Management Application of Statistical Population Reconstruction to Wild Game
Populations

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Abstract

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Historically, management agencies in the United States have monitored most

game populations through an ad hoc approach which combines indices, harvest data,

hunter surveyed data, and occasional demographic evaluation. However, changing

management priorities and increased scrutiny require more informative and defensible

means of monitoring harvested populations. Statistical population reconstruction (SPR) is

a flexible modeling system which simultaneously analyzes age-at-harvest data, hunter

effort data and any additional demographic data which are available, producing estimates

of abundance, natural survival and harvest rate, as well as their associated variances. An

SPR based monitoring framework provides comprehensive analysis of commonly

collected data and represents a statistically rigorous and defensible alternative to the currently popular approaches. However, applications of SPR have previously been limited to small scale, highly monitored populations, primarily due to a lack of formal evaluation of data requirements and guidance for management application. In this dissertation I provide the guidance necessary for broad scale application of SPR modeling to monitor harvested species. I rigorously evaluate the relative utility of auxiliary data sources as well as minimum harvest and hunter effort data requirements for SPR models, providing necessary guidance for resource managers seeking to apply SPR. I present a historic population reconstruction based on SPR parameter estimates as an illustrative example of the management application potential of SPR output. I comprehensively evaluate models to project reconstructed abundance into the future in order to further increase the management utility of statistical population reconstruction. I provide a detailed explanation of model structure and assumptions, allowing resource managers to critically evaluate SPR models. Finally, I offer guidance on the customization of SPR models necessary to adequately model the harvest regimes and data collection methodologies which are unique to each harvested population, thus increasing the number of populations which can be modeled. This dissertation will facilitate the broad scale management application of SPR, thus increasing the rigor and efficiency with which harvested game populations are monitored.

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Chapter 1. INTRODUCTION

When modern wildlife management began in the United States, the goal was to recover depleted populations and end overexploitation (Schmidt 1980). In most areas, for most game species, this effort has been a resounding success. Contemporary management now focuses on maintaining game populations at consistent harvestable levels that do not cause undue conflict with humans (Strickland et al. 1994). In order to successfully manage harvested populations, managers must monitor status and trends of the resource. Censusing wildlife populations is financially and logistically intractable in almost all game management situations, so managers must choose cost-effective, defensible monitoring solutions that are logistically feasible.

Today wildlife managers face an increasingly difficult task. Wildlife budgets across the country are shrinking as states deal with economic problems (Lueck 2000). The wild land base is shrinking, allowing less core habitat and increasing human animal conflict. Managers are under increased scrutiny from an ever widening group of stake holders (Jacobson and Decker 2006). Where once it was only hunters and land owners, managers now find their stakeholder groups to also include non-consumptive users, anti-hunting activists, non-governmental organizations (NGO's) and the general public (Jacobson and Decker 2006). Due to the increased pressures and reduced resources, managers need a reliable, rigorous, and efficient monitoring tool to help them steward our wildlife resources into perpetuity.

The least expensive and most widely used method of monitoring is through annual assessment of trends in indices. Indices are easily and inexpensively measured population metrics whose value is assumed to be proportional to the abundance or rate of change of the

population. Common indices include scat or pellet density (Don 1968), catch-per-unit effort (CPUE) (Hatter 2001), visual counts and encounters (Skalski et al. 2005 p. 385, Kishimoto et al. 2010), car-animal collisions (Hewitt 2011), and demographic structure of the harvest (Caughley 1974). Unfortunately, the relationship between the observed index value and the state of the population is generally unknown and often unexamined, which can result in misinformed management (Seber 1982, Anderson 2001;2003). The use of indices can be especially troublesome if the functional relationship between the index and population abundance changes based on the abundance of the population (Anderson 2001;2003). Despite well documented concerns, most harvested species are monitored primarily through indices (Rupp et al. 2000, Mason et al. 2006, Sands and Pope 2010, Collier et al. 2013). Managers often augment trend information from indices with occasional localized intensive monitoring efforts (Vangilder and Kurzejeski 1995, Rönnegård et al. 2008).

Direct monitoring efforts are typically of short duration, limited geographic area, and generally targeted at estimating a single demographic parameter of concern, thus limiting their inferential capabilities outside of the study site and time. Intensive monitoring efforts often include marking animals, either for mark-recapture (Robson and Regier 1964) or radio-telemetry (Millspaugh and Marzluff 2001) studies. Mark-recapture and radio-telemetry are widely used, have been applied over long periods, and are logistically feasible ways to estimate vital rates of the population (Seber 1982). Larger species can be monitored through GPS collars, which provide detailed spatial information that can be used to answer a wide range of ecological questions (Waller and Servheen 2005, Rauset et al. 2012). Genetic sampling is increasing in popularity, especially in the study of elusive species (DeYoung and Honeycutt 2005). Genetic

sampling requires genetic material to be collected from the population, usually through hair snare or fecal samples (Waits and Paetkau 2005). Genetic samples from the population are then analyzed to determine the number of individuals in the sampled area as well as other detailed demographic information (DeYoung and Honeycutt 2005, Waits and Paetkau 2005). The scale necessary for population wide monitoring, in terms of statistically rigorous sample collection and analysis can be logistically difficult and expensive to achieve, with genetic sampling. Additionally, genetic identification of individuals is prone to error and traditionally, genetic samples are not randomly distributed, making inference to the population as a whole difficult (Anderson 2001, Waits and Paetkau 2005).

In some cases population-wide surveys are conducted to estimate overall abundance. Population surveys across large geographic scales are expensive, time consuming and often dangerous, usually involving helicopters and planes to fly transects (Unsworth et al. 1990, Anderson et al. 1998, Jones et al. 2006). In order to make such surveys logistically and financially feasible, they are often conducted infrequently (once a decade) or at small spatial scales, limited to areas of greatest concern (Rabe et al. 2002, Whittaker et al. 2003). Often these studies save money by not estimating sightability correction factors (the probability of seeing animals at varying distances), essentially turning the study into a minimum animal count; a very expensive uncalibrated index to abundance (Whittaker et al. 2003). Finally, the infrequent surveys make accurate trend information difficult to obtain.

Monitoring tools based on harvest data are popular, because they provide a low cost annual source of information (Rupp et al. 2000, Skalski et al. 2005, Sands and Pope 2010). Most management agencies collect some form of age-at-harvest and hunter effort information

(Strickland et al. 1994). Historically, these data have been used in simple accounting methods or as indices, or in some cases in slightly more advanced demographic analysis (Skalski et al. 2005). One such model is the sex-age-kill (SAK) model, which estimates male abundance based on harvest information and conditional probabilities of mortality (Millspaugh et al. 2009). Unfortunately, the SAK model is data intensive, leading managers to make assumptions concerning stable and stationary populations to relax the data requirements. Violations of the SAK model assumptions can result in very poor model performance (Millspaugh et al. 2009). The Downing model is a special case of the Fry model, which estimates only minimum abundance, and is subject to the assumption of constant harvest and survival rates (Fry 1949, Downing 1980, Davis et al. 2007). Alternatively, managers will populate population dynamics models with parameter estimates from the literature to guide their management decisions (Connelly et al. 2005). Using demographic parameters from other populations has obvious drawbacks. Directly estimating demographic parameters from the population to be managed is preferable (Skalski et al. 2005). Over the last decade, statistical population reconstruction (SPR) has emerged as a viable option for managers to use age-at-harvest data to monitor populations over broad spatial and temporal scales (Broms et al. 2010, Gast et al. 2013a, Gast et al. 2013k).

SPR analysis uses age-at-harvest data, hunter effort data, and other available auxiliary information to simultaneously estimate age-specific abundance, natural survival and harvest probabilities. SPR has several advantages over more traditional monitoring methods. Simultaneously analyzing multiple sources of data increases the precision with which individual parameters are estimated (Schaub and Abadi 2011). Estimates of age-specific abundance allows managers to identify which population segments are driving trends (e.g., recruitment, adult

survival, a low abundance cohort etc). Abundance estimates also allow harvest goals to be set based on harvest rate and the potential impact of changes to harvest regulations to be modeled. SPR does not require the annual input of demographic parameters, estimated from intensive field studies, like population dynamics models and the SAK model (Millspaugh et al. 2009, Broms et al. 2010, Gast et al. 2013a). Instead SPR uses data that are already commonly collected. SPR provides annual estimates of abundance and recruitment as well as their associated standard errors; an aspect generally lacking in many of the deterministic or *ad hoc* methods detailed above (Seber 1982, Skalski et al. 2005). Variance estimates of parameters allow practitioners to objectively assess the quality of the information upon which they base management decisions. This information can then be used to guide future monitoring efforts to improve the precision of parameters of greatest management concern. Additionally, SPR models can be augmented to accommodate complex harvest regimes, account for interannual variability in demographic parameters and incorporate a wide range of auxiliary information. Making SPR suitable to model a wide range of harvested populations.

SPR models typically consist of at least three likelihood components; the age-at-harvest likelihood, aging likelihood, and auxiliary likelihood. The age-at-harvest likelihood is a multinomial likelihood which models the cohort structure of the population; relating observed harvest numbers to survival and harvest probabilities. The auxiliary likelihood uses data independent of age-at-harvest data to estimate at least one of the demographic parameters from the age-at-harvest likelihood. The aging likelihood accounts for incomplete aging or reporting of harvest. Other data sources and likelihoods can be included based on data availability, season structure or other considerations. Gove et al. (2002) first used age-at-harvest data in conjunction

with hunter effort data in a joint-likelihood framework. Since then the method has been applied, tested and refined. Skalski et al. (2007) tested indices for use as auxiliary information in SPR. Conn et al. (2008) used SPR in a Bayesian context to model black bears (*Ursus americana*) in Pennsylvania. Fieberg et al. (2010) used SPR with a chi-square objective function, instead of the standard maximum likelihood approach, to model black bears in Minnesota. Broms et al. (2010) used SPR to model greater sage-grouse (*Centrocercus urophasianus*) with radio-telemetry auxiliary information. Skalski et al. (2011) applied SPR to a furbearer population in Michigan. Skalski et al. (2012b) used SPR with limited age class information (0, 1, 2+). Most recently Gast (2012) made significant improvements to the general SPR model structure by, estimating abundance with a Horvitz-Thompson type estimator, removing the catch-effort likelihood traditionally included in SPR models and adding random effect parameters to demographic processes. These improvements by Gast (2012) reduce bias, provide more accurate variance estimates, increase reliability and account for natural variability in demographic processes.

Despite the advantages of using SPR, there are also some drawbacks to the method. The largest initial hurdle to SPR is the mathematical complexity of the approach, which can be difficult to communicate to stakeholders and consequently may reduce buy in or confidence in the resulting estimates. Another major hurdle to implementation is that there is a steep learning curve associated with the statistical theory and software necessary to analyze SPR data (i.e., Automatic Differentiation Model Builder (ADMB)). Generally, auxiliary data are required, making SPR more costly than uncalibrated indices alone; however, SPR provides substantially more information. Finally, SPR requires several consecutive years of representative age-at-harvest data. If management agencies are not currently collecting the correct data, it may be

several years before they can successfully implement SPR. With proper planning, collaboration, and execution, the majority of challenges associated with SPR can be overcome to produce an efficient adaptive management tool.

Despite being an efficient, flexible, and powerful tool for monitoring harvested species, SPR has not been widely applied in management contexts. One of the principal reasons for the lack of adoption of new statistical methods is the lack of an instructional bridge to cross the chasm between model development and management application. Too often models are developed and posited for use with no guide for application, leaving practitioners to sink or swim on their own. Model development is only half of the battle, confronting models with the actual data from resource agencies presents a unique set of challenges (Hilborn and Mangel 1997). The application of complex models can require detailed knowledge of model structure and assumptions, which many mangers lack. This provides an obvious need for a thorough, practical, guide for managers, in order to apply advanced statistical models to a wide range of scenarios. The majority of the previous work done concerning SPR has focused on the construction, selection, and evaluation of SPR models. This dissertation is meant to provide the necessary tools and guidance for managers to apply statistical population reconstruction to monitor harvested populations. It will answer the most pressing questions about data needs, model modifications and application of output for SPR models and provide guidance through illustrative examples. The broad scale management application of SPR models, facilitated by this dissertation, has the potential to increase the efficiency and rigor with which harvested wildlife are monitored.

Chapter 2, which has been previously published, will assess the utility of abundance auxiliary data relative to radio-telemetry harvest probability auxiliary data SPR (Clawson et al. 2013). Chapter 3, which has also been previously published, will illustrate the use of SPR analysis to historically reconstruct 50 years of wild turkey population dynamics and hunter response to this reintroduced small game species of Missouri (Clawson et al. 2015). Chapter 4 will evaluate methods to project next year game abundance based on simple demographic models and output from statistical population reconstruction. Finally, chapter 5 will provide detailed guidance on data requirements, sampling considerations, spatial scaling, model modifications and multi sex modeling. Chapter 5 will also offer further assessments of potential SPR auxiliary and methods for the inclusion of covariate data into SPR modeling frameworks. Together, these five chapters will provide a blueprint for managers wishing to apply statistical population reconstruction to monitor harvested species.

Chapter 2. THE UTILITY OF AUXILIARY DATA IN STATISTICAL POPULATION RECONSTRUCTION

In recent years, statistical population reconstruction (SPR) has emerged as a feasible method for estimating the demographics of harvested wildlife over large geographic areas using age-at-harvest data which are commonly collected by wildlife agencies (Gove et al. 2002, Skalski et al. 2007, Skalski et al. 2011, Broms et al. 2010). Its origin can be found in the vast history of quantitative stock assessment in fisheries (Quinn & Deriso 1999). In wildlife science, where methods such as the Downing (1980) method and sex-age-kill (Millspaugh et al. 2009) are still the norm, there are advantages in using SPR which offers flexibility and robustness not available in traditional techniques. Further, SPR allows for the simultaneous estimation of survival, abundance, recruitment, and harvest mortality whereas traditional reconstruction techniques estimate only total abundance.

Age-at-harvest data provide the primary source of information in SPR models; however age-at-harvest data alone are insufficient to reconstruct population demographics using SPR. In addition to age-at-harvest data, one or more sets of auxiliary data are needed to estimate one or more of the parameters from the age-at-harvest likelihood, either survival rates, harvest rates, recruitment, or abundance. The joint likelihood structure of SPR models is flexible enough to incorporate almost any form of auxiliary data. In the past, it has been common to include catch-effort data as auxiliary information for SPR models. Skalski et al. (2007) calibrated a black-tailed deer (*Odocoileus hemionus*) SPR model using catch-effort data. That was possible because hunter effort was deliberately manipulated to produce a strong contrast in harvest rates

with alternative levels of effort. Similarly, Skalski et al. (2011) used a five-fold change in trapping effort over time to construct a catch-effort relationship and reconstruct the abundance of American martens (*Martes americana*) in the upper peninsula of Michigan. In other populations where hunter or trap effort may be relatively constant over time, catch-effort data will likely be an insufficient form of auxiliary information. Thus, although catch-effort data has been a staple in SPR analyses, other types of auxiliary data may be more useful.

Several other types of auxiliary data have been used in previous SPR analyses including radiotelemetry information on harvest rates and independent estimates of abundance. Broms et al. (2010) used radiotelemetry to help reconstruct greater sage-grouse (*Centrocercus urophasianus*) abundance in Oregon. Radiotelemetry data were used to estimate vulnerability coefficients associated with harvest mortality of greater sage-grouse in Oregon. Fieberg et al. (2010) also used radiotelemetry to estimate harvest rates and reconstruct the abundance of a Minnesota black bear (*Ursus americanus*) population. Other researchers have used independent estimates of total abundance as auxiliary data. For example, Gast et al. (2013a) used independent mark-recapture estimates of total abundance to help calibrate an SPR model of elk (*Cervus elaphus*) in the upper peninsula of Michigan. Alternatively, Fieberg et al. (2010) chose not to use independent DNA mark-recapture estimates of abundance when reconstructing the Michigan black bear population. Instead, they elected to use that information as an independent source of confirmatory information. In contrast, Skalski et al. (2007) found an independent browse damage index of deer abundance had little or no benefit in reconstructing a black-tailed deer herd. Such index data can help characterize the trend of a population but not its absolute abundance. These examples illustrate the flexibility of SPR, but also raise questions about the

potential utility of various types and quality of auxiliary data. Uncertainty remains as to the effect of auxiliary data on model stability and how much auxiliary data are needed. Also, it is unclear how the precision of the auxiliary data (i.e., CV) changes the precision of the reconstructed abundance estimates. Additionally it is unclear if the timing of auxiliary studies changes their effectiveness.

The purpose of this paper is to provide game managers with guidance on how best to incorporate auxiliary studies in SPR. We evaluate whether precision of the auxiliary study is the sole consideration, or whether the types of parameters being estimated is also important. To this end, we compare the performance of SPR where independent estimates of abundance or harvest mortality are available. We also consider the timing of the auxiliary studies in relationship to the duration of an SPR and the relative benefit of more than one auxiliary study in the precision of SPR.

