_i = \alpha N_i$ relationship

Model selection. I picked the best-fitting model using AIC selection criterion. The small-sample AIC_c could not be applied satisfactorily to the joint-likelihood model because the sample size could not be extracted satisfactorily.

The telemetry data consisted of 4 years of observations and had a strong effect on the model's calculability—without this data, the model would not converge or the parameters converged to their boundaries. Each year of telemetry data had a much greater effect on the model estimates than any year of the harvest data. The index data consisted of 14 years of observations and did not have a strong effect on the model, its inclusion did not ensure that the model would converge and its inclusion did not have a significant effect on the parameter estimates. In order to calculate the sample size, all the observations from the index data, telemetry data and harvest data would have to be added equally. As discussed above, many observations came from different data sources and should not be treated as equal.

The small sample AIC_c was therefore not used for the model selection. Instead, models were compared through likelihood ratio tests and AIC. Both methods selected the same model, providing extra support for the chosen model.

The models including and excluding the index likelihood could not be directly

compared through the model selection criteria because they consisted of different data sets. The 2 best-fitting models, one including the index and one excluding it, were compared through the χ^2 -values associated with the expected age-at-harvests.

4.4 Results

The model including the radiotelemetry data and 4 survival parameters, separated by both sex and age (model Radio1c4s), was chosen as the best fitting model (Table 4.4). It estimated juvenile male survival as 0.37 (SE = 0.134), juvenile female survival as 0.25 (SE = 0.063), adult male survival as 0.61 (SE = 0.163), adult female survival as 0.82 (SE = 0.052), and the vulnerability coefficient as 0.033 (SE = 0.017), leading to an average harvest mortality of 0.028 (Figure 4.2). Total abundances ranged from a low of 26,286 in 1995 to a high of 39,492 in 2004 (Figure 4.3). The average estimated abundance was 33,071. Over the 14 years of the data set, the juvenile male, juvenile female, and adult male populations increased in size, while the adult females remained steady (Figure 4.4).

A summary of the output from all models is provided in the last section of the Chapter.

Table 4.4: Log-likelihood, AIC and chi-square goodness-of-fit. $\ln[L(\hat{\theta})]$ is the log-likelihood value. $AIC = 2k - 2\ln[L(\hat{\theta})]$, where k = the number of parameters estimated. $\chi^2 = \frac{\sum (Obs-Exp)^2}{Exp}$ are the chi-square values. The top 4 models excluded the index likelihood, the bottom 4 included it. The two groups of models' AIC values could not be directly compared because they have different data sets.

Model	$\ln[L(\hat{\theta})]$	k	AIC	χ^2 Values
Radio1c1s	-330.4	17	694.7	155.7
Radio1cMsFs	-305.2	18	646.4	104.5
Radio1cJsAs	-302.4	18	640.9	92.1
Radio1c4s	-298.2	20	636.4	85.5
RadioIndex1c1s	-365.2	19	768.3	156.4
RadioIndex1cMsFs	-339.1	20	718.1	105.1
RadioIndex1cJsAs	-338.1	20	716.3	92.3
RadioIndex1c4s	-332.0	22	708.0	87.5

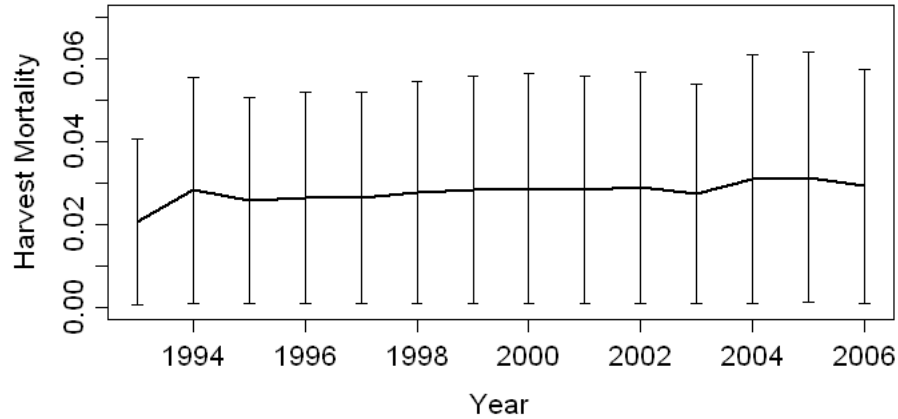


Figure 4.2: Harvest mortalities ($1 - e^{-cf_i}$) of sage grouse in Oregon, 1993-2006, estimated from the Radio1c4s model.

4.4.1 Goodness of Fit

In Chapter 3, the erroneous use of χ^2 values as a model selection tool was discussed. Nevertheless, a comparison of the observed age-at-harvests and expected age-at-harvests gave a qualitative measurement of the model's fit and provided insight into the model's estimates. The expected age-at-harvests were $\hat{a}_{i,j,k} = \hat{N}_{i,j,k} \cdot \hat{H}_{i,j,k} \cdot \hat{p}_{samp,i}$. The juvenile male, juvenile female, and adult male expected harvests matched the observed harvests (Figure 4.5). The adult female expected values strayed further from the observed values, but with no apparent pattern. The resulting chi-square values were still high (Table 4.4), but overall, this comparison of observed versus expected values supported the population reconstruction results.

4.5 Discussion

The population reconstruction led to plausible parameter estimates, but the standard errors associated with the abundance estimates were high (Table 4.5): the coefficients

Table 4.5: Estimated grouse abundances just prior to the hunting season. Statewide population sizes in Oregon, 1993-2006, estimated from the Radio1c4s model.

	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
$\hat{N}_{M,1}$	6,278	6,820	4,053	6,305	7,487	5,750	9,439	5,978	9,176	9,770	7,992	9,738	9,075	8,238
SE	3,163	3,392	2,050	3,159	3,748	2,886	4,685	2,986	4,573	4,863	3,983	4,821	4,490	4,101
$\hat{N}_{F,1}$	6,548	8,233	5,616	8,570	8,566	5,918	10,582	7,108	9,620	9,477	9,933	11,605	9,314	9,471
SE	3,299	4,085	2,823	4,282	4,281	2,972	5,257	3,548	4,785	4,718	4,933	5,742	4,617	4,706
$\hat{N}_{M,2}$	5,237	5,421	5,685	4,850	5,169	5,788	5,518	6,691	6,128	6,957	7,660	7,443	7,918	7,956
SE	2,638	2,681	2,805	2,418	2,555	2,855	2,733	3,308	3,034	3,435	3,786	3,680	3,914	3,938
$\hat{N}_{F,2}$	11,980	11,214	10,932	10,092	10,140	10,178	9,546	10,178	9,827	10,166	10,395	10,706	11,319	11,243
SE	5,960	5,534	5,392	4,984	4,998	5,012	4,719	5,014	4,853	5,013	5,128	5,271	5,581	5,559
\hat{N}_{\dots}	30,043	31,688	26,286	29,816	31,362	27,634	35,084	29,954	34,751	36,370	35,980	39,492	37,626	36,908
SE	14,896	15,596	12,963	14,730	15,492	13,635	17,305	14,758	17,151	17,943	17,733	19,422	18,506	18,203

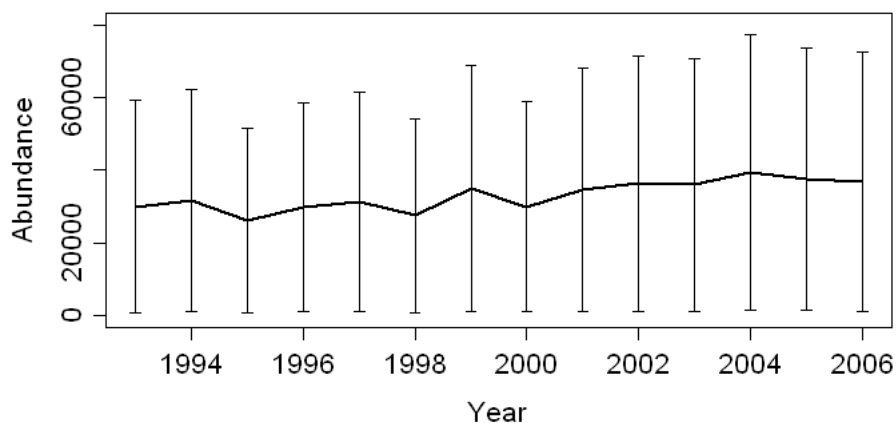


Figure 4.3: Grouse total abundance trends in Oregon, 1993-2006, estimated from the Radio1c4s model.

of variation (CV) were approximately 50%. While not a desirable result, the simulations of models with low harvest mortalities and telemetry data similarly had high standard errors.

The standard errors associated with the survivals were reasonable, with CVs ranging from 6% for adult females to 36% for juvenile male survival. The standard error associated with the vulnerability coefficient was small, but because the harvest rates were so low, it led to a CV of 52% for the harvest mortalities. Still, the population reconstruction work led to a 95% confidence interval for the harvest mortalities of 0-5%. Even with a high coefficient of variation, the model gave a small range for the harvest mortalities.

The harvest mortalities and abundances were correlated, especially the adult abundances which were derived in part from the harvest mortalities. The high CV associated with the harvest mortality may therefore be the cause behind the high CVs of the abundances. A graph of the CV of 2006 total abundance versus the number tagged in the radiotelemetry study confirms this conclusion (Figure 4.6).