2.1 METHODS

2.1.1 Overview of statistical population reconstruction

Statistical population reconstruction is based on age-at-harvest data collected over time by game management agencies. The observed counts $h_{ij} \left(i = 1, \ldots, Y; j = 0, \ldots, A \right)$ are modeled as a function of the initial abundance of a cohort and the subsequent natural survival and harvest over time and perhaps probabilities of reporting and age determination. Skalski et al. (2007) modeled the diagonals of this age-at-harvest matrix as independent multinomial distributions (L_{ij}) where the joint likelihood can be written as

$$L_{\text{Age-at-harvest}} = \prod_{j=0}^{A} L_{1j} \cdot \prod_{i=1}^{Y} L_{i0} \, .$$

This likelihood is often accompanied by a likelihood model describing the annual probabilities of harvested animals being report and/or aged, i.e.,

$$L_{\text{Reporting}} = \prod_{i=1}^{Y} L_i$$

and where L_i are binomial sampling models for the fractions of animals harvest in year i being reported and/or aged. This likelihood can be omitted if there is 100% reporting and aging of all harvested animals.

Together, these two likelihoods are incapable of estimating the demographic parameters of annual abundance, recruitment, natural survival, and harvest mortality of interest. Gove et al. (2002) proved that at least one demographic parameter must be estimated independent of the age-at-harvest data for statistical population reconstruction to be possible. Sometimes there may be, say, k independent auxiliary studies contributing to the reconstruction; hence, the joint likelihood model may be written as

$$L = L_{\text{Age-at-harvest}} \cdot L_{\text{Reporting}} \cdot \prod_{i=1}^{k} L_{\text{Auxiliary}_i} \, . \tag{1}$$

Skalski et al. (2007) suggested using a catch-effort likelihood as an auxiliary where the annual harvest numbers are modeled as binomial random variables as a function of the unknown total abundance in year i (i.e., N_i) and hunter effort (f_i) where

$$L_{\text{Catch-effort}} = \prod_{i=1}^{Y} \binom{N_i}{\sum_{j=0}^{A} h_{ij}} p(f_i)^{\sum_{j=0}^{A} h_{ij}} \left(1 - p(f_i)\right)^{N_i - \sum_{j=0}^{A} h_{ij}} \tag{2}$$

and where $p(f)$ is the probability of harvest modeled as a function of effort. A common parameterization for the probability of harvest is

$$p_i = 1 - e^{-cf_i}$$

where c is the vulnerability coefficient (Quinn & Deriso 1999:40, Seber 1982:296). Unless hunter effort has varied dramatically over time, this catch-effort auxiliary may not be adequate to support statistical population reconstruction.

2.1.2 Auxiliary likelihoods

We considered two alternative forms of auxiliary likelihoods in our evaluation. In one case, an unbiased annual abundance estimate $(\hat{N}_i)$ was assumed to be available with estimated standard error $\hat{\sigma}_i$. The auxiliary likelihood then assumed the estimate was asymptotically normally distributed with the likelihood

$$L_{\text{Aux}} = \frac{1}{\sqrt{2\pi}\sigma_i} e^{-\frac{1}{2}\frac{(N_i - \hat{N}_i)^2}{\sigma_i^2}}. \tag{3}$$

We took this approach to allow the auxiliary likelihood to be independent of the form of the abundance survey and simply reflect survey precision (i.e., CV $= \sigma_i/N_i$). The second auxiliary approach was based on a hypothetical radio-telemetry study to estimate harvest mortality during the hunting season. A binomial of the form

$$L_{\text{Aux}} = \binom{T_i}{d_i} (1 - e^{-cf_i})^{d_i} (e^{-cf_i})^{T_i - d_i}, \tag{4}$$

where T_i = number of animals tagged and at risk of harvest, and d_i = number of tagged animals harvested, and where harvest mortality was reparameterized in terms of a vulnerability coefficient (c) and annual year-specific hunter effort [Equation (1)]. Precision in the case of the radio-telemetry study was expressed in terms of

$$CV = \sqrt{\frac{p_i(1-p_i)}{T_i}} \Bigg/ p_i \quad .$$

2.1.3 Monte Carlo simulations

A Monte Carlo simulation study was used to determine the precision of population reconstruction estimates based on the amount, type, and timing of auxiliary studies. A stochastic Leslie matrix model was used to generate age-at-harvest data for populations with different levels of natural survival rates, and harvest rates. Recruitment levels were adjusted to produce populations with stationary abundance of approximately 6000 animals in expectation. Recruitment was generated using a Poisson process, and natural survival and harvest were modeled as binomial processes.

In each simulation, 20 years of data were generated to establish demographic trends with years 21–44 used in the population reconstruction analysis. The full age-class data were generated and used in standard population reconstruction models. The same data were also reanalyzed after pooling the adult age-at-harvest data (i.e., 2.5+ year olds) using the pooled adult reconstruction of Skalski et al. (2012).

Demographic scenarios were performed to represent a range of scenarios expected for harvested large mammal populations. Natural survival probabilities were simulated at 0.75 or

0.90 and harvest rates at 0.10 or 0.25. To minimize the number of scenarios investigated, survival and harvest rates were assumed constant across all age classes. Auxiliary data were simulated to estimate either annual abundance $\left(\hat{N}_i \right)$ or a harvest probability $\left(\hat{P}_i \right)$ with coefficients of variation (CV) equal to 0.05, 0.125, 0.25, or 0.50. The CVs of 0.05, 0.125, and 0.25 correspond to precision levels described by Robson and Regier (1964) as appropriate for accurate research, accurate management, and rough management. A fourth CV, of 0.50, was simulated to represent a minimum information scenario. At this level of precision, a parameter is estimated within ±100% of the true value, 95% of the time. The effect of timing of the auxiliary data was tested for each parameter combination by staging the auxiliary study at either the beginning, middle, near end (i.e., year 23 of the reconstruction), or end (i.e., year 24) of the reconstruction.

Average measurement error of the reconstructed abundance estimates was estimated from the variance component expression

$$E\left(s^2_{\hat{N}_{\bullet j}} - s^2_{N_{\bullet j}} \right) = \left(\sigma^2_{N_{ij}} + \overline{\mathrm{Var}\left(\hat{N}_{ij} \middle| N_{ij} \right)} \right) - \sigma^2_{N_{ij}} = \overline{\mathrm{Var}\left(\hat{N}_{ij} \middle| N_{ij} \right)},$$

where $s^2_{\hat{N}_{\bullet j}} = \dfrac{\sum\limits_{i=1}^{10,000} \left(\hat{N}_{ij} - \bar{\hat{N}}_{ij} \right)^2}{(10,000-1)}$ is the empirical variance among the abundance estimates in the jth

year of reconstruction and $s^2_{N_{\bullet j}} = \dfrac{\sum\limits_{i=1}^{10,000} \left(N_{ij} - \bar{N}_{ij} \right)^2}{(10,000-1)}$ is the empirical variance among the true

abundance values in the jth year of the reconstruction. A total of 10,000 simulations per scenario were used to obtain precise estimates of $s^2_{\hat{N}_{\bullet j}}$ and $s^2_{N_{\bullet j}}$. This approach provides a model-

independent estimate of measurement error. Across the 24 years of reconstruction, reported precision was calculated in terms of median CV of measurement error.

2.1.4 **Black-tailed deer sensitivity analysis**

The previous Monte Carlo simulation studies looked at the relationship between the precision of abundance estimates from population reconstruction and the use of auxiliary data. This section examines the effect of auxiliary data on the stability of reconstructed population trends for one particular realized dataset. The black-tailed deer reconstruction of Skalski et al. (2007) was selected for illustration because no auxiliary likelihood was incorporated in the original population reconstruction. Over a 24-year period, the abundance ranged between 1500 and 3500 does. Only catch-effort data were used to calibrate the model. The example is therefore convenient for illustrating the relative merits of population reconstruction without and with auxiliary data of varying degrees.

Skalski et al. (2012) recommended using point-deletion techniques to determine the stability of population reconstruction to varying amounts of historical information. For a reconstruction to be reliable, the estimated abundance trends should be relatively insensitive to the amount of historical data used in the demographic analysis. They recommended determining how stable the reconstruction abundance estimates were when 0, 1, 2, … years of the historical data were sequentially eliminated for the analysis. Following the advice of Skalski et al. (2012), simulated survey data to estimate abundance $\left(\hat{N}_i \right)$ and harvest probability $\left(\hat{P}_i \right)$ were added to the original population reconstruction with coefficients of variation of CV = 0.05, 0.125, 0.25, or 0.50. One such survey was assumed to have occurred either at the middle (i.e. 1991) or at the

end (2002) of the 24-year population reconstruction (1979–2002). Stability was measured by the

relative absolute deviation (RAD) in abundance defined as

$$\text{RAD} = \frac{1}{y} \sum_{i=1}^{y} \frac{|N_{ik} - N_i|}{N_i} \times 100\%$$

where N_i = abundance estimate in year i from original population reconstruction using all years

of data, N_{ik} = abundance estimate in year i from a reconstruction with k historical years of age-at-

harvest data deleted, and y = number of years in the truncated reconstruction. The number of

years deleted ranged from k = 0, 2, 4, 6, 8, 10, and 12 of the original 24 years of reconstruction.

2.2 RESULTS

2.2.1 Monte Carlo simulations

As the precision of the auxiliary studies increased, precision of the reconstructed

abundance estimates increased roughly proportional. With minimal information from an

auxiliary study with a CV of 50%, the median CVs of the abundance estimates were intolerably

large, usually greater than 100% (Table 1). As the CV of an auxiliary study used in estimating

abundance went from 0.25 to 0.05, the median CV of the reconstructed abundance estimates was

reduced by more than half and ranged from 0.354–0.798 to 0.082–0.354, respectively. The use

of auxiliary data in conjunction with pooled age-class data (i.e., age classes 0.5, 1.5, and 2.5+)

had the same pattern of improvement in precision as occurred for full age-class reconstruction

(Table 2.1). The only difference was a slight additional reduction in the anticipated CVs.

Auxiliary abundance studies had a greater influence on the precision of reconstructed

abundance estimates than auxiliary harvest probability studies for equal precision (Table 2.1).

For example, when the auxiliary abundance study had a CV of 12.5% (i.e., with ±25% of the true value 95% of the time), the resulting median CVs for the reconstructed abundance estimates ranged from 19.8% to 58.3% (Table 2.1). For a similar level of precision in an auxiliary harvest mortality study, the population reconstruction estimates had CVs in the range 57.4% to 92.8%. In general, reducing the CV of an auxiliary study produced a commensurate reduction in the CVs of the reconstructed abundance estimates.

Timing of the auxiliary studies was generally not important. The same improvement in the precision of the population reconstruction estimates occurred regardless of whether the auxiliary study was conducted at the beginning, middle, or near the end of the investigation. The only exception was when the auxiliary study was performed in the last (i.e., current) year of reconstruction. Under this circumstance, precision of the population reconstruction will not be measurably improved until a year thereafter.

Incorporating multiple auxiliary studies, 1/3 and 2/3 of the way through the reconstruction period, increased precision of the resulting abundance estimates (Table 2.1). The effect is most substantial with auxiliary studies of minimal precision (Table 2.1). However, a single auxiliary study with a CV of 0.125 results in better precision than two auxiliary studies with a CV of 0.250 each (Table 2.1).

Table 2.1 Median coefficient of variation (CV) of measurement error in simulated population reconstruction models when including either abundance or harvest probability auxiliary studies at varying levels of precision in the middle of the reconstruction. Further, we considered one (single abundance auxiliary) and two abundance auxiliary studies (double abundance auxiliary). Populations were simulated at high and low levels of harvest and natural survival probabilities.

| | | | $CV(\hat{N})$ | | | Pooled model |
| | | | Full model | | | |
Survival probability	Harvest probability	Auxiliary CV	Single abundance auxiliary	Double abundance auxiliary	Single harvest probability auxiliary	Single abundance auxiliary
0.75	0.1	0.05	0.082	0.044	0.25	0.119
0.75	0.1	0.125	0.198	0.124	0.574	0.188
0.75	0.1	0.25	0.369	0.280	0.88	0.317
0.75	0.1	0.5	0.953	0.474	2.038	0.895
0.75	0.25	0.05	0.344	0.231	0.573	0.248
0.75	0.25	0.125	0.583	0.467	0.928	0.372
0.75	0.25	0.25	0.798	0.672	1.333	0.538
0.75	0.25	0.5	1.877	0.876	2.441	1.758
0.9	0.1	0.05	0.09	0.068	0.229	0.120
0.9	0.1	0.125	0.221	0.151	0.536	0.191
0.9	0.1	0.25	0.354	0.239	0.795	0.318
0.9	0.1	0.5	0.79	0.404	1.741	0.954
0.9	0.25	0.05	0.325	0.232	0.563	0.218
0.9	0.25	0.125	0.55	0.467	0.883	0.415
0.9	0.25	0.25	0.719	0.642	1.467	0.578
0.9	0.25	0.5	0.894	0.813	2.708	0.861

2.2.2 Black-tailed deer example

Augmenting the original black-tailed deer data with an auxiliary abundance survey or a telemetry study, to estimate the vulnerability coefficient, greatly improved the stability of the population reconstruction when the amount of historical data was reduced. Without any auxiliary data, the black-tailed deer reconstruction was very sensitive when 4 or more years of harvest data were omitted from the analysis (Table 2.2, Figure 2.1). With 6 of 24 years of

historical data removed, the RAD exceeded 150%. With even more years of data deleted, the reconstruction virtually disintegrated (Table 2.2). However, the presence of rough auxiliary studies with a CV = 25% (i.e., ±50% of the true value, 95% of the time) resulted in reasonable stability of the reconstructed population trends. When the auxiliary data estimated the harvest probability $\left(\hat{P_i} \right)$ with a CV ≤ 0.25, the RAD ≤ 7.48% with as many as 12 years of historical data eliminated (Table 2.2, Figure 2.2). When the auxiliary data provided an abundance estimate within a CV = 0.25, the RAD ≤ 22.25% with as many as 12 years of data deleted (Table 2.2, Figure 2.3). By the time the auxiliary studies had a precise level suitable for accurate management purposes (Robson & Regier 1964, CV = 0.125), the RADs ≤ 6.32% with 12 years of data deleted (i.e., 50%) when auxiliary telemetry data were available.

Smaller RADs were obtained using radio-telemetry auxiliary data to estimate harvest probabilities rather than auxiliary abundance surveys for equal levels of precision (Table 2.2, 2.3). Stability of the population reconstruction was not affected by whether the auxiliary study was conducted in the middle or near the end of the time series (Table 2.3).

Table 2.2. Relative absolute deviation $\left(\overline{\mathrm{RAD}}\right)$ in annual abundance estimates from point-deletion sensitivity analyses performed on a statistical population reconstruction of female black-tailed deer (Skalski et al. 2007). Models had either no auxiliary data or auxiliary data that estimated abundance or the vulnerability coefficient. Auxiliary studies have a coefficient of variation (CV) of 0.05, 0.125, 0.25, or 0.50 and were simulated in the final year of study.

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

Table 2.3 Relative absolute deviation $\left(\overline{\text{RAD}}\right)$ of abundance estimates from a point-deletion sensitivity analysis of female black-tailed deer comparing auxiliary studies simulated at the end (i.e., 2002) or the center of the reconstruction (i.e., 1991).

CV	Abundance auxiliary data		Vulnerability coefficient auxiliary data	
	2002	1991	2002	1991
0.05	2.17%	1.76%	1.71%	1.75%
0.125	3.75%	3.76%	1.48%	1.52%
0.25	11.70%	11.77%	3.05%	3.36%
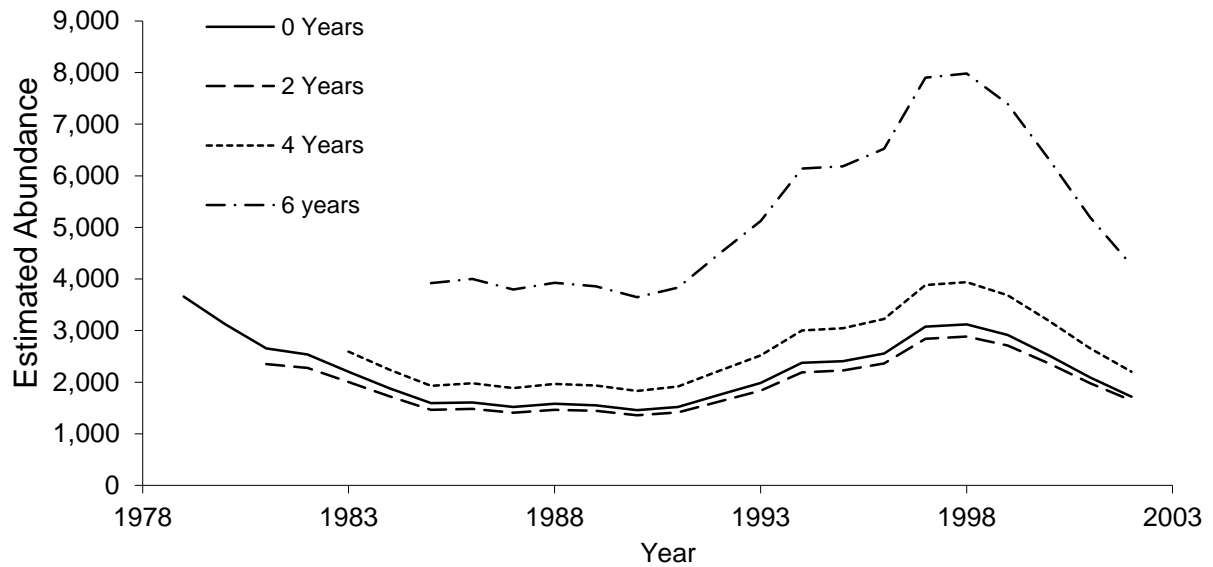
Figure 2.1 Alternative population reconstructions of the black-tailed deer population with 0, 2, 4, or 6 years of historical data removed in the absence of any auxiliary data.
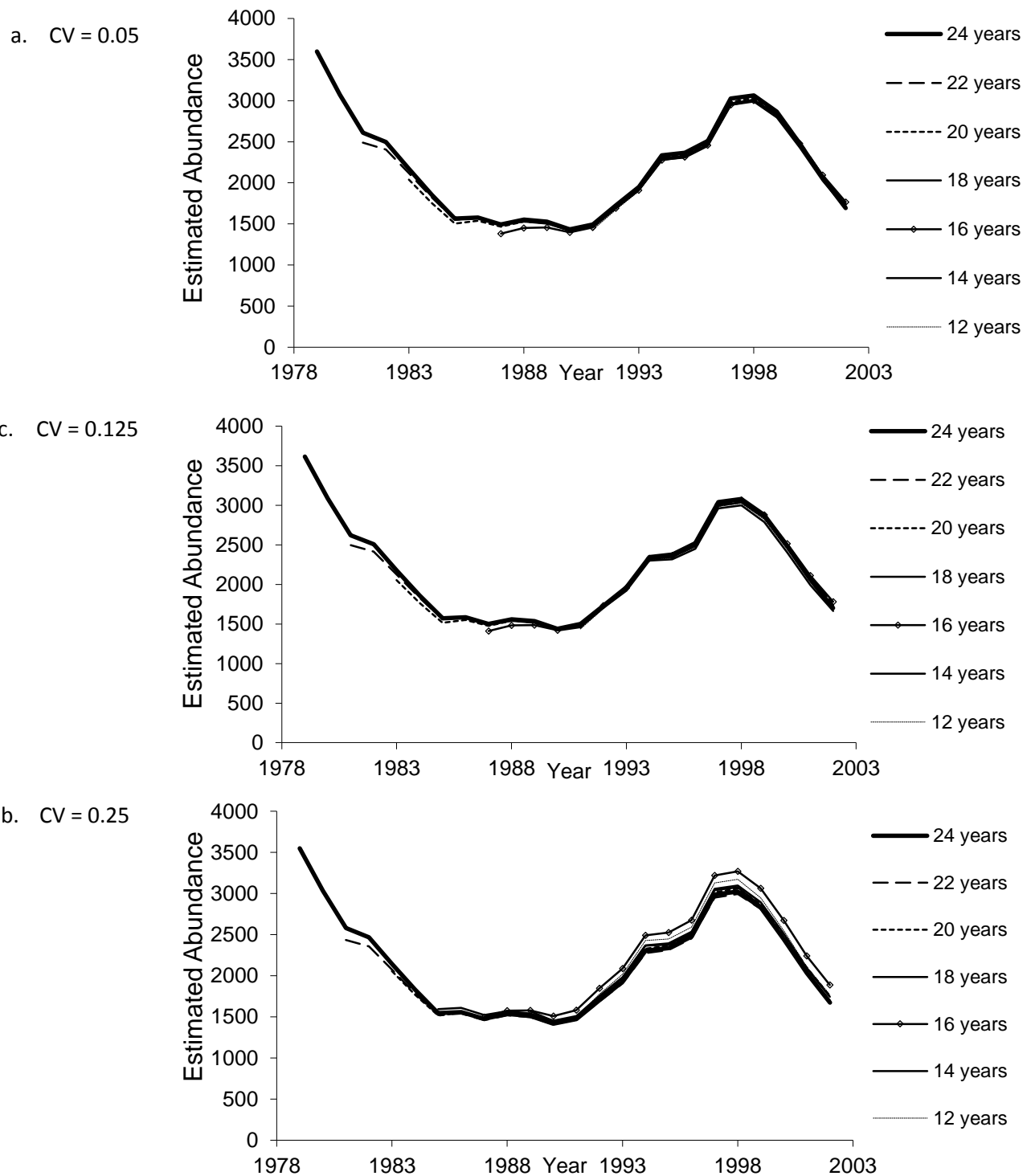
Figure 2.2. Annual abundance trends from a point-deletion sensitivity analysis, with historic data removed, on a statistical population reconstruction of female black-tailed deer, with a simulated auxiliary study to estimate harvest probability in 2002 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.
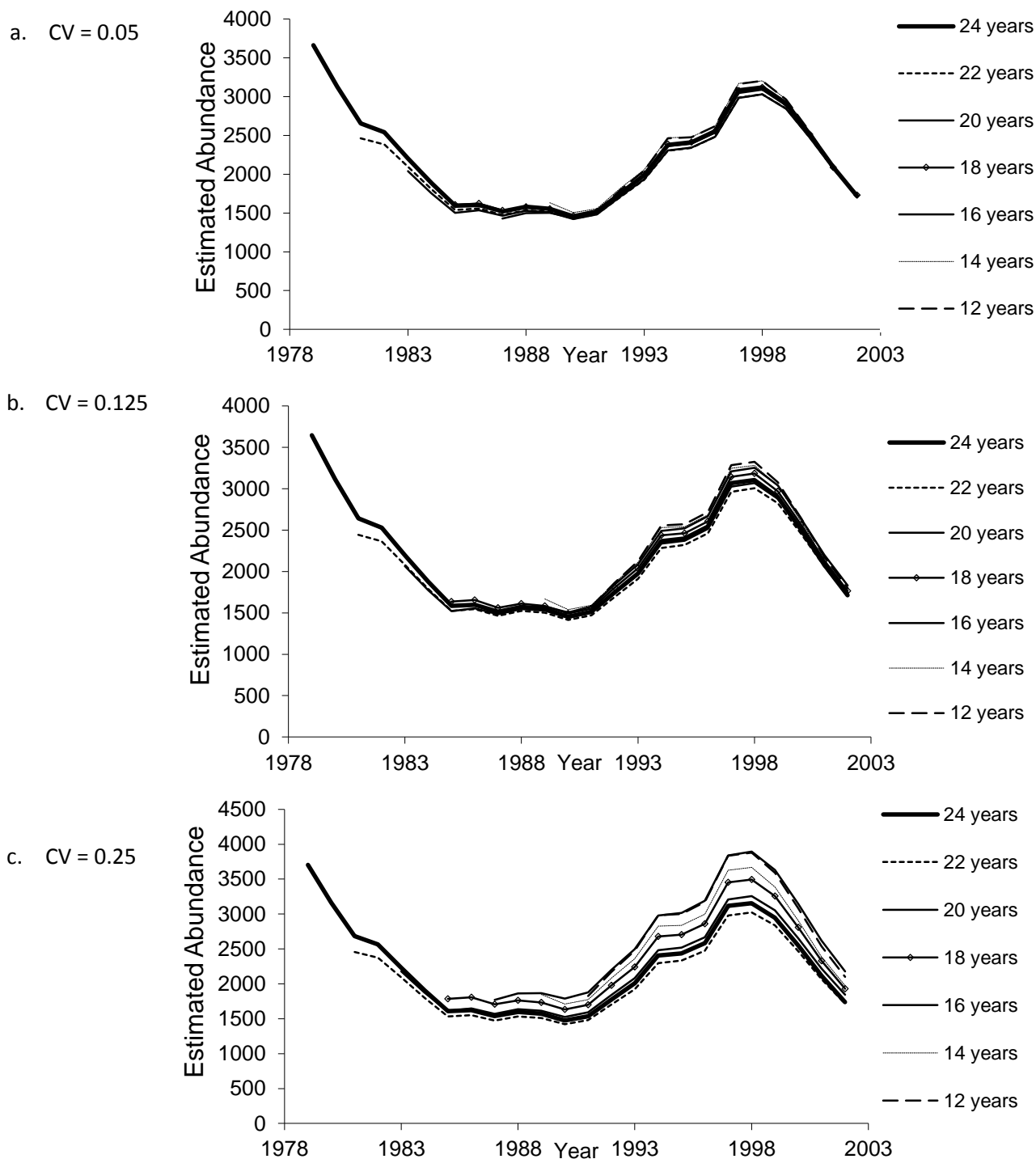
Figure 2.3 Annual abundance trends from a point-deletion sensitivity analysis, with historic data removed, on a statistical population reconstruction of female black-tailed deer, with a simulated auxiliary study to estimate abundance in 2002 with a CV of (a) 0.05, (b) 0.125, and (c) 0.250.

2.3 **DISCUSSION**

Our simulation and sensitivity analyses illustrate several important trade-offs in the quality and type of auxiliary studies used in SPR modeling. First, the value of even rather imprecise auxiliary data (e.g., CVs = 25%) on the precision and stability of population reconstruction were evident. This finding demonstrates the general utility of auxiliary information in SPR and can be used by managers as a guide on the required quality of future auxiliary studies. Second, different types of auxiliary data have different benefits to SPR estimates and the choice of auxiliary data components ultimately depends on the goal of the resource manager. If the primary concern is precision of the abundance estimates, auxiliary abundance studies are more beneficial than auxiliary radio-telemetry studies for comparable levels of precision. However, managers might be more interested in the inter-annual stability of abundance estimates when designing harvest regulations. If so, auxiliary radio-telemetry studies are more beneficial than abundance auxiliary studies for comparable levels of precision.

Another important question in SPR modeling relates to the timing of auxiliary data collection and our findings suggested improvements in precision are expected when auxiliary data is collected at any point during the reconstruction except the last year. This finding is important for wildlife managers who might have historical age-at-harvest data and are considering conducting a contemporary auxiliary study. These results suggest the continued value of collecting auxiliary data after the collection of age-at-harvest data has begun. In other words, age-at-harvest and auxiliary data do not need to be collected simultaneously from the start of the study. Further, because auxiliary data can be collected at nearly any point during the reconstruction, a manager can be less concerned if data collection during an auxiliary study

proves unsuccessful. For example, if radio-collars malfunction, a manager can attempt a telemetry study at a later date or alter plans and collect another type of auxiliary data without losing the ability to use SPR.

Our analyses also indicate that multiple auxiliary studies can further enhance the precision of population reconstruction estimates. In an adaptive management framework where decisions are updated as more and more information becomes available through time, this finding is relevant. SPR is not only flexible enough to handle multiple auxiliary data types, but we can expect precision of the resulting estimates to improve. However, if a manager is considering whether to complete one or two auxiliary studies that estimate abundance, it is important to consider that one study with high precision will improve precision of SPR estimates compared with two auxiliary studies with low precision. Although precision of demographic estimates is generally not considered in traditional models of population reconstruction (Millspaugh et al. 2009), we encourage managers to carefully consider the quality of auxiliary data and how it ultimately affects the results of SPR.

Our assessment, however, is void of any cost-precision comparison for radio-telemetry versus auxiliary abundance surveys. The feasibility for each type of survey will vary by species, geographic factors and labor cost. Given that precision of population reconstruction estimates improve roughly proportional to the improvement in precision (i.e. reduction in CV) of auxiliary studies, it should be fairly straightforward to perform a cost benefit analysis. Field investigators should consider their end goals and perform a cost-benefit analysis when planning auxiliary studies to augment SPR models. Such an approach is likely to produce the most useful

population estimates and gain support from administrators and stakeholders holding managers

accountable for costs and reliability of modeling results.

Chapter 3. TRENDS IN MALE WILD TURKEY ABUNDANCE AND HARVEST FOLLOWING RESTORATION EFFORTS IN THE SOUTHEAST REGION OF MISSOURI, 1960–2010

Current wild turkey (*Meleagris gallopavo*) populations in Missouri, USA, are the result of extensive reintroduction efforts combined with >50 years of harvest management (Lewis 2001). In 2010, >100,000 hunters participated in Missouri's spring wild turkey season, harvesting >40,000 wild turkeys (Isabelle 2010). Wild turkeys have not always been so plentiful in Missouri; in 1952 there were as few as 2,500 statewide (Dickneite 1973). Extensive restoration efforts began in 1954 with the initiation of a trap-and-transfer program that used birds from remnant populations in Missouri to repopulate other areas of the state. In order to generate interest in wild turkey management and further restocking efforts, the Missouri Department of Conservation (MDC) established the first modern spring turkey season in 1960 (Lewis 2001). Other than a few scattered releases, the wild turkey restoration program in Missouri was completed in 1979 (Lewis 2001). Although there were reintroductions, restocking, and recovery projects of many wildlife species across the country from 1930–1980, there has been little historical assessment of these recovering populations and hunter response to emerging game populations (Kallman 1987).

A historical population assessment can be useful in informing future management actions. Rates of population increase can be used to estimate recovery times, and exploitation rates used to assess how hunting may affect population recovery. Hunter response to harvest opportunities may also affect the rate of population growth depending upon species and harvest

rate. A delayed response by hunters may allow a population to grow more quickly. In Missouri and elsewhere, hunters are often used as a primary means of harvest data collection, which can be used to assess wildlife population dynamics. An understanding of hunter motivation and behavior can impact harvest management decisions. Generally, managers assume hunter satisfaction is linked to high success rates (Diefenbach et al. 2012); however, aesthetic and social values may have a greater impact (Kennedy 1974, Ringelman 1997). Outside of factors affecting hunter satisfaction, little is known about hunter behavior, despite harvest being the primary management tool of game species (Stedman et al. 2004). Hunter distribution and density, in response to an emerging population, can provide information about hunter behavior and motivation. If hunters are primarily driven by high success rates, one might expect the distribution of hunter densities to be related to game densities.

In addition to providing information useful in assessing hunter behavior, historical reconstructions can be helpful in identifying potential drivers of wildlife abundance trends. Long-term series of demographic parameters can elucidate trends not seen in short-term studies (Miller et al. 1998). For ground-nesting, short-lived, highly fecund species, weather and recruitment are often highly influential factors in population dynamics (Bridges et al. 2001). Cold and wet spring weather has been shown to negatively affect eastern wild turkey nest success and poult survival (Vangilder and Kurzejeski 1995; Roberts and Porter 1998*a, b;* Lowrey et al. 2001). Given that previous wild turkey studies have linked weather and reproductive metrics, it is likely that weather is a driving factor in annual wild turkey abundance fluctuations (Porter et al. 1990). In contrast to the potential effects of weather on wild turkey abundance, moderate levels of spring male wild turkey harvest (<30%) are thought to have

minimal effects on wild turkey abundance, but may affect the juvenile:adult male ratio (Kurzejeski and Vangilder 1992, Vangilder 1992, Vangilder and Kurzejeski 1995, Healy and Powell 2000, Kimmel 2000). Autumn either-sex harvests, however, can impact wild turkey abundance, where removing >10% of the population is likely to result in population decline (Suchy et al. 1983, Little et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008).

The objectives of this study were 1) estimate abundance of the male turkey population in the Ozarks East turkey productivity region from 1960 to 2010 at both the regional and county spatial scales; 2) use the resulting abundance distribution at the county level to assess hunter responses to an emerging population; and 3) use the regional abundance estimates to assess possible drivers of population dynamics, specifically weather and autumn harvest pressure. Using the fitted catch-effort relationship from a contemporary (2006–2010) statistical population reconstruction (SPR) of the male wild turkey population in the East Ozarks by Gast et al. (2013k), we reconstructed male wild turkey abundance within the region back in time from 1960 to 2010. Using this 50-year trend in reconstructed abundance, we fit a population growth model and assessed factors that might influence abundance fluctuations. We also examined hunter response to the emerging population as additional harvest opportunities became available. The result is a half-century of spatial–temporal trends in male wild turkey abundance and hunter response to restoration efforts and harvest management in southeastern Missouri.

3.1 STUDY AREA

In Missouri, wild turkeys are managed within areas of similar habitat known as turkey productivity regions (TPR; Figure 3.1). We reconstructed the male wild turkey population in the

Ozarks East TPR in southeastern Missouri. The Missouri Ozarks have a rugged terrain, and are 90% covered by fairly homogeneous oak (*Quercus* spp.) forests and areas of mixed oak and shortleaf pine (*Pinus echinata;* Vangilder 1996). There were 13 counties in the Ozarks East TPR.

Prior to restoration efforts, wild turkeys existed at low population levels throughout the Ozarks East TPR (Lewis 1957). In an effort to increase wild turkey abundance, a statewide trap-and-transfer program involving wild-captured birds was initiated in 1954 by the MDC. The first documented releases occurred in the Ozarks East TPR in 1960. Within the region, 198 wild turkeys were translocated during 14 releases in 7 counties over a 14-year time span from 1960 to 1974. Releases of 21, 36, and 39 birds occurred in Butler, Ripley, and Oregon counties, respectively, 2–3 years prior to these counties establishing hunting seasons (Figure 3.1). Wild turkeys were also released in Carter, Dent, Wayne, and Reynolds counties, concurrent with harvest (Figure 3.1).