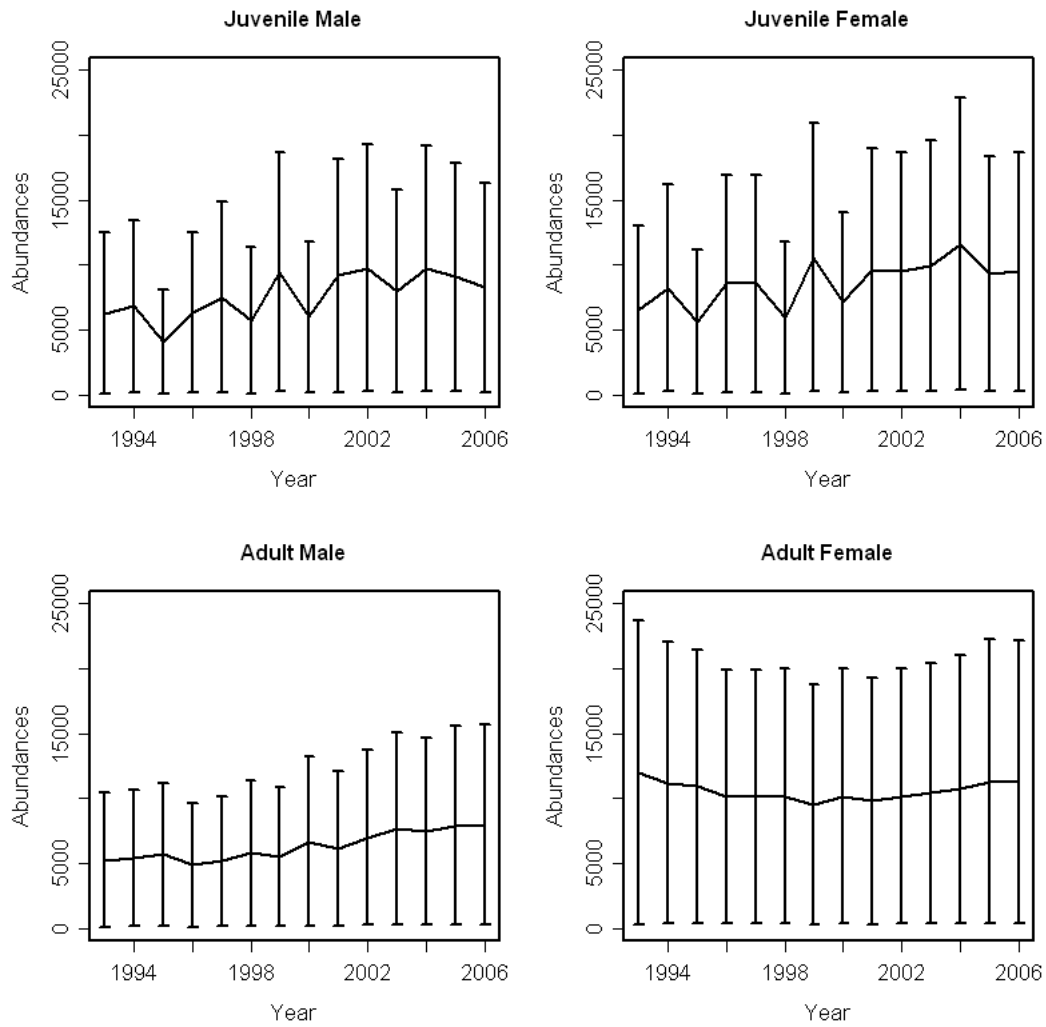


Figure 4.4: Statewide grouse sex and age-class population trends in Oregon, 1993-2006, estimated from the Radio1c4s model.

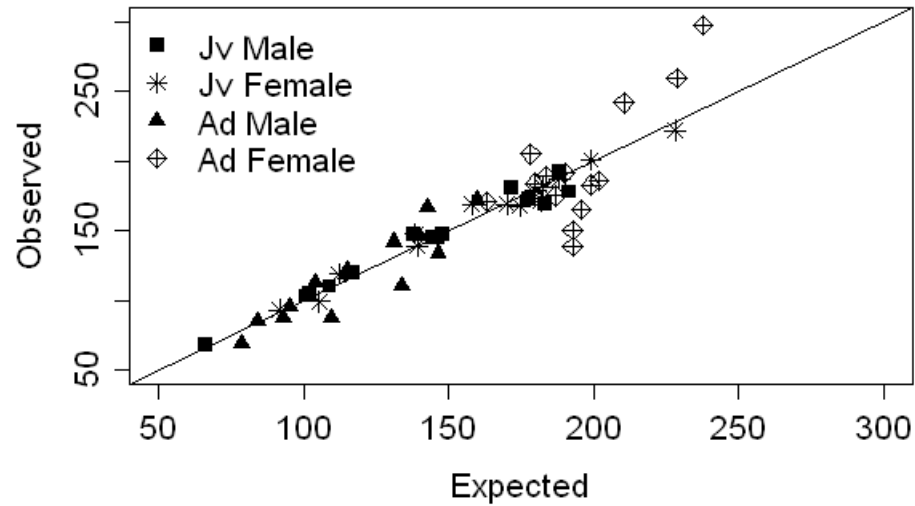


Figure 4.5: The observed and expected age-at-harvests were similar, with most of the deviation coming from the adult female harvests.

For the Oregon sage grouse, the model was rerun changing the number of grouse tagged but keeping the proportion of tagged and harvested grouse constant.

As the number tagged increased, the CV of total abundance decreased exponentially. The model that used the true number tagged had a CV of 49%. If twice as many birds had been tagged each year, this CV would have dropped to 28%. For this data set, the minimum CV of total abundance was 20%, approached when 400 birds were tagged.

4.5.1 Method-of-Moments Values

As with the mourning doves in Chapter 3, a method-of-moments model based on the telemetry results was built from the data. A contingency table showed no difference between years for the radiotelemetry study, so the 4 years of telemetry were pooled

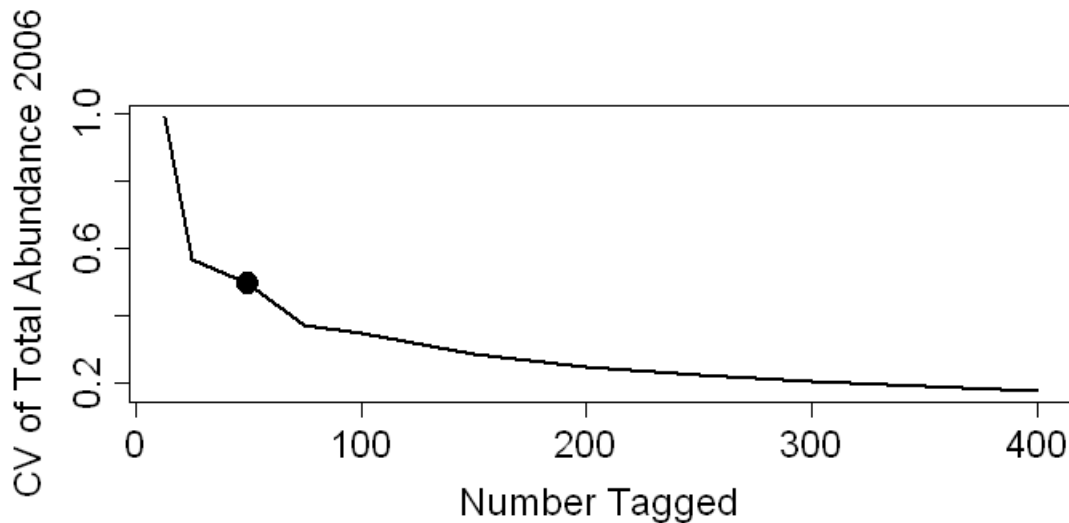


Figure 4.6: The CV of total abundance in 2006 versus hypothetical numbers of grouse tagged in the radiotelemetry study. In the real study, 50 birds were tagged in 1998 and the CV of total abundance was 49%.

to obtain the method-of-moments harvest rate:

$$\hat{H}_{determ} = \frac{\sum_{i=1998}^{2001} h_i^{(r)}}{\sum_{i=1998}^{2001} T_i^{(r)}} \quad (4.8)$$

The method-of-moments harvest mortality from the telemetry was 0.0328 (SE = 0.016). Using this estimate and assuming the harvest rate was constant across all years, gave method-of-moments abundance estimates when combined with the harvest information from the hunter surveys (Table 4.1), and Equation 1.17 from Chapter 3.

For the sage grouse, both the method-of-moments and population reconstruction models led to similar trends (Figure 4.6), with the reconstruction estimating larger abundances (Table 4.7). One noted difference is that the method-of-moments model concluded a population increase from 1993-94, from 16,714 to 29,768 grouse. A doubling of the population without cause is suggestive of an unrealistic model.

As mentioned in Chapter 3, the reconstruction was the preferred model because

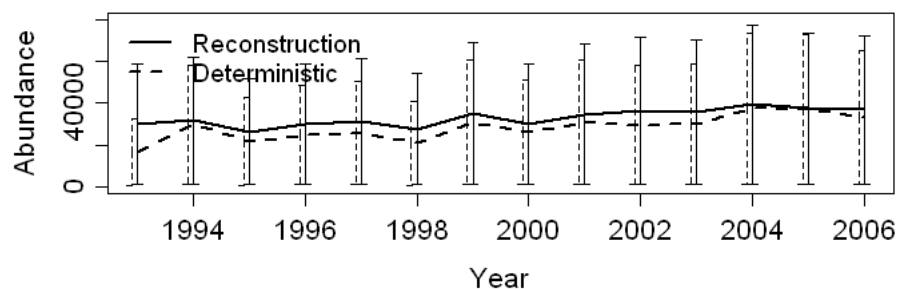


Figure 4.7: Grouse method-of-moments trends compared graphically to population reconstruction model estimates.

it took into account the inherent variability in the data and the relationship between juvenile and adult abundances in successive years. The reconstruction incorporated more information, making it more robust to anomalies in the data.

4.5.2 Lek Count Trends

The lek counts measured trends in breeding male populations which in turn measure trends in overall abundance. As mentioned earlier, the exact relationship between these variables was unknown. Fortunately, the reconstruction provided abundance estimates against which to compare the lek trends. Graphs of the trends supported the use of leks to measure abundance trend (Figures 4.8 and 4.9).

Making the common assumption that $E[I_i] = \alpha N_i$, straight linear regression through the origin yielded $\alpha = 0.000534$, and $\hat{\sigma} = 4.028$. The correlation associated with this relationship was low, ($r^2 = 0.429$) suggesting that a different relationship between the index and abundance may be more appropriate.

Because the lek surveys only count adult male sage grouse, a better relationship between the lek counts and abundance was to assume that the index represented a fraction of the adult male grouse population, $E[I_i] = \alpha N_{M,2,i}$. This equation led to

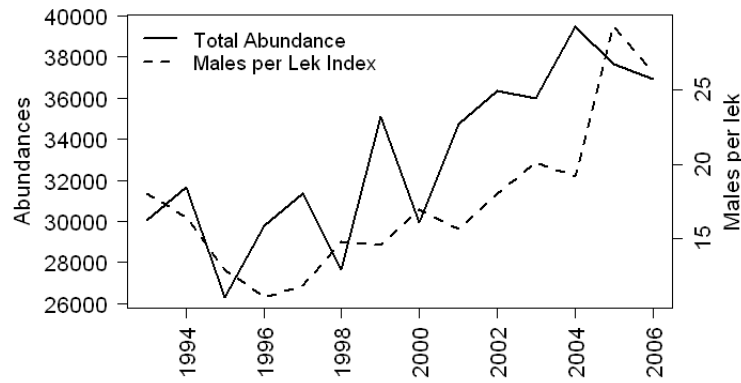


Figure 4.8: Comparison of males per lek and total abundance trends, 1993-2006, for state of Oregon. $r^2 = 0.429$.