Today, wild turkeys are harvested in Missouri during 2 seasons; a predominantly male harvest in spring, followed by an autumn harvest of both males and females. In the Ozarks East TPR, a spring firearms harvest season was opened in 10 counties in 1960 and in all 13 counties by 1972. An autumn firearms harvest season was initiated in 1978. Until 2005, landowners could harvest wild turkeys without a permit during the spring and autumn hunting seasons. Aging and sexing of harvested animals in Missouri historically occurred at hunter check stations, but more recently, animals have been sexed and aged by hunters as part of a call-in registration program (Hansen et al. 2006). In autumn, it can be difficult for hunters to distinguish female turkeys from juvenile males, calling into question the reliability of some autumn age and sex data. Because of these limitations, the contemporary SPR model by Gast et al. (2013k) and the reconstruction

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presented here include only male wild turkeys.
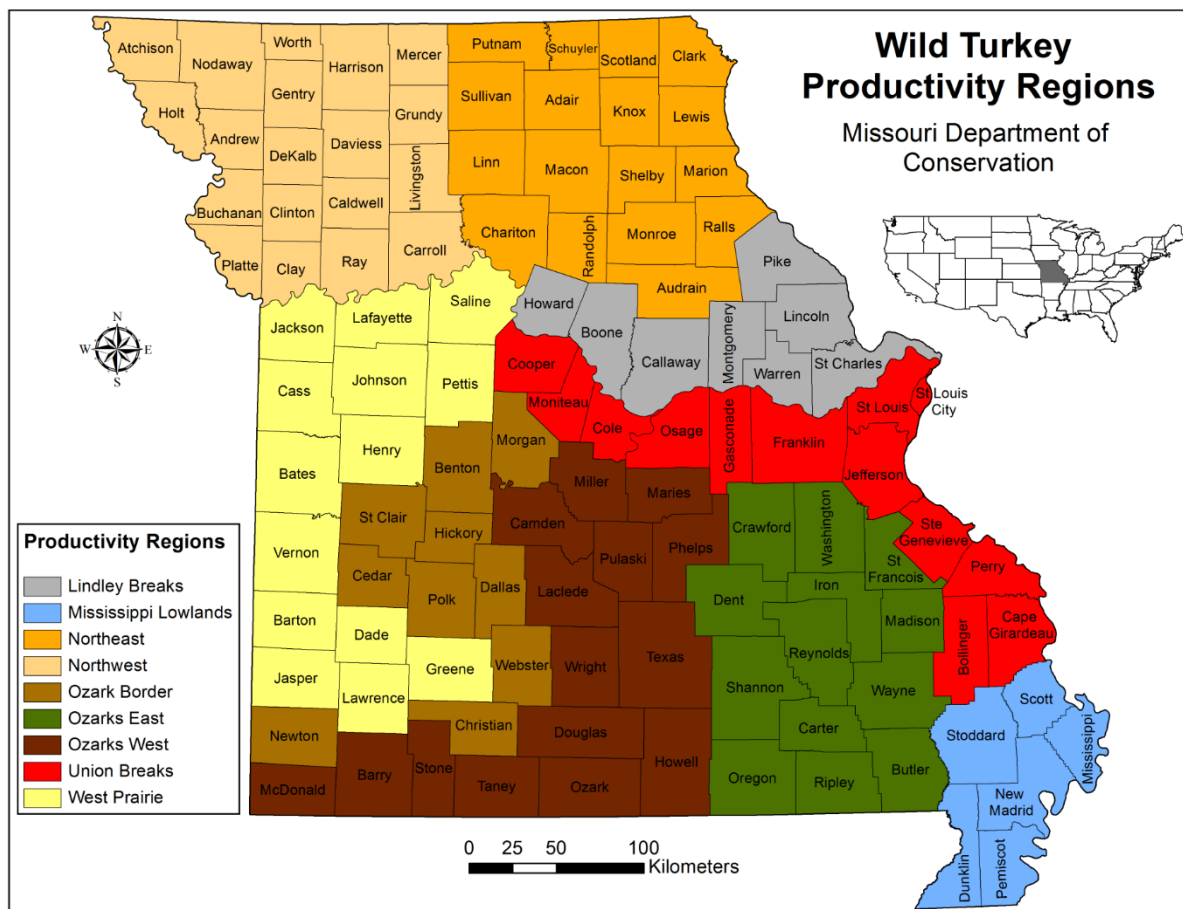
Figure 3.1 A map of turkey productivity regions (TPR) in Missouri, USA, with the Ozarks East TPR in the southeastern corner of the state.

3.2 **METHODS**

3.2.1 **Historical reconstruction**

The MDC began collecting wild turkey harvest records in the Ozarks East TPR in 1960. Annual harvest data consist of total harvest, permittee harvest (harvest by permitted hunters, because landowners did not need permits), and the proportion of yearlings in the harvest (1960–2010; Appendix A). Hunter-effort data include permits sold statewide (1960–2010 annually), the number of hunters in the Ozarks East TPR (1963–1982 annually, 1984–1996 semiannually, 1998–2010 annually), and the number of hunting trips taken in the Ozarks East TPR (1984–1996 semiannually, 1998–2010 annually; Table 3.1). In addition to harvest and hunter-effort data, an archer index beginning in 1983 was available, which provides the number of wild turkeys seen per 1,000 archer-hours (Appendix A).

To address data gaps and in order to take full advantage of the 50-year harvest and hunter-effort data set, we estimated missing values using time series and regression techniques. We lacked data for 12 years on the number of hunters in the Ozarks East TPR. We used data from the remaining 38 years that had both state-wide permit numbers and number of hunters in the Ozarks East TPR to establish a functional relationship between statewide permits sold and the number of hunters who hunted in the Ozarks East TPR. Based on an examination of the data, we chose to model the relationship between state-wide permit sales and hunters in the Ozarks East TPR as

$$\text{Hunters} = \frac{a \times \text{Permits}}{1 + \beta \times \text{Permits}}. \qquad (5)$$

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Table 3.1. Statewide and Ozarks East turkey productivity region (TPR) hunter effort in Missouri, USA, 1960–2010, with missing values indicated.

Year	Statewide permits	Hunters in Ozarks East TPR	Hunter trips in Ozarks East TPR	Year	Statewide permits	Hunters in Ozarks East TPR	Hunter trips in Ozarks East TPR
1960	698			1986	77,972	15,454	75,496
1961	1,001			1987	85,723		
1962	1,400			1988	94,301	17,204	82,616
1963	1,778	998		1989	92,901		
1964	2,958	1,404		1990	92,094	14,347	72,864
1965	3,099	1,392		1991	89,025		
1966	4,873	1,884		1992	89,720	12,831	64,756
1967	6,702	2,712		1993	89,899		
1968	8,102	3,436		1994	90,703		68,220
1969	7,577	3,067		1995	99,412		
1970	10,072	4,492		1996	99,879	14,991	69,298
1971	12,306	5,365		1997	99,933		
1972	20,077	8,937		1998	105,518	12,220	65,854
1973	29,633	11,912		1999	120,215	13,309	71,273
1974	26,363	11,671		2000	124,533	13,461	62,601
1975	28,621	10,252		2001	125,157	14,683	76,457
1976	35,932	12,460		2002	130,021	15,346	74,921
1977	36,596	11,289		2003	110,939	15,232	69,350
1978	42,244	11,485		2004	114,529	15,713	81,414
1979	46,008	13,515		2005	115,190	16,483	82,299
1980	56,133	13,084		2006	115,897	14,304	67,334
1981	63,914	13,729		2007	117,736	15,096	80,017
1982	67,150	15,436		2008	115,049	13,368	60,511
1983	73,347			2009	112,303	13,505	67,649
1984	76,053	17,600	84,394	2010	104,955	12,682	62,808
1985	69,945			2010	104,955	12,682	62,808

This relationship was fit using non-linear regression, assuming a normal error structure. It is reasonable to assume some degree of regional hunter fidelity and, therefore, a relationship between statewide permit and Ozarks East hunter numbers based on hunter preference,

familiarity, and regional proximity. We then used the fitted relationship to predict the number of hunters in the Ozarks East TPR based on the number of permits sold statewide, for the 12 years that lacked regional hunter data.

In addition to estimating hunter numbers in the Ozarks East TPR for years with missing data values, we also estimated permittee harvest in the 2 years in which data were missing. In 1966 and 1970, permittee harvest was not recorded; however, total harvest data were recorded. Therefore, we estimated permittee harvest in these years based on the proportional change of total harvest, applied to permittee harvest in the previous and subsequent years, and averaged according to the formula

$$\hat{X}_i = \frac{\dfrac{Y_i}{Y_{i-1}} \times X_{i-1} + \dfrac{Y_i}{Y_{i+1}} \times X_{i+1}}{2}, \quad (6)$$

assuming X_i is the permittee harvest in year i and Y_i is the total harvest in year i.

In order to reconstruct abundance at both the regional and county spatial scale, we needed both hunter-effort and harvest data at each spatial scale. The MDC collected hunter-effort and harvest data at the county-level; therefore, data could be aggregated to the regional scale. We estimated missing hunter-effort data (1983–1997 semiannually) at the regional scale (Eq. 1) and scaled to the county level using an averaged proportional change method,

$$\hat{C}_i = \frac{\dfrac{R_i}{R_{i-1}} C_{i-1} + \dfrac{R_i}{R_{i+1}} \times C_{i+1}}{2}, \quad (7)$$

where C_i is the estimated number of hunters in the county in year i and R_i is the estimated

number of hunters in the region in year i. These data imputation measures allowed us to complete the data set and subsequently estimate abundance from 1960 to 2010 at both the regional and county spatial scales.

Gast et al. (2013b) used a statistical population reconstruction model to estimate spring male wild turkey abundance, harvest vulnerability, and natural survival in the Ozarks East TPR from 1996 to 2010. We used the estimated vulnerability coefficient (c) from this analysis to reconstruct abundance back to 1960. We estimated age-specific (yearling and adult) abundance of males just prior to the spring harvest season using a Horvitz–Thompson (Horvitz Thompson 1952) -type estimator of the form:

$$\hat{N}_{j,i} = \frac{H_{j,i}}{\hat{P}_{j,i}}, \quad (8)$$

where $H_{j,i}$ is the permittee harvest of age class j (i.e., yearlings and adults) in year i (Appendix A), $\hat{N}_{j,i}$ is the estimated male abundance for age class j in year i and $\hat{P}_{j,i}$ is the estimated harvest probability for age class j in year i. Probability of harvest is parameterized as

$$\hat{P}_{j,i} = 1 - e^{-\hat{c}_j f_i}, \quad (5)$$

where $\hat{c}_j$ is the harvest vulnerability coefficient estimated by Gast et al. (2013b) for age class j, using statistical population reconstruction from this same population (1996–2010) and f_i is the hunter density in the Ozarks East TPR in year i.

In 1960, only 10 of the 13 counties within the Ozarks East TPR were open for harvest (Appendix A), with the entire region not open for harvest until 1972. We scaled effort

measurements and harvest vulnerability parameters to account for the changes in huntable area; consequently, all effort metrics used in the models are densities (hunters per square mile). In order to reconstruct pre-1996 harvest probabilities, we assumed that the catch–effort relationship estimated in the SPR remained constant from 1960 to 2010. We assessed the assumption of constant hunter behavior, as an index of harvest vulnerability, comparing hunter trips to estimated hunter numbers (Table 3.1). We found a strong relationships between hunter numbers in the Ozarks East TPR and statewide hunter permits (Figure 3.2; Pearson $r = 0.822$), and between hunter numbers and hunter trips (Figure 3.3; Pearson $r = 0.845$), which permitted estimation of missing hunter statistics (Table 3.1) and the subsequent historical population reconstruction.
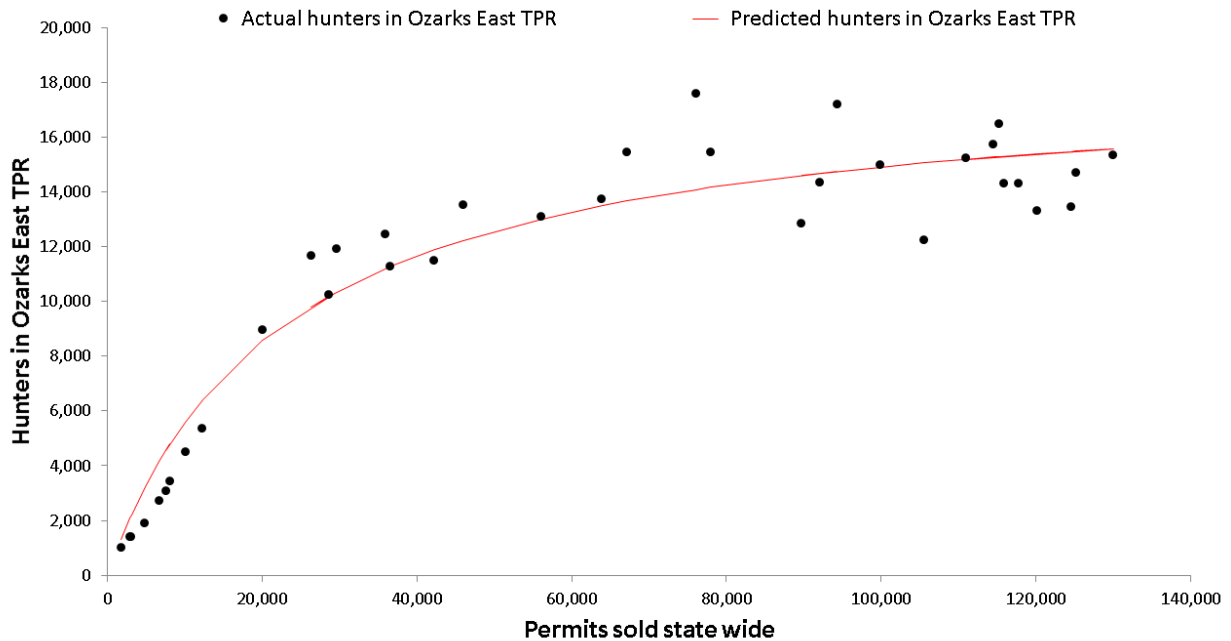
Figure 3.2. Number of permitted spring hunters in the Ozarks East turkey productivity region (TPR), Missouri, USA (1960–2010), versus statewide turkey spring hunting permits and fitted regression model (Eq. 1).
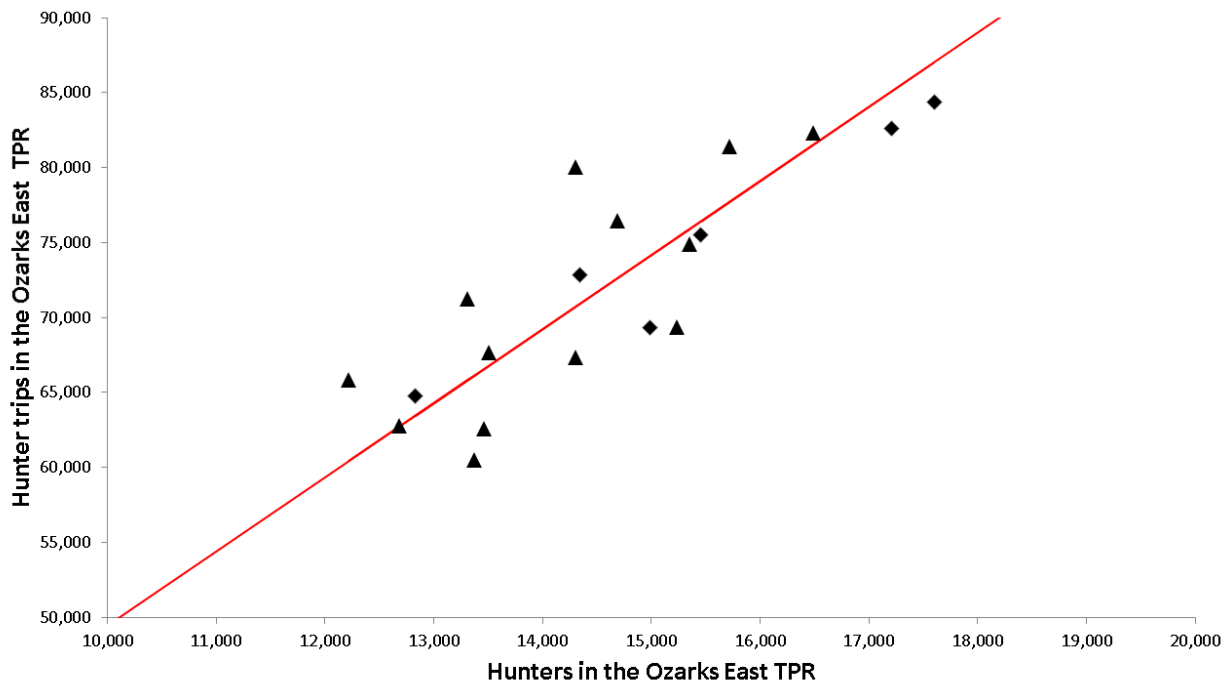
Figure 3.3. Number of spring turkey hunter trips taken in the Ozarks East (OE) turkey productivity region (TPR), Missouri, USA (1984-2010), versus number of turkey hunters in the Ozarks East TPR (horizontal axis). Model fitted was a straight-line regression through the origin. Data include both the 14-day (diamonds, $n = 6$) and 21-day (triangles, $n = 13$) harvest seasons.

3.2.2 Hunter response

We assessed the growth of the number of hunters relative to the number of male wild turkeys available for harvest at the regional level with visual assessments and regression analysis. To quantify hunter motivation, we developed 2 hypotheses:

1) Hunter distribution is driven primarily by high turkey densities.