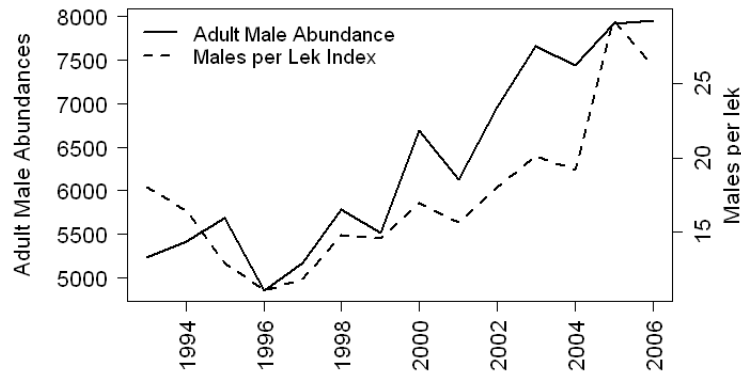


Figure 4.9: Comparison of males per lek and adult male abundance trends, 1993-2006, for the state of Oregon. $r^2 = 0.721$.

an estimate of $\alpha = 0.0028$ and $\hat{\sigma} = 2.972$, with a higher correlation ($r^2=0.721$).

It must be noted that the abundance estimates used in the regression were subject to measurement error because they were estimates, not the true abundance values. Generally, measurement error in the independent variable leads to an underestimated regression coefficient (Kutner et al. 2005). In the comparison of the reconstruction estimates of $\alpha = 0.00275$ and $\hat{\sigma} = 2.50$ (for the model with Radio+Index auxiliaries and 4 survivals), and the regression estimates, there did not appear to be a large difference for this case.

The correlation between the lek counts and the population reconstruction trends was encouraging. Because the true abundance is never known, the strong relationship between two independent measurements was an important check on both data sources.

4.5.3 Adult Male Lek Counts

A total number of males are counted each spring season during the lek surveys. If the model was working correctly, the total number of males seen each spring would be less than the reconstruction estimate because not all male can be counted, and not all leks are counted. Moreover, if a similar number of leks were assessed each year, the number of adult males seen should also roughly follow the population trend. A comparison of the males counted and the reconstruction estimate showed that this was indeed the case for all years besides 2006 (Figure 4.10), further supporting the reconstruction results.

4.5.4 Previous parameter estimates

Abundance Estimates. Different models based on lek-count data have led to previous spring population estimates of 27,505 in 1992 (Willis et al. 1993), a minimum estimate of 20,000 in 1998 (Braun 1998), and approximately 40,000 sage grouse in 2003 (Hagen 2005). The reconstruction estimates were for late summer, just prior to

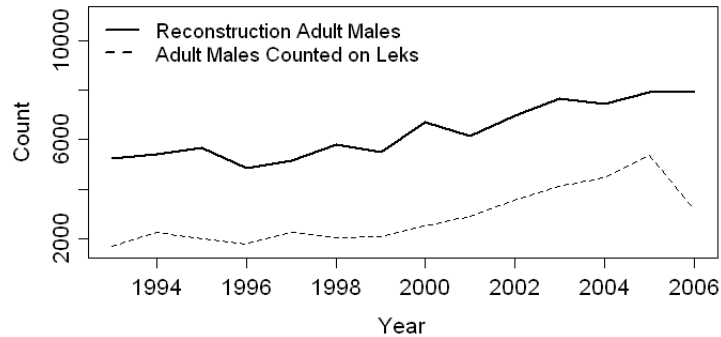


Figure 4.10: Comparison of adult males counted on all leks each spring and adult male abundances from reconstruction model, 1993-2006, for state of Oregon.

the hunting season, but the model estimates were still supported by these previous estimates. The reconstruction only goes back to 1993, but its estimate of 30,043 grouse for that year was in line with Willis' estimate for 1992. Braun provided a minimum population size of 20,000 for 1998, the reconstruction estimate of 27,634 was well above that estimate. In 2003, the reconstruction estimate was 35,980 grouse; while this number was lower than Hagen's estimate, it was inside the confidence interval of that estimate (34,393 to 45,268) (Hagen 2005).

Survival Rates. A wide range of survival estimates have been reported in the literature. The juvenile survival estimate varied from 0.10 (Crawford et al. 2004) from hatching until first breeding season to 0.88 (Battazzo 2007) during the winter months. Two studies (Battazzo 2007, Beck et al. 2006) reported very high winter survivals for juvenile sage grouse, 0.88 and 0.80. Other studies reported yearly juvenile survivals at 0.40, 0.33, 0.63 and 0.10 (Wallestad 1975, Johnson and Braun 1999, Zablan et al. 2003, Crawford et al. 2004). The reconstruction estimated juvenile male survival at 0.373 and juvenile female survival at 0.252. These estimates were within the range reported in the literature.

Adult male survival estimates have ranged from 0.37 to 0.59 (June 1963, Connelly et al. 1994, Zablan et al. 2003, Crawford et al. 2004). The population reconstruction estimated adult male survival at 0.609, slightly greater than the range found in the literature. Moynahan (2006) concluded that adult female survival could vary between 0.247 and 0.96, while most other studies pinned the rate as being slightly higher than the adult male survival. Past studies reported adult female survivals of 0.67, 0.35, 0.78, 0.73, 0.59, and 0.85 (June 1963, Wallestad 1975, Connelly et al. 1994, Johnson and Braun 1999, Zablan et al. 2003, Battazzo 2007). The population reconstruction estimated adult female survival at 0.818, which was in line with previous studies.

Hunter vulnerability. Few studies have estimated harvest mortalities of sage grouse. Connelly et al. (2000a) reported that harvest rates vary between 0-25%, with little difference between the sexes, for all of North America. In Oregon, Willis et al. (1993) concluded that the overall harvest rate there is $< 3\%$. In fact, the ODFW goal is a harvest of 5% of the population (Rowland and Wisdom 2002). The average harvest mortality from the reconstruction was 2.8%, matching the previous work.

4.5.5 Simulations

The simulations from Chapter 2 suggested that models with 1 vulnerability coefficient, many years of data and an auxiliary telemetry study obtain unbiased abundance estimates. Comparisons of the reconstruction results with the deterministic model (Section 4.5.1), the lek counts (Section 4.5.2), and various parameter estimates from the other literature (Section 4.5.4) all suggested that the reconstruction provided reasonable estimates for this population.

The simulations from Chapter 2 also suggested that it is difficult to estimate parameters for a population with very low harvest mortality and no telemetry data. Coinciding with the simulation results, grouse models that excluded the telemetry data led to unpredictable results, with abundance estimates at their upper boundary

and harvest rates at their lower boundary.

4.6 Management Implications

Like the mourning dove example, the sage grouse results reinforced the need of a telemetry study in order for the model to work. Without such a study, estimates were unobtainable. With a telemetry study, estimates were unbiased and fairly consistent across the models (Section 4.7).

With more birds tagged in the telemetry study or with more auxiliary information, the standard errors could be decreased to reasonable levels. Even with the high standard errors, the results shown here suggest the population reconstruction can be a powerful management tool for small game and a useful augmentation to the lek counts. The population reconstruction supported previous studies estimating abundances, survivals, and harvest mortalities; it reaffirmed the assumed index-abundance relationship; and provided statistically rigorous estimates.

Table 4.6: Grouse method-of-moments model estimates compared to population reconstruction model estimates.

Model	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
<i>Deterministic</i>														
$\hat{S}E$	16,714	29,768	21,838	24,644	25,590	20,770	30,958	26,138	30,958	29,676	29,860	37,454	37,271	33,214
<i>Reconstruction</i>														
$\hat{S}E$	8,256	14,675	10,776	12,156	12,620	10,251	15,260	12,890	15,260	14,630	14,720	18,455	18,365	16,370
$\hat{S}E$	30,043	31,688	26,286	29,816	31,362	27,634	35,084	29,954	34,751	36,370	35,980	39,492	37,626	36,908
$\hat{S}E$	14,896	15,596	12,963	14,730	15,492	13,635	17,305	14,758	17,151	17,943	17,733	19,422	18,506	18,203

4.7 Alternate Model Results

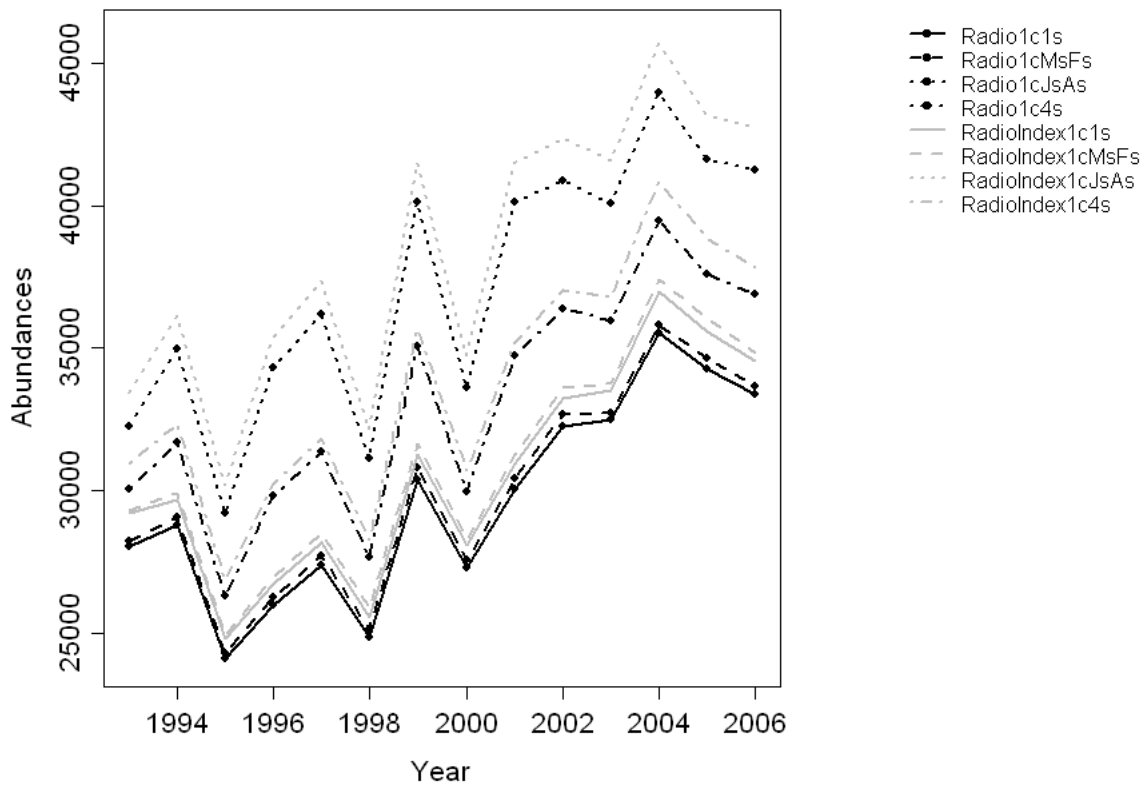


Figure 4.11: Reconstruction estimates of total yearly sage grouse abundance from each of the working models. Model Radio1c4s was chosen as the best-fitting.