2) Hunter distribution is driven primarily by convenience.

We assessed support for each of the hypotheses using data on hunter density in each county, distance of the county from the nearest major metropolitan area (St. Louis, MO) and estimated turkey density in the county, from 1960 to 2010. Using multiple regression, we fit the model:

$$\text{HunterDensity}_{i,k} = \alpha + \beta_{0,d} \times \text{Decade}_i + \beta_1 \times \text{Distance}_k + \beta_2 \times \text{TurkeyDensity}_{i,k} \quad (6)$$

where,

> $\text{HunterDensity}_{i,k}$ is the hunter density in year i and county k,
>
> Decade_i is a factor variable indicating which decade the observations from year i arose,
>
> Distance_k is the distance of county k from St. Louis, Missouri,
>
> $\text{TurkeyDensity}_{i,k}$ is the estimated male wild turkey density in year i and county k.

Decade was included to control for the magnitude of changes in turkey abundance over time. Each variable was evaluated based on its coefficient of partial determination (Kutner et al. 2004: 268), which describes the amount of variation in hunter density that is explained by a certain parameter, given all other parameters are in the model. Turkey density explaining the highest proportion of variation in hunter density would provide support for hypothesis 1; distance explaining the highest proportion of variation in hunter density would provide support for hypothesis 2. A decadal snapshot of the county-level distribution of hunter density and turkey abundance are provided in Figures 3.4 and 3.5.
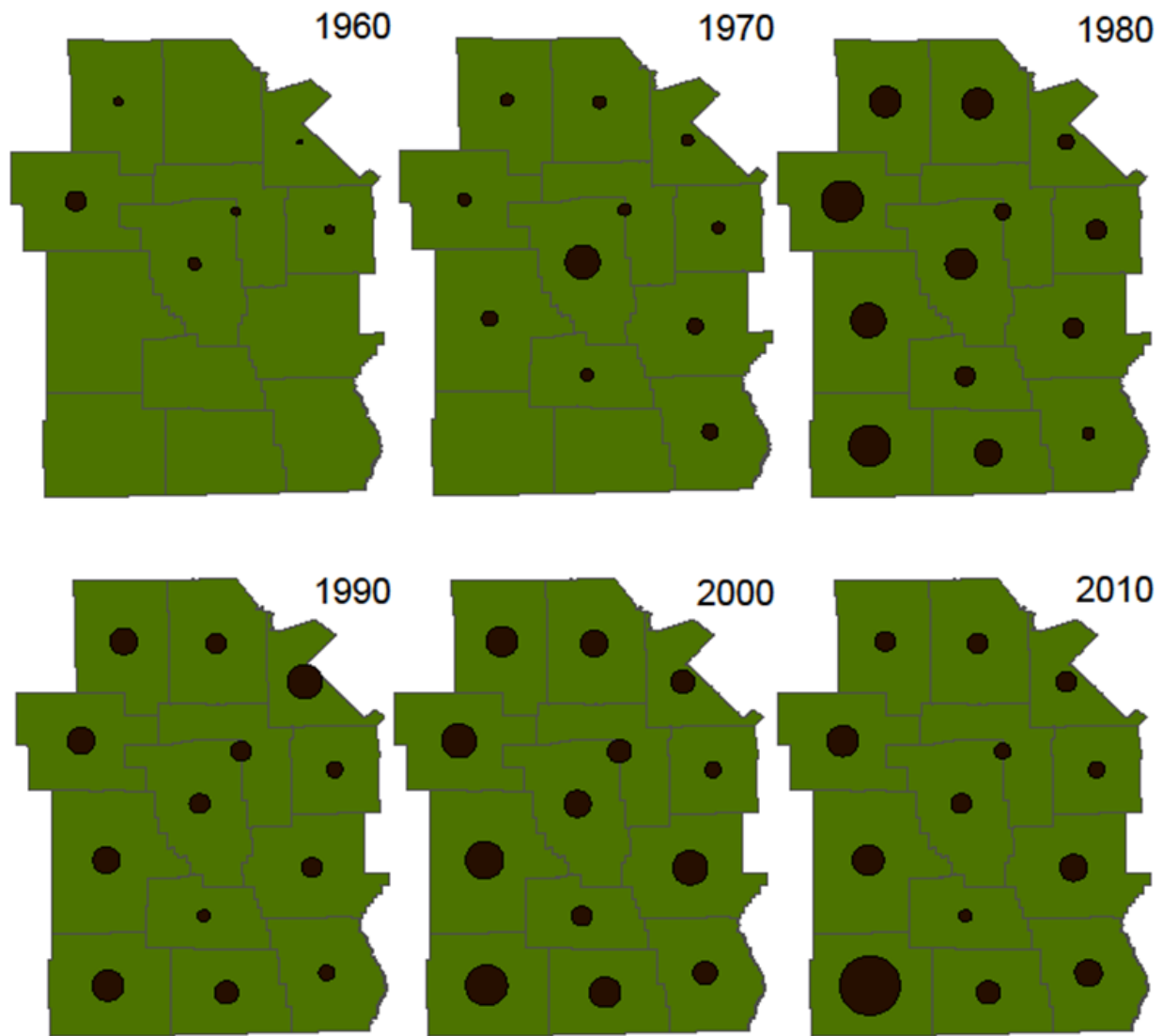
Figure 3.4. Decadal snapshots of male wild turkey abundance by county in the Ozarks East turkey productivity region, Missouri, USA (1960–2010). Dot sizes are proportional to abundance levels • 1–200 wild turkeys, ● 1,000–1,200 wild turkeys, ● 2,000–2,200 wild turkeys, ● 3,000–3,200 wild turkeys.
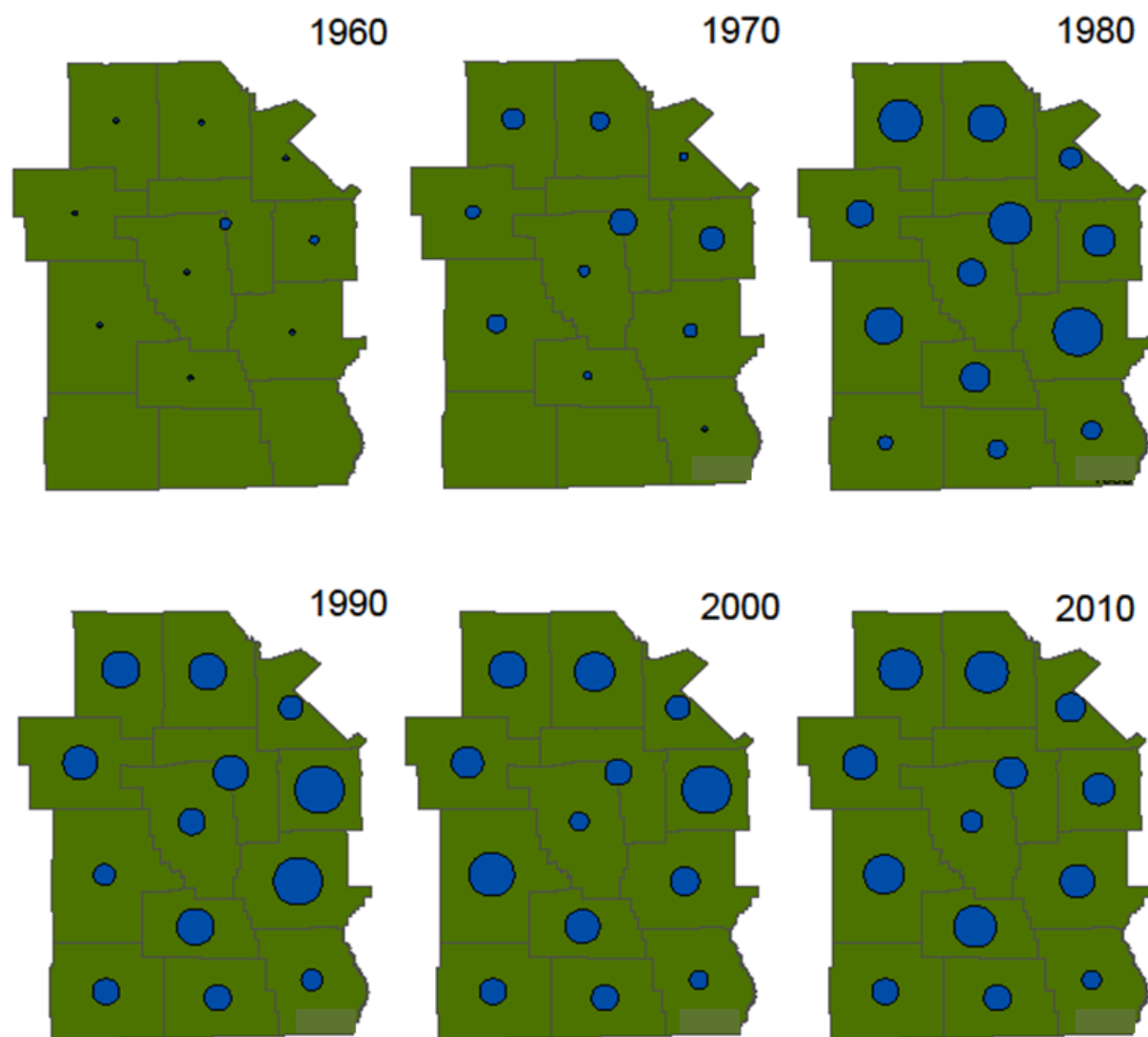
Figure 3.5. Decadal snapshots of spring turkey hunters per square mile by county in the Ozarks East turkey productivity region of Missouri, USA, (1960–2010). Dots are proportional to hunter density: 0.001–0.150 hunters per square mile, 0.90–1.05 hunters per square mile, 1.50–1.65 hunters per square mile, 2.10–2.25 hunters per square mile.

3.2.3 **Drivers of population dynamics**

Once we estimated male wild turkey abundance in the Ozarks East TPR, we wanted to assess the causes of variation in male abundance, the most obvious of which was the growth of the newly expanded population. Therefore, we fit a logistic population growth curve of the form

$$N_t = \frac{K \times N_0}{N_0 + (K - N_0) \times e^{-rt}}, \quad (7)$$

to male wild turkey abundance estimates from the historical reconstruction using a non-linear least-squares approach (Kutner et al. 2004:512). Using the logistic growth model as a baseline, we were able to assess causes of variation in abundance attributable to more than simple population growth. We used relative deviance from the fitted logistic population growth model (DEV), calculated

$$DEV_t = \frac{N_t^{Historic} - N_t^{Logistic}}{N_t^{Historic}} \quad (8)$$

as our response variable, rather than using the raw abundance estimates, in order to assess inter-annual variation in abundance not described by the underlying growth. Yearling recruitment was used as an additional population metric, because recruitment has been shown to be a primary driver of turkey populations (Lobdell et al. 1972). In our model, yearlings are recruited into the population the spring after they are born, making them approximately 1 year old, depending on the timing of hatching and harvest season. We chose to use the natural log of the yearling:adult ratio (YAR) as the recruitment metric. The YAR of males was calculated based on the abundance of yearling males and the abundance of adult males estimated from Eq. 4. The natural log transformation was used to help achieve normality of the ratio estimate. Spring YAR is a

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metric of realized recruitment over an entire year encompassing the effects of nest success, clutch size, poult survival, autumn juvenile harvest, and juvenile overwinter survival.

There are 2 competing hypotheses as to what is primarily driving fluctuations of abundance in this population: 1) autumn harvest rates, or 2) other external forces, primarily weather. In order to quantify the influence of autumn harvest on the population, we used linear regression to relate autumn hunter effort (as an index to harvest rate) in year i to the relative deviance of spring male abundance from the fitted logistic growth model (DEV) and spring YAR of males (YAR) in year $i + 1$ (Porter et al. 1990). Data for autumn harvest effort are only available from 1996 to 2010. In order to quantify weather in the study region, monthly regional weather metrics were chosen to approximate stages of the breeding season, including pre-breeding (Mar), nesting (Apr and May), and early brood-rearing (May and Jun). Wild turkey nesting chronology can be variable (Vangilder and Kurzejeski 1995), especially over multiple decades, so monthly metrics were used as an approximation to these stages of the breeding season. Many factors affect turkey reproductive success, including the timing of breeding and nesting, breeding hen survival, nest success, poult survival, and juvenile survival, and juvenile autumn harvest; some of which have been found to be correlated with weather metrics. Cold temperatures in March and April may delay breeding and nest initiation (Rolley et al. 1998). Vangilder and Kurzejeski (1995) found warmer March temperatures to be correlated with increased nest success. Additionally, dry weather during incubation (Apr and May) has been correlated with increased nest success (Roberts et al. 1995, Roberts and Porter 1998*b,* Lehman et al. 2008). Cold and wet weather within 2 weeks of hatch (late May and early Jun) has been correlated with poult mortality (Healy and Nenno 1985, Roberts et al. 1995). We obtained

climatological data (min. daily temp, max. daily temp, and total daily precipitation) from the

National Oceanic and Atmospheric Administration for each county within the Ozarks East TPR

(National Climatic Data Center 1960–2010). We used these data to calculate 6 weather metrics

relevant to wild turkey reproduction (Table 3.2). We calculated each weather metric for each

month in the breeding season (Mar, Apr, May, and Jun), resulting in 24 individual metrics. We

then averaged county metrics to form regional metrics (Miller et al. 1998). Furthermore, we

assumed extrinsic factors would have the greatest influence on turkey abundance after the

exponential growth phase of the population, so these analyses were limited to the years 1980–

2010 when the population had reached carrying capacity. Multiple regression was performed

using forward stepwise selection to select the most parsimonious model of weather variables to

explain the variation in the population metrics of interest (DEV or YAR; Kutner et al. 2004:214).

We tested each weather metric, the variable with the smallest significant ($\alpha = 0.10$) *P*-value was

included in the model. This process was repeated until all significant covariates were included in

the model (Table 3.3).

Table 3.2. Weather variables included in an examination of the relationship between weather and wild turkey reproduction and male abundance in the Ozarks East turkey productivity region of Missouri, USA, from 1960 to 2010.

Variable	Definition	Explanation	Citation
Cold days (CD)	The no. of days the min. temp is in the lower one-third quantile of daily min. temps	Cold temps during the nesting season may affect the timing and success of nests.	Rolley et al. (1998), Latham (1958)
Heating degree days (HDD)	The sum of heating degree days, Heating degree − day = (65° F − AVGTEMP if AVGTEMP <65° F); [AVGTEMP = (MIN + MAX)/2].	An alternate way to measure cold temps. See above explanation.	Roberts and Porter (1998*a, b*)
Zero degree days (ZDD)	The no. of days the min. temp dropped below zero degrees (C)	An alternate way to measure cold temps. See above explanation.	Vangilder and Kurzejeski (1995)
Rainy days (RD)	The no. of days that max. recorded precipitation is >0 mm	Wet weather during the nesting season may increase predation, lower nest success, and affect poult mortality.	Lowrey et al. (2001), Palmer et al. (1993), Roberts et al. (1995), Vangilder and Kurzejeski (1995)
Total precipitation (TP)	The sum of precipitation for all days in the period (mm)	An alternate way to measure wet weather. See above explanation.	Lowrey et al. (2001)
Bad weather days (BWD)	The no. of days the min. temp is in the lower one-third quantile of daily min. temps and the precipitation is in the upper one-third quantile of daily precipitation values	A combination of cold and wet weather has been shown to be detrimental to poults. Additionally, cold and wet weather may have an interactive effect on nest success.	Healy and Nenno (1985), Lehman et al. (2008)

Table 3.3. Multiple regression of weather parameters used in an examination of the relationship between weather and wild turkey reproduction and male abundance in the Ozarks East turkey productivity region of Missouri, USA, from 1960 to 2010. June total precipitation (JTP) and April cold days (ACD) were included in the best fit model for the yearling:adult ratio (YAR). June total precipitation (JTP) and April bad weather days (ABWD) were included in the best fit model for the deviance from the fitted logistic model (DEV). March total precipitation (RTP) and May bad weather days (MBWD) were found to be non-significant ($\alpha = 0.10$) for the YAR and DEV models respectively.

Model	Last parameter P-value	r^2
$YAR_{i+1} = e^{-0.419+0.0007JTP_i}$	0.001	0.335
$YAR_{i+1} = e^{0.94-0.08913ACD_i}$	0.002	0.268
$YAR_{i+1} = e^{0.353+0.0007JTP_i-0.096ACD_i}$	<0.001	0.630
$YAR_{i+1} = e^{0.353+0.0007JTP_i-0.096ACD_i+0.001783RTP_i}$	0.117	0.662
$DEV_{i+1} = 0.1371-0.1223ABWD_i$	0.003	0.251
$DEV_{i+1} = -0.1763+0.00015JTP_i$	0.150	0.066
$DEV_{i+1} = 0.0004-0.1256ABWD_i+0.00016JTP_i$	0.074	0.330
$DEV_{i+1} = 0.0781-0.1227ABWD_i+0.00017JTP_i-0.0486MBWD$	0.179	0.373

3.3 RESULTS

3.3.1 Historical reconstruction

The SPR in the Ozarks East TPR from 1996 to 2010 by Gast et al. (2013b) adjoins well

with the historical reconstruction from 1960 to 1996 we performed using the catch–effort

relationship of Gast et al. (2013b) and the Horvitz–Thompson abundance estimator (Eq. 4; Figure 3.6). The 2 approaches independently estimate the 1996 regional male wild turkey abundance within 16% of each other, or within one standard error of the original estimate.
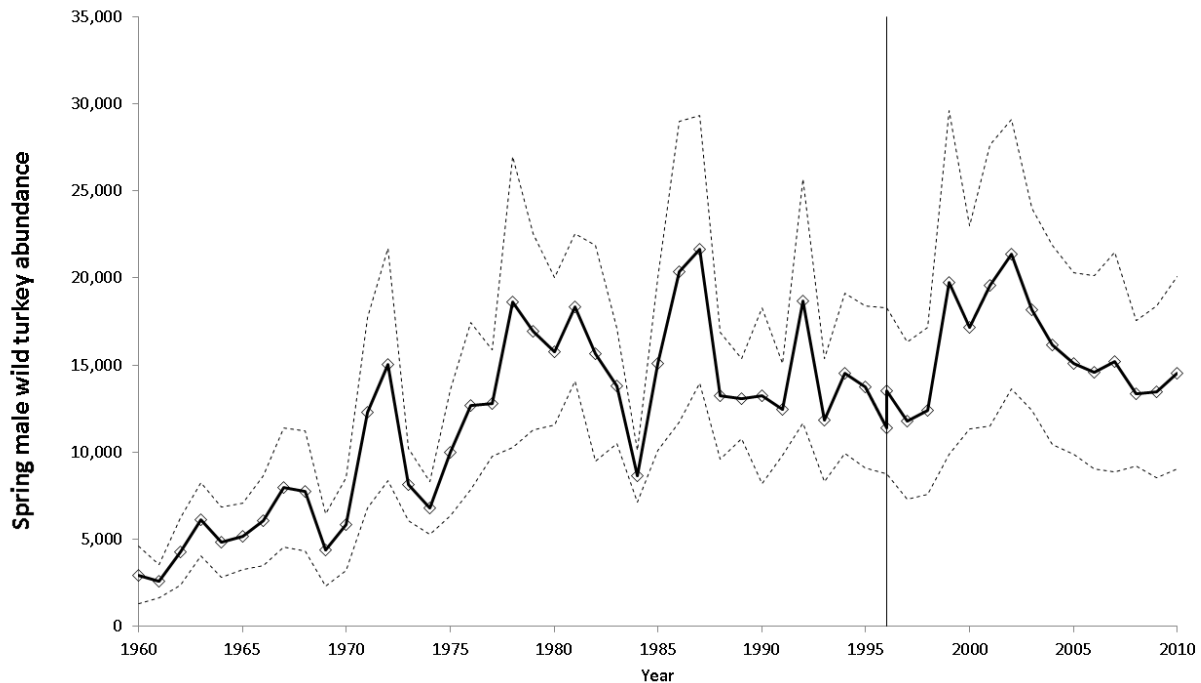
Figure 3.6. Spring male wild turkey abundance (black line) and associated 95% confidence interval (dashed lines) estimated based on historical reconstruction (1960–1996), and statistical population reconstruction (1996–2010) for the Ozarks East turkey productivity region, Missouri, USA. Separation of modeling methods is indicated by the vertical black line.

In 1960, only 6 of the 10 counties open to spring wild turkey hunting in the Ozarks East TPR reported any harvest; we estimated male total wild turkey abundance at 2,923 ($\hat{SE}$ = 843.5;Figure 3.6). The initial abundance estimate agrees reasonably well with crude population surveys conducted in 1952 and 1957, which estimate approximately 2,500 wild turkeys (male and female; Dickneite 1973). Male wild turkey abundance grew steadily following restoration, with regional abundance reaching 5,835 ($\hat{SE}$ = 1,021.0) in 1970. By 1980, the male wild turkey

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abundance reached 15,763 ($\hat{SE}$ =2,159.7). The estimated male wild turkey abundance in the

Ozarks East TPR increased to a peak of 21,652 ($\hat{SE}$ = 3,911.7) in 1987, and subsequently

returned to 11,361 ($\hat{SE}$ = 1,410.3) in 1996. Since 1980, spring male abundance has varied

annually about a constant mean or carrying capacity (*K*), with a range between 9,000 and 22,000

regionally.

Regional abundance estimates from the historical population reconstruction fit a logistic

growth curve (Figure 3.7). The logistic growth model (Eq. 5) estimates an initial regional

population size of 1,997 male wild turkeys ($\hat{SE}$ = 1,356.6), an instantaneous rate of growth, $\hat{r}$,

of 0.207 (i.e., $\hat{\lambda} = 1.230$ $\hat{SE}$ = 0.067), and a carrying capacity, $\hat{K}$, of 15,260 ($\hat{SE}$ = 624.0)

male wild turkeys.

The logistic model estimated realized annual population growth rates of 18.8% in 1960,

slowing to 9.3% by 1970 and 1.3% by 1980. The total male wild turkey abundance estimated by

the regional reconstruction agrees with the sum of the county-level population reconstructions

(Figure 3.8). The archer index of wild turkey abundance (1983–2010) also correlates reasonably

well with our estimates of regional male wild turkey abundance (Pearson *r* = 0.49). These

regression and separate reconstruction analyses lend support to the veracity of our overall

historical reconstruction.
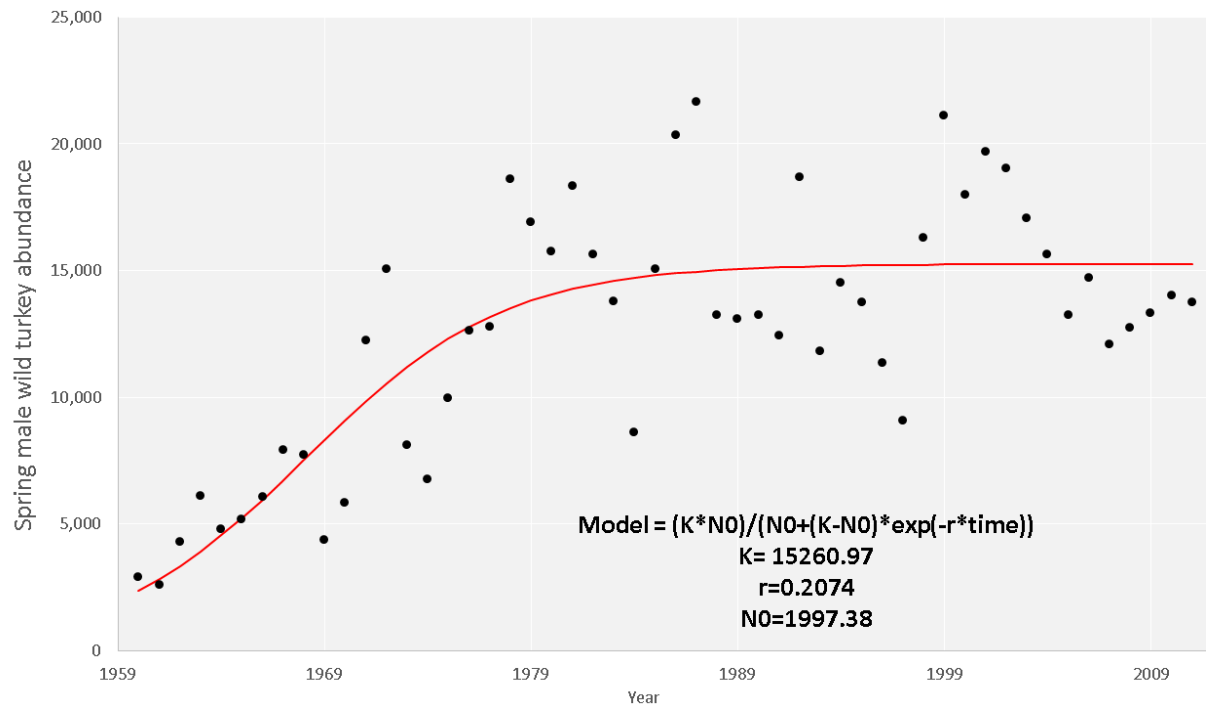
Figure 3.7. A continuous logistic population growth model (line) fitted to abundance estimates (dots) of male wild turkeys in the Ozarks East turkey productivity region of Missouri, USA, 1960–2010.
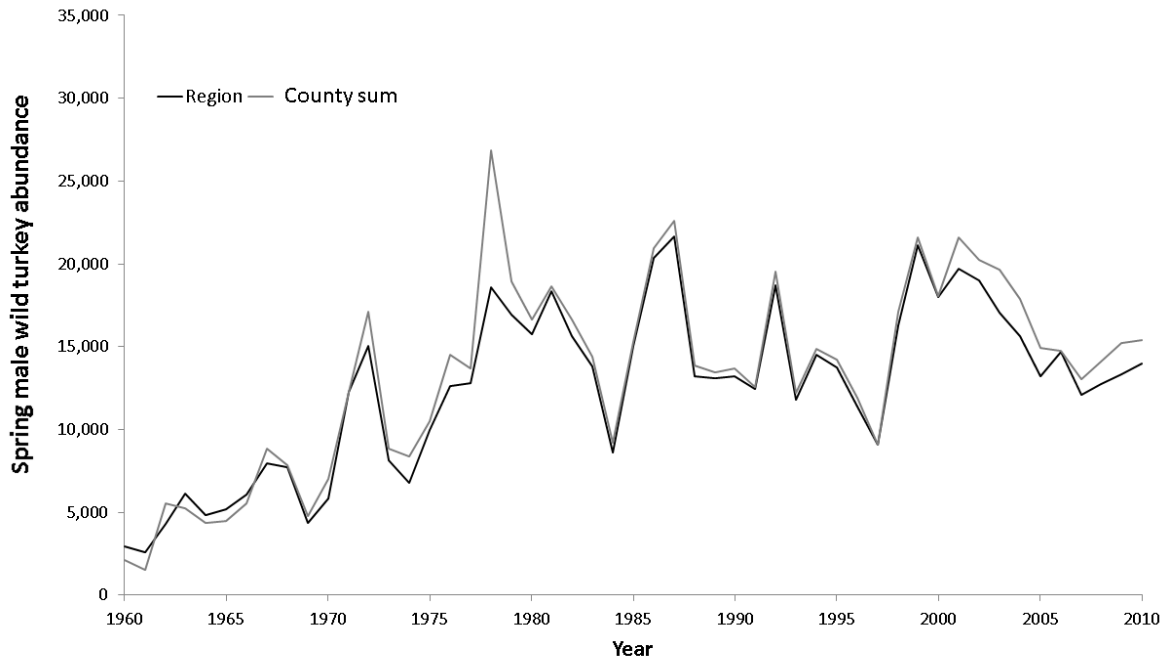
Figure 3.8. Spring male wild turkey abundance (1960–2010) in the Ozarks East turkey productivity region, Missouri, USA, based on a region-wide reconstruction (black line) and the aggregate of corresponding county reconstructions (grey line).

By 1980, a pattern emerged of higher abundances in the west and southwest counties within the region, with the eastern and northeastern counties having comparatively lower male wild turkey numbers (Figure 3.4). The number of male wild turkeys varied widely among counties, ranging from 60 to 805 in 1960 and from 600 to 3,063 in 2010 (Figure 3.4). Despite county-level variations in abundance, individual county abundances showed similar trends as the Ozarks East TPR overall, suggesting similar controlling factors regionally (Figure 3.9).
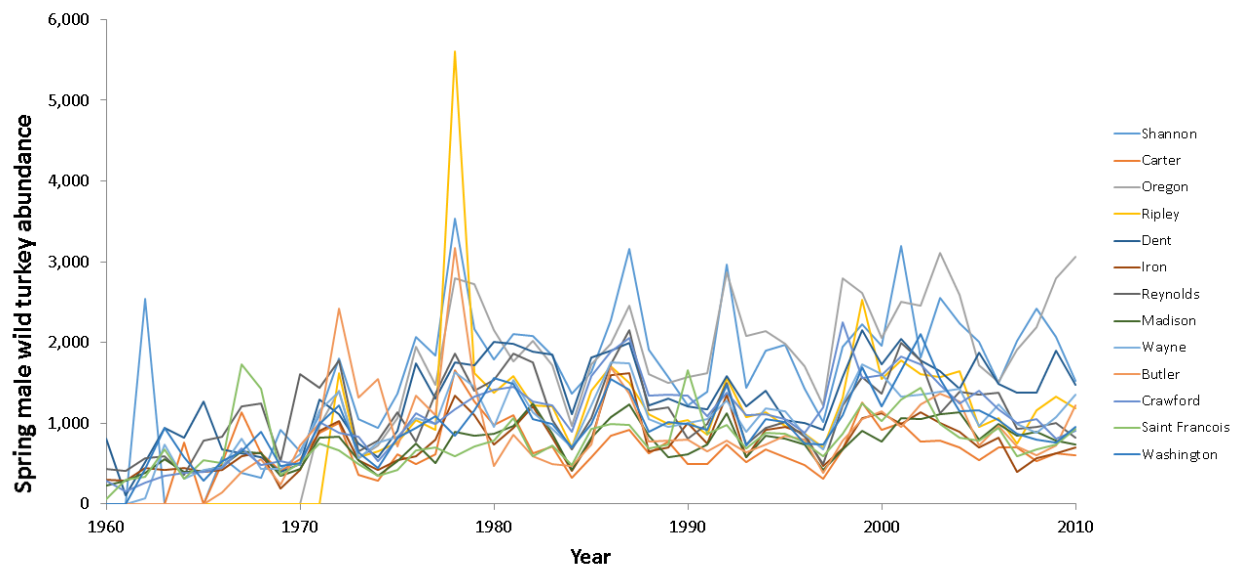
Figure 3.9. Male wild turkey abundance by county in the Ozarks East turkey productivity region, Missouri, USA (1960–2010). Estimates based on historical Horvitz–Thompson reconstruction.

3.3.2 **Hunter response**

Overall number of hunters in the Ozarks East TPR grew commensurate with the increase in regional turkey abundance (Pearson $r = 0.738$; Figure 3.10). The number of hunters regionally peaked in 1984 and remained relatively stable from 1980 to 2010 (Figure 3.10). At the county-wide level, the distance from St. Louis, Missouri, explained 19.9% of the variation in hunter density, while turkey density explained only 1.1% of the variation in hunter effort (Eq. 6). Hunter density tends to be higher in the northeastern corner of the region, while turkey density is highest in the west and southwest portions of the Ozarks East TPR (Figure 3.4 and Figure 3.5).
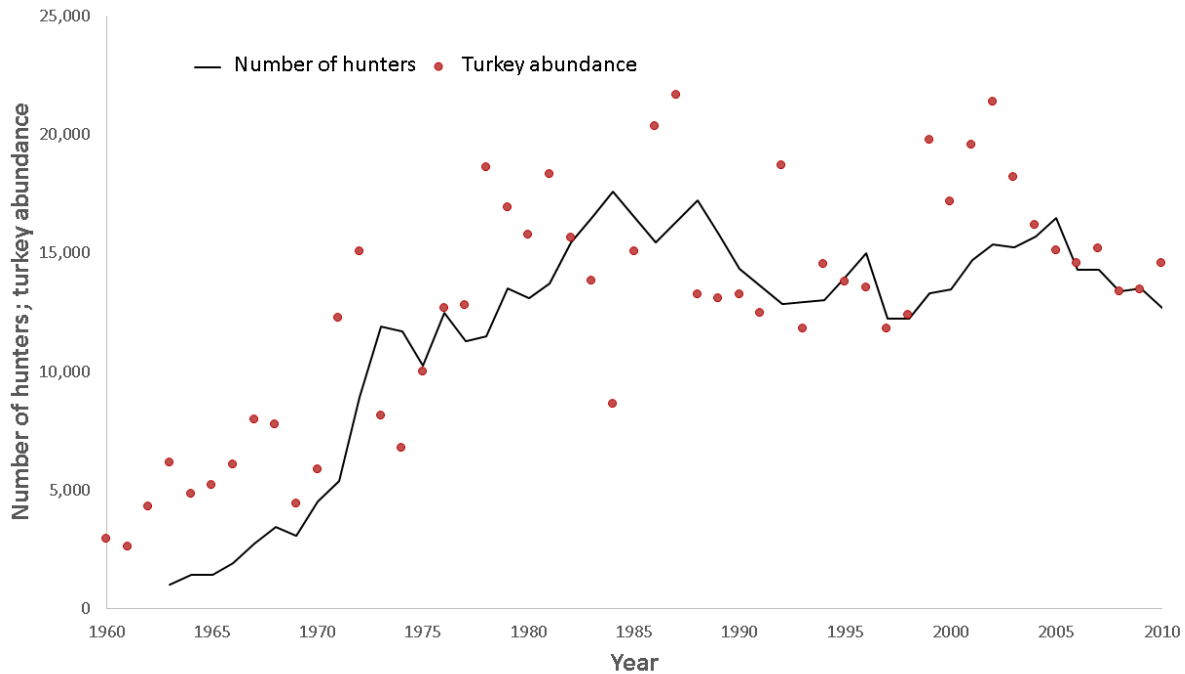
Figure 3.10. Spring male wild turkey abundance based on a region-wide historical reconstruction (dots), and number of hunters (line) in the Ozarks East turkey productivity region, Missouri, USA (1960–2010).