Model: Radio1c1s		
Parameter	Est.	SE
S	0.534	0.010
c	0.037	0.019
\hat{h}	0.031	0.015
\hat{N}_{JM}	6,267	3,111
\hat{N}_{JF}	8,197	4,063
\hat{N}_{AM}	6,176	3,045
\hat{N}_{AF}	8,985	4,426
$\hat{N}_{..}$	29,625	14,563

Model: Radio1cMsFs		
Parameter	Est.	SE
S_M	0.481	0.012
S_F	0.569	0.011
c	0.037	0.018
\hat{h}	0.031	0.015
\hat{N}_{JM}	6,860	3,406
\hat{N}_{JF}	7,787	3,862
\hat{N}_{AM}	5,714	2,821
\hat{N}_{AF}	9,566	4,713
$\hat{N}_{..}$	29,927	14,714

Model: Radio1cJsAs		
Parameter	Est.	SE
S_J	0.143	0.028
S_A	0.901	0.029
c	0.030	0.015
\hat{h}	0.025	0.012
\hat{N}_{JM}	8,428	4,203
\hat{N}_{JF}	9,746	4,844
\hat{N}_{AM}	7,175	3,533
\hat{N}_{AF}	11,789	5,812
$\hat{N}_{..}$	37,138	18,288

Model: Radio1c4s		
Parameter	Est.	SE
S_{JM}	0.373	0.134
S_{JF}	0.252	0.063
S_{AM}	0.609	0.163
S_{AF}	0.818	0.052
c	0.033	0.017
\hat{h}	0.028	0.014
\hat{N}_{JM}	7,578	3,779
\hat{N}_{JF}	8,611	4,289
\hat{N}_{AM}	6,316	3,127
\hat{N}_{AF}	10,565	5,216
$\hat{N}_{..}$	33,071	16,310

Model: RadioIndex1c1s		
Parameter	Est.	SE
S	0.532	0.010
c	0.036	0.018
\hat{h}	0.030	0.015
\hat{N}_{JM}	6,459	3,208
\hat{N}_{JF}	8,476	4,205
\hat{N}_{AM}	6,387	3,152
\hat{N}_{AF}	9,269	4,569
$\hat{N}_{..}$	30,592	15,050
α	0.00276	0.00136
σ	2.72	0.581

Model: RadioIndex1cMsFs		
Parameter	Est.	SE
S_M	0.479	0.012
S_F	0.569	0.012
c	0.036	0.018
\hat{h}	0.030	0.015
\hat{N}_{JM}	7,077	3,515
\hat{N}_{JF}	8,037	3,988
\hat{N}_{AM}	5,895	2,911
\hat{N}_{AF}	9,875	4,868
$\hat{N}_{..}$	30,883	15,194
α	0.00301	0.00148
σ	2.53	0.548

Model: RadioIndex1cJsAs		
Parameter	Est.	SE
S_J	0.148	0.028
S_A	0.895	0.029
c	0.029	0.014
\hat{h}	0.024	0.012
\hat{N}_{JM}	8,707	4,347
\hat{N}_{JF}	10,096	5,022
\hat{N}_{AM}	7,435	3,664
\hat{N}_{AF}	12,192	6,017
$\hat{N}_{..}$	38,430	18,944
α	0.00237	0.00117
σ	3.08	0.593

Model: RadioIndex1c4s		
Parameter	Est.	SE
S_{JM}	0.449	0.113
S_{JF}	0.241	0.062
S_{AM}	0.515	0.137
S_{AF}	0.826	0.052
c	0.033	0.016
\hat{h}	0.027	0.013
\hat{N}_{JM}	7,746	3,860
\hat{N}_{JF}	8,809	4,389
\hat{N}_{AM}	6,456	3,198
\hat{N}_{AF}	10,807	5,336
$\hat{N}_{..}$	33,819	16,683
α	0.00275	0.00136
σ	2.50	0.556

Chapter 5

CONCLUSION

The results presented in this thesis demonstrated that reliable estimates of the natural survivals, harvest mortalities, and abundances were obtainable with the small game population reconstruction model but depended on the qualities of the inputted data. As mentioned at the end of Chapter 2, harvest mortalities should be 20-50%, hunter effort should be variable, and at least 5 years of collected data must be used, with more years being preferable. More accurate and precise estimates consistently came from models where age-classes shared a common vulnerability coefficient. Including radiotelemetry data significantly improved the accuracy and reliability of all parameter estimates while including population index data did not.

Concerning the inclusion of auxiliary information, the results from the simulations and examples were conclusive and substantive. The addition of a radiotelemetry study aided in the reliability of all parameter estimates, and combined with high harvest mortalities led to very low measurement errors. Model parameters were highly correlated, especially between the vulnerability coefficients and the juvenile abundances. This high correlation made it important to provide an estimate of the vulnerability coefficient(s) through an independent tagging study. It also meant that the telemetry data had a significant effect on the model estimates.

The addition of population index data did not improve model results. The purpose of the auxiliary index data was to add abundance trend information into the model; it did not directly help estimate any of the model parameters. I believe this trend information, however, was already being incorporated in the model through the yearly catch-effort data.