3.3.3 **Drivers of population dynamics**

The number of hunter trips in year i explained only 3.1% of the variation in annual abundance about the fitted logistic growth model in year $i + 1$, 1980–2010. Of the 24 climatic variables examined, only the number of bad weather days in April and total June precipitation in year i were significantly related to annual population fluctuations in year $i + 1$. A bivariate model with these 2 covariates explained 33.0% ($P = 0.003$) of the annual variation about the fitted logistic growth model during the period 1980–2010 (Table 3.3).

The total number of autumn hunter trips taken in year i explained only 4.1% of the variation in spring YARs in year $i + 1$. On the other hand, a bivariate model composed of total June precipitation and number of cold days in April in year i explained 63% ($P < 0.001$) of the

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annual variation in YAR in year $i+1$ (Table 3.3). None of the other climatic variables were found to be correlated with YARs.

3.4 DISCUSSION

In this 50-year reconstruction of male wild turkey abundance, we observed a logistic growth trend followed by high inter-annual abundance fluctuation around a stable carrying capacity ($\hat{K}$ = 15,260), which was not discernible with the shorter duration (1996–2010) reconstruction performed by Gast et al. (2013b). Our historical reconstruction illustrates the exponential growth phase commonly found in emergent populations, followed by oscillation about an equilibrium (*K*), characteristic of logistic population growth (Morrison 2009). The observed abundance fluctuations are consistent with Mosby (1967), who suggested that high inter-annual variation, up to ±50% of the stable mean, is common in wild turkey populations. This evidence of a stable population with high inter-annual variation in abundance lends support for consistent hunting regulations rather than altering regulations annually to accommodate short-term fluctuations in abundance. Furthermore, a 50-year time series of abundance estimates is a rare and powerful tool when conveying management strategies to stakeholders.

Expected hunter response can be an important consideration in managing the reintroduction of harvestable animals. Our analysis yielded 2 interesting insights into aspects of hunter behavior. First, hunters may not exert full harvest pressure in the first few years after reintroduction. Hunters in the Ozarks East TPR of Missouri did not exert their full hunting pressure on the newly reestablished turkey population until decades after reintroduction (Figure 3.10). This time lag in autumn hunter participation may have contributed to the healthy growth of the turkey population. This information may be useful for managers planning future

introductions or reintroductions of harvestable species.

Second, game abundance is not the only consideration in a hunter choice of where to hunt. Our analysis of hunter densities by county from 1960 to 2010 lends support for the hypothesis that hunters' choices were driven more by convenience than high turkey densities. This has important implications in setting game management goals. Maximizing hunter opportunity may be more important than high game densities to the hunting public.

There has been much concern about the impact of autumn hunting seasons on wild turkeys (Suchy et al. 1983, Little et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008). However, fluctuations in the male wild turkey population in the Ozarks East TPR seem to be controlled primarily by weather rather than autumn harvest. That autumn hunter effort was completely unrelated to deviance from the logistic growth model and YAR supports the idea that observed levels of autumn harvest have not noticeably impacted the population. The combined weather model explained a moderate portion of the variation in deviations from the logistic model. On the other hand, weather covariates explained a substantial portion of the inter-annual variation in the YAR; especially considering this realized recruitment metric includes an entire year of natural mortality and autumn harvest not modeled here. The much higher correlation with the recruitment metric rather than the abundance metric suggests that weather primarily affects recruitment, which in turn affects overall abundance. Based on this historical analysis, spring weather is at least a partial driver of inter-annual variation in wild turkey recruitment and, subsequently, in abundance fluctuations.

The negative effect of cold days in April on recruitment we observed is consistent with the available literature that suggests cold temperatures during the nesting season negatively

impacts recruitment (Vangilder and Kurzejeski 1995; Roberts and Porter 1998*a,b*). Our finding that the total precipitation in June is positively correlated with our recruitment index seems in direct opposition to much of the available literature, which says that cold and wet weather can cause poult mortality. Poult survival is usually only studied in a 1–4 weeks post-hatch, which generally occurs at the end of May and beginning of June. Healy and Nenno (1985), in a 2-year study of 21 hens, found that temperatures below 11° C in conjunction with rainfall are correlated with poult mortality in West Virginia, USA. Similarly, Lehman et al. (2008), in a study of 57 hens over 3 years, found that poult survival was negatively correlated with cold and wet weather in June in South Dakota, USA. Roberts and Porter (1998*a,b*), in a study of 26 hens over 3 years, found precipitation in May and early June to be negatively correlated with survival of wild turkey nests and poults in New York, USA. In Missouri, in a study of 69 hens over 7 years, the number of days of heavy precipitation in June were shown to be detrimental to poult survival, which the authors attributed, at least partially, to localized flooding (Vangilder and Kurzejeski 1995). Total June precipitation has not previously been shown to be detrimental to wild turkey populations; however, successful wild turkey nests were associated with fewer rainfall events in Mississippi, USA, from March to June (Lowrey et al. 2001). Conversely, drought conditions have been shown to negatively impact highly fecund, ground-nesting species (Bridges et al. 2001). It is possible that high levels of June precipitation may produce favorable foraging conditions over the summer and into the autumn (Beasom and Pattee 1980). Considering that water availability can adversely affect invertebrates (Huberty and Denno 2004) and acorn production (Sork et al. 1993), which are important wild turkey food sources (Korschgen 1967, Healy 1985), increased precipitation may increase food availability and positively impact survival.

Previous research has mainly focused on specific mechanisms, such as directly estimating poult survival, with short-duration, low-sample-size studies. These previous studies have been unable to evaluate the realized effect on the number of animals recruited into the harvestable population. Our 30-year data set allowed us to view long-term realized population metrics, offering a broader view of the driving factors of a population. Our results suggest that weather effects may extend beyond simply nest success and poult mortality in some systems. Results of this study and others highlight the variability in both the number and magnitude of factors potentially affecting wild turkey recruitment.

Our reconstruction study of wild turkeys is not without its limitations. Male animals, which we modeled here, are not typically the driving force of populations with a polygamous mating system (Vangilder 1992). However, extreme sexual disparities can cause depression in reproduction, thus affecting population dynamics (McGhee et al. 2008). Future studies of this population may benefit from focusing on the female portion of this population, specifically autumn female harvest rates, which we were unable to reconstruct because of data limitations.

Our analysis offers an initial assessment of the relationship between the dynamics of this wild turkey population and weather. Future research should include targeted long-term studies to determine the ecological mechanisms that relate spring weather to realized recruitment, into the harvestable population, in Missouri wild turkey populations. It may also be prudent to assess weather impacts at multiple spatial scales. Further studies should also consider predation and oak masting, 2 factors that have previously been shown to impact wild turkey populations which were not assessed here (Sork et al. 1993, Miller et al. 1998, Norman et al. 2001, Ryan et al. 2004, Fuller et al. 2013).

3.5 MANAGEMENT IMPLICATIONS

Following exponential growth for 20 years post-restoration, the current male wild turkey population in the Ozarks East TPR seems to be oscillating ($\hat{N}$ of 9,000–22,000) about a stable equilibrium of approximately 15,000 since 1980. Annual recruitment appears to be at least partially controlled by weather factors including the total amount of June precipitation and the number of cold days in April. Appropriately, harvest regulations for the Ozarks East TPR wild turkey population have remained unchanged in response to short-term population fluctuations. The result has been relatively static harvest regulations that the hunting population can rely upon as the turkey population fluctuates in response to short-term environmental perturbations. Although our results indicate that current levels of autumn and spring harvest had little effect on wild turkey abundance, managers should monitor harvest rates to ensure that they do not exceed thresholds that may negatively impact population growth and abundance.

Chapter 4. EVALUATION OF MODELS TO PROJECT THE ABUNDANCE OF HARVESTED SPECIES.

Accurate estimates of abundance are necessary for the effective management of harvested wildlife (Roseberry 1979, Rabe et al. 2002, Connelly et al. 2005, Hewitt 2011, Alisauskas et al. 2014). There are several established methods to estimate the abundance of a wildlife population including mark-recapture, mark-harvest, line transect, distance methods and cohort reconstructions (Seber 1982, Skalski et al. 2005). Integrated population models which reconstruct abundance based on age-at-harvest information, such as statistical population reconstruction (SPR), are among the most cost efficient ways to produce annual abundance estimates over large spatial scales and long time periods (Gove et al. 2002, Conn et al. 2008, Skalski et al. 2012b, Gast et al. 2013a, Gast et al. 2013k). All methods for estimating abundance are retrospective, estimating abundance in the past or current year. The primary concern of game managers is how many animals will be available for harvest in the subsequent year(s) (Eberhardt 1987).

There are several benefits to obtaining accurate estimates of future abundance. Most game populations are managed conservatively due to uncertainty about the abundance state of the population (Connelly et al. 2005). Increased certainty about the population state allows for increased recreational opportunity and economic gain (Connelly et al. 2005, Hewitt 2011). More importantly, a clear idea of past, present and future abundance will decrease the probability of management mistakes and make it easier for managers to convey management objectives to stakeholders (Freddy et al. 2004, Lukacs et al. 2011). Clear communication and consistent

quality management decisions will increase trust and cooperation with the growing list of stakeholder groups with which wildlife managers are faced (Murphy and Noon 1991, Rabe et al. 2002, Hewitt 2011, Clawson et al. 2015).

Accurately projecting the future abundance of a harvested wildlife population, even a single year into the future, is difficult (Eberhardt 1987, Fewster et al. 2000, Krebs 2002). Future abundance depends primarily on three main demographic factors: current abundance, realized recruitment (including both fecundity and survival to a harvestable age), and adult mortality (both natural and harvest). Both fisheries (Gallucci et al. 1996, Quinn and Deriso 1999, Hilborn 2012) and waterfowl managers (Byron and Johnson 1995, Williams and Johnson 1995, Johnson and Williams 1999) spend large amounts of money collecting data on these three aspects of their managed populations annually, in order to produce reliable future abundance estimates. Fisheries stock assessment models include data from catch-effort surveys, harvest data, and possible trawl and hydroacoustic surveys, as well as long studied stock-recruitment relationships (Gallucci et al. 1996, Quinn and Deriso 1999, Francis et al. 2005, Hilborn 2012). Waterfowl managers collect breeding pond surveys, nest count data, as well as harvest and survival rate estimates from large scale banding programs (Hawkins et al. 1984, Williams and Johnson 1995, Johnson et al. 2002). Even with several annual data sources, waterfowl managers project abundance only a single year into the future, reevaluating model structure annually (Johnson et al. 2002). In contrast, most non-migratory game populations do not support a commercial harvest and are not federally managed according to international treaties, so resources to collect detailed demographic data annually are often limited.

The amount of demographic data collected on traditional game populations varies greatly

depending on the state and species managed (Rupp et al. 2000, Rabe et al. 2002, Freddy et al. 2004, Lukacs et al. 2011). Harvest data are usually collected, including estimates of total harvest and age composition, but are rarely used to estimate abundance (Rupp et al. 2000, Beston and Mace 2012). More often, traditional game populations are monitored based on indices to abundance such as partial counts, catch per-unit-effort and other harvest based indices, as well as browse indices or pellet counts. Theses indices to abundance are generally used to infer population trend. Additionally, some management agencies simply manage to indices, balancing hunter and land owner satisfaction or reducing animal vehicle collisions (Hewitt 2011). This index-based management strategy is generally augmented with occasional field studies to estimate population parameters of concern (White and Lubow 2002, Bender et al. 2004). The occasional demographic inquiries are used to collect information on survival, harvest rate, abundance or some aspect of recruitment (e.g., nest success, pregnancy rates or neonate survival) (Kurzejeski et al. 1987, Diefenbach et al. 2000, Gilbert and Raedeke 2004, Delgiudice et al. 2006, Fuller et al. 2013). Alternatively, managers who use SPR have estimates of annual abundance, survival, harvest rate and annual realized recruitment in addition to age composition and hunter effort data (Gove et al. 2002, Skalski et al. 2011, Skalski et al. 2012b). However, recruitment from SPR is not associated with the previous breeding abundance so it is not as useful for projection as the stock-recruit models used by fisheries managers or the annual nest counts collected by waterfowl managers.

The purpose of this paper is to evaluate simple methods of projecting the abundance of wild populations, from year t to year t+1, in ways consistent with current levels of demographic data. We will also examine whether additional demographic data on survival, recruitment and

harvest improve the accuracy of annual population projections. Specifically, whether information from SPR can be used to improve annual abundance projections.

4.1 METHODS

4.1.1 Projecting abundance without additional demographic data

Data sets of annual abundance were obtained from the Global Population Dynamics Database (GPDD) (NERC 2010). This database includes more than 4500 time series of abundance and indices to abundance from more than 1800 animal species (Inchausti and Halley 2001). Using data from the GPDD allowed us to evaluate alternative projection models on a large number of populations. We established several criteria for inclusion of datasets in this effort. Only data from harvestable birds and mammals were included. The demographic data sets had to consist of actual abundance estimates or direct abundance counts, indices to abundance such as tracks, scat or pelt counts were not included in this analysis. The data sets had to include a minimum of 11 years of consecutive abundance estimates because some of the projection models evaluated required a minimum of ten years of data. Populations that exhibited a clear logistic growth pattern were not included. These types of demographic patterns have been previously well studied (Alpizar-Jara et al. 2001, Eberhardt 2002, Krebs 2002, Eberhardt and Breiwick 2012). Based on our criteria the GPDD yielded 71 populations appropriate for our analysis. We then divided these 71 populations into four classes based on two categories, taxa (bird vs mammal) and trend (clear trend vs no clear trend) (Table 4.1, Figure 4.1-4). The distinction between taxa differentiated, to a large degree, intrinsically (Hewitt 2011) and extrinsically (Fleming and Porter 2007) controlled populations. The distinction in trend was made because we expected projection models to perform differently when applied to populations

with and without a clear temporal trend. Furthermore, trend and taxa classifications were not

independent of one another (Pearson chi sq, $P < 0.001$), indicating they should be evaluated

separately.

Table 4.1. Median of the absolute deviance relative to the observed abundance of projections
made with models to project abundance without additional demographic data, averaged across
populations within taxa and trend class (Mammal, Bird, Trend, No Trend). Projected populations
come from the Global Population Dynamics Database. Models are ranked based on overall
performance without regard for trend or taxa (Overall).

| Model | Absolute relative deviation | | | | | Overall Rank |
	Mammal, Trend	Bird, Trend	Mammal, No Trend	Bird, No Trend	Overall	
M_0	0.112	0.168	0.183	0.343	0.221	1
$M_{\lambda-Y}$	0.100	0.144	0.203	0.371	0.232	2
$M_{\lambda\ NL-Y}$	0.117	0.156	0.193	0.370	0.235	3
$M_{\lambda\ NL-5}$	0.108	0.191	0.222	0.381	0.245	4
$M_{\lambda-5}$	0.106	0.182	0.229	0.396	0.252	5
M_{A-3}	0.140	0.223	0.209	0.410	0.264	6
$M_{\lambda-3}$	0.117	0.189	0.221	0.445	0.272	7
$M_{\lambda\ NL-3}$	0.122	0.195	0.222	0.451	0.276	8
M_{REG-Y}	0.149	0.228	0.282	0.445	0.300	9
M_{REG-5}	0.128	0.215	0.238	0.503	0.303	10
M_{A-5}	0.169	0.282	0.246	0.467	0.306	11
M_{REG-3}	0.133	0.312	0.233	0.539	0.320	12
$M_{\lambda-2}$	0.153	0.227	0.255	0.544	0.331	13
M_{A-Y}	0.330	0.469	0.258	0.457	0.361	14
Projections	406	41	370	491	1308	
Populations	27	5	17	22	71	
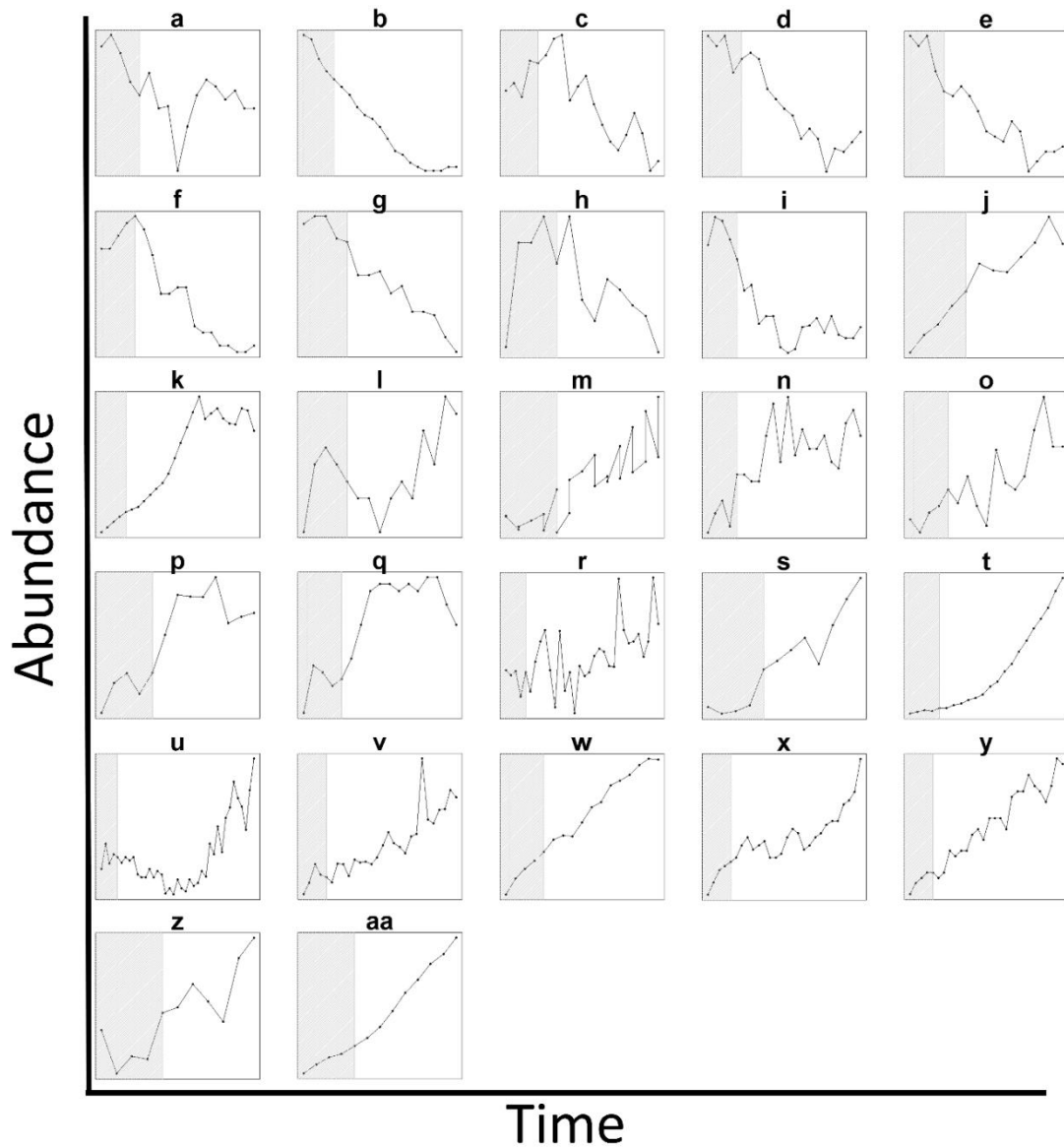
Figure 4.1. Mammal populations from the Global Population Dynamics Database that exhibit a clear trend, used to project abundance with no additional demographic data. Species are indicated by letter as follows a) Spotted dolphin (*Stenella attenuata*), b) Spotted dolphin, c) Bobcat (*Lynx rufus*), d) Harbour seal (*Phoca vitulina*),e) Harbour seal, f) Harbour seal, g) Grey wolf (*Canis lupus*), h) Grey wolf, i) Mule deer (*Odocoileus hemionus*), j) Cape buffalo (*Syncerus caffer*), k) Blue Wildebeest (*Connochaetes taurinus*), l) Harbour seal, m) Sea otter (*Enhydra lutris*), n) Grey wolf, o) Eurasian lynx (*Lynx lynx*), p) Eurasian lynx, q) Lion (*Panthera leo*), r) Arctic fox (*Alopex lagopus*), s) Sea otter, t) Muskox (*Ovibos moschatus*), u) Grizzly Bear (*Ursus arctos*), v) Florida manatee (*Trichechus manatus*), w) Northern elephant seal (*Mirounga angustirostris*), x) White rhino (*Ceratotherium simum*), y) Amur tiger (*Panthera tigris*), z) Mountain goat (*Oreamnos americanus*), aa) Père David's deer (*Elaphurus davidianus*).
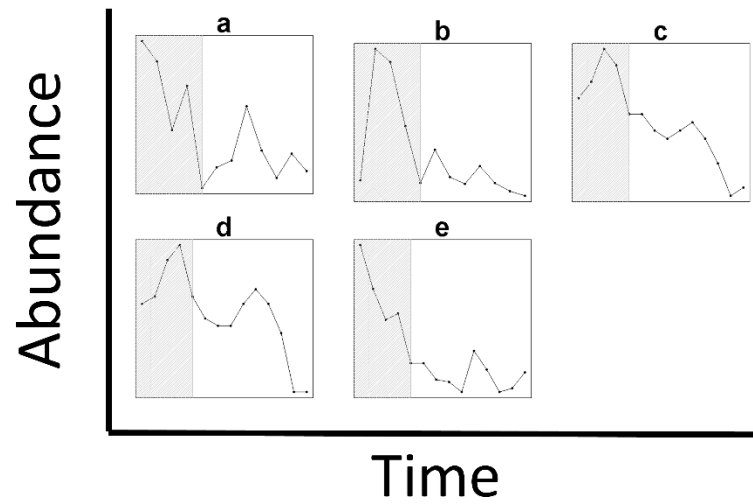
Figure 4.2. Bird populations from the Global Population Dynamics Database that exhibit a clear trend, used to project abundance with no additional demographic data. Species are indicated by letter as follows a) Blue grouse (*Dendragapus obscurus*), b) Blue grouse, c) Wood grouse (*Tetrao urogallus*), d) Black grouse (*Tetrao tetrix*), e) Grey partridge (*Perdix perdix*).
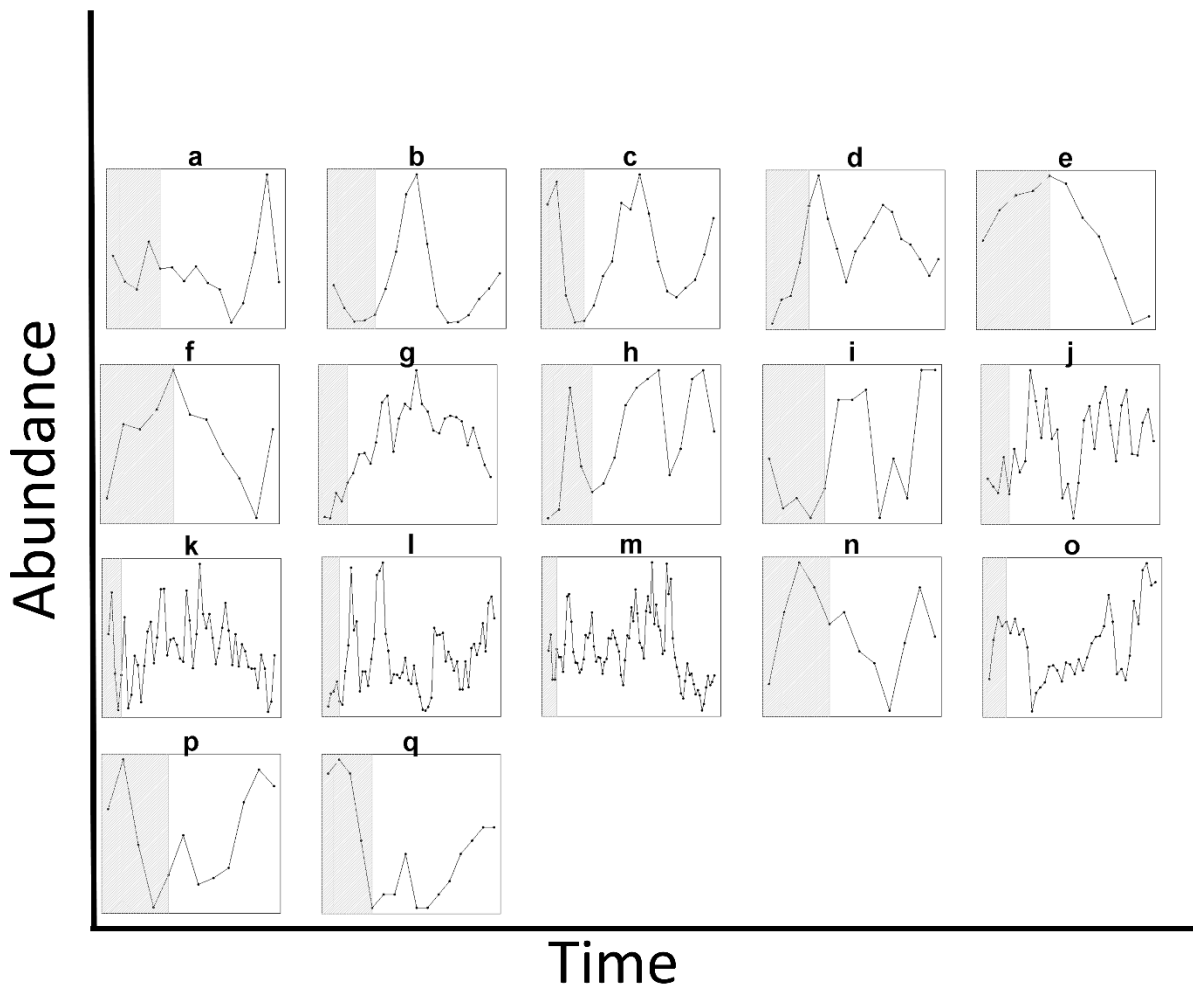
Figure 4.3. Mammal populations from the Global Population Dynamics Database that exhibit no clear trend, used to project abundance with no additional demographic data. Species are indicated by letter as follows a) San Joaquin kit fox (*Vulpes macrotis*), b) Canadian lynx (*Lynx canadensis*), c) Canadian lynx, d) Chamois (*Rupicapra rupicapra*), e) Greater kudu (*Tragelaphus strepsiceros*), f) Greater kudu, g) Lion, h) Grey wolf, i) African wild dog (*Lycaon pictus*), j) American marten (*Martes Americana*), k) Fox (*Vulpes spp.*), Wolverine (*Gulo gulo*), m) Wolverine , n) Dall Sheep (*Ovis dalli*), o) Chamois , p) Brown bear , q) Black rhinoceros (*Diceros bicornis*).
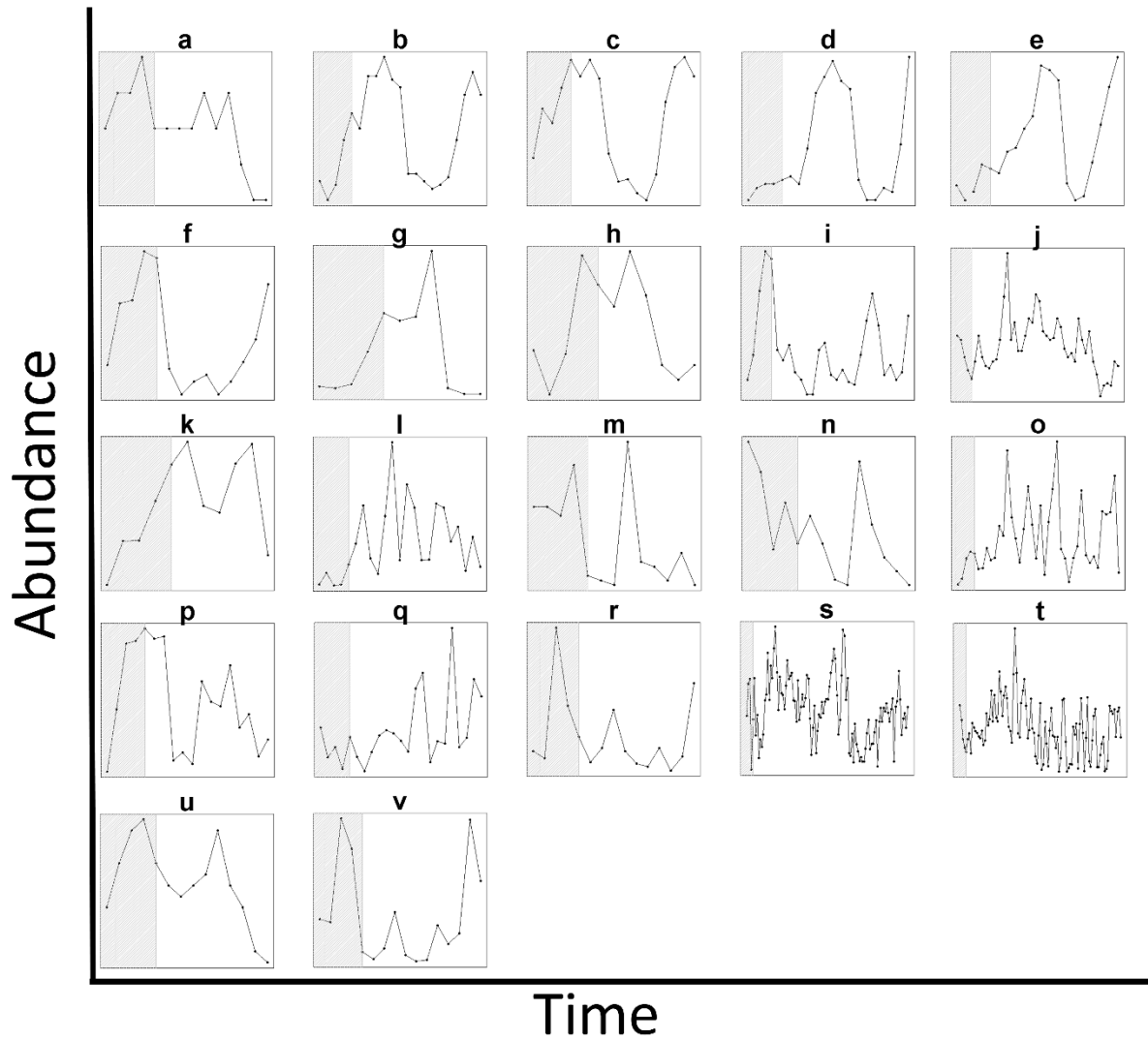
Figure 4.4. Bird populations from the Global Population Dynamics Database that exhibit no clear trend, used to project abundance with no additional demographic data. Species are indicated by letter as follows a) Willow grouse (*Lagopus lagopus*), b) Rock ptarmigan(*Lagopus mutus*), c) Rock ptarmigan, d) Rock ptarmigan, e) Rock ptarmigan, f) Rock ptarmigan, g) Rock ptarmigan, h) Ruffed grouse (*Bonasa umbellus*), i) Hazel grouse (*Bonasa bonasia*), j) Bobwhite (*Colinus virginianus*), k) Grey partridge, l) California quail (*Callipepla californica*), m) Willow grouse, n) Red-legged partridge, o) Black grouse, p) Northern bobwhite, q) Rock ptarmigan, r) Wood grouse, s) Red grouse (*Lagopus lagopus*), t) Red grouse, u) Hazel grouse, v) Wood grouse.

The simplest projection model assumed abundance (N) in year t+1 equals the abundance observed in the current year (t) i.e.,

$$M_0: N_{t+1} = N_t \ .$$

Thus no change in abundance is projected from the final year of observed data to the projected year. This was considered the base model(M_0), to which all population models were compared. The next set of projection models examined moving averages(M_A). Moving averages were taken across the most recent 3, 5 or all years of available data, constituting models

$$M_{A-3} : N_{t+1} = \frac{N_t + N_{t-1} + N_{t-2}}{3} ,$$

$$M_{A-5} : N_{t+1} = \frac{N_t + N_{t-1} + N_{t-2} + N_{t-3} + N_{t-4}}{5} ,$$

$$M_{A-Y} : N_{t+1} = \frac{\sum_{i=1}^{i=t} N_i}{t} \ .$$

Note the base model (M_0) is a moving average with a window of one year. The next three projection models are based on the regression (M_{REG}) of abundance versus time (i), using the linear model

$$N_i = \alpha + \beta * i$$

using the most current 3, 5, or all available years of data. Population projections were then

$$M_{REG-3} : N_{t+1} = \hat{\alpha} + \hat{\beta} * (t+1), (\hat{\alpha}, \hat{\beta} \rightarrow t, \dots t-2),$$

$$M_{REG-5} : N_{t+1} = \hat{\alpha} + \hat{\beta} * (t+1), (\hat{\alpha}, \hat{\beta} \rightarrow t, \dots t-4),$$

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$$M_{REG-Y} : N_{t+1} = \hat{\alpha} + \hat{\beta} * (t + 1), (\hat{\alpha}, \hat{\beta} \rightarrow t, \dots 1).$$

These first seven projection models ignore the fact that the time series of abundance arises from the biological processes of birth and death.

Our simplest demographic models condense the birth and death process into a single parameter (λ), the finite population growth rate. Seven projection models were examined based on estimates of the finite rate of population growth (λ). The simplest model estimated the population growth rate (λ) based on the previous two years of abundance such that,

$$M_{\lambda-2}: \quad N_{t+1} = N_t * \left(\frac{N_t}{N_{t-1}} \right) = N_t * \hat{\lambda} .$$

Alternatively, λ was estimated by regressing the abundance in year i+1 against the abundance in year i using the linear model

$$N_{i+1} = \lambda * N_i,$$

for varying numbers of years 3, 5, or all available years. Population projections were then

$$M_{\lambda-3}: N_{t+1} = N_t * \hat{\lambda}, (\hat{\lambda} \rightarrow t, \dots t - 2) ,$$
$$M_{\lambda-5}: N_{t+1} = N_t * \hat{\lambda}, (\hat{\lambda} \rightarrow t, \dots t - 4),$$
$$M_{\lambda-Y}: N_{t+1} = N_t * \hat{\lambda}, (\hat{\lambda} \rightarrow t, \dots 1).$$

The potential drawback of this model is that if the observed abundances (N_i) are measured with error, then the slope term (λ) would be negatively biased