The results of the simulation studies were supported by both the mourning dove and sage grouse examples. The doves had a very high harvest mortality, sometimes > 50%, and only 5 years of data. As predicted from the simulations, the data required the addition of radiotelemetry data to produce estimates. The sage grouse population had a low harvest mortality, around 5%, and therefore also required the radiotelemetry data to produce stable parameter estimates. Including or excluding the lek count information in the sage grouse population reconstruction did not have a large effect on the abundance estimates.

Some models that excluded the telemetry data were able to estimate abundances but did not provide good estimates of the survival rates or harvest mortalities. Models with 1 common vulnerability coefficient achieved accurate abundance estimates with high harvest mortalities (30%-50%). Models with 2 vulnerability coefficients required 10 years of data, high harvest mortalities (30%-50%), and high variation in hunter effort to achieve accurate abundance estimates. All of these models had positively biased survivals and vulnerability coefficients and high standard errors associated with these estimates, but the abundances and their standard error estimates were accurate. These results demonstrated that robust abundances could be estimated even though the survival or vulnerability coefficients were known to be unreliable. One such situation were the mourning doves in Missouri. The model was unable to estimate adult survival, but the above simulation results suggest the abundance estimates were accurate.

The question of how to select the best-fitting model is unanswered. The natural choice, AIC_c , is problematic for joint likelihoods because of the complication in determining sample size. Including an auxiliary study increases the number of observations, but, not all sample observations are created equal, and simply summing counts over likelihood components does not properly represent sample size. In the examples for this thesis, AIC, χ^2 goodness-of-fit values, and likelihood ratio tests (LRTs) were calculated. For the sage grouse, all three values agreed, and one model

was selected as best-fitting. For the mourning doves, the AIC and LRT also picked the same model, but did not agree with the χ^2 goodness-of-fit results. This anomaly, that the AIC and χ^2 goodness-of-fit values do not agree has been noted before and is not uncommon (Burnham and Anderson 2002). There is no single best approach for the model selection for a joint likelihood model such as population reconstruction.

The simulations provided some ideas on which models resulted in the most accurate and precise estimates. The sensitivity analysis simulations concluded that if the data came from a population with separate juvenile and adult vulnerability coefficients and survivals, then separate juvenile and adult vulnerability coefficients and survivals should be included in the model for the best abundance estimates. Models that assumed only 1 vulnerability coefficient, but came from a population with 2 vulnerability coefficients had abundances underestimated by 10% or more. On the other hand, the first set of simulations concluded that if data came from a population with one common vulnerability coefficient, it provided better estimates overall than a similar population with 2 vulnerability coefficients (Table 2.11).

The best way to pick a model may be to determine *a priori* how many parameters (1 versus 2 vulnerability coefficients, 1 versus 2 survivals) should be included in the model using biological knowledge to guide model development, and then test the robustness of the estimates to model misspecification.

Even with the identified problems, small game population reconstruction models are a better tool than the current demographic alternatives, which are relying solely on index data or using the method-of-moments technique. The method-of-moments technique is tempting in its simplicity but I believe its weaknesses, described in Chapter 3, are greater than the statistical population reconstruction that I presented. The faults of index data have been enumerated many times in the literature (Skalski et al. 2005).

The population reconstruction model provides information on both population status and trends. The reconstruction model results should be compared to the index

data when available, which provides an independent check on the model's credibility. In many cases, such as sage grouse, the index data can confirm the trends predicted by population reconstruction.

5.1 Management Implications

One of the strongest conclusions from the simulations is that radiotelemetry data improves all parameter estimates and should be used if at all available. If telemetry data are not available, the population reconstruction model should only be used on species with a harvest mortality of 20-50% and with at least 10 years of data. Index data should be used as an independent confirmation rather than as part of the population reconstruction model.

Three conclusions can be derived from this thesis. The first result was that a minimum of 5 years of age-at-harvest data was needed to calculate all of the parameters. Second, more variability in hunter effort led to better accuracy and precision for the estimates. Thirdly, trends in recruitment did not affect the precision or accuracy of the abundance estimates. In other words, population reconstruction is robust to the trends in the population.

The mourning doves and sage grouse population reconstructions both followed the patterns predicted by the simulations.

Species that shared a common harvest vulnerability or a common natural survival yielded better results. However, if the juveniles and adults were previously known to have different vulnerabilities to harvest and/or different survival rates, then multiple vulnerability coefficients and multiple survival rates should be included in the model. If the number of vulnerability coefficients and survivals are not known *a priori*, the best-fitting model should be selected by a combination of biological insight, AIC and goodness-of-fit.

The population reconstruction model, for many simulation scenarios, estimated the survival and vulnerability coefficients inaccurately or was unable to estimate all

of the parameters. The survival parameters tended to be estimated least accurately. This unreliability of the survival estimates has also been noted in the statistical catch-at-age models used in fisheries (Hilborn and Walters 1992). Still, these models produced accurate abundance estimates. Abundances estimates were also reasonably robust to model misspecification. Therefore, abundance estimates may be valid even if the predicted survival or harvest mortalities are known to be flawed. For situations where survival parameters are inestimable, literature values could be used in place of the MLE's to evaluate the robustness of the abundance estimates.

Finally, demographic parameters estimated from population reconstruction should be compared to values reported in the literature and predicted trends compared to the population indices. This “ground truthing” is an important component to the model evaluation, and should be used whenever possible.

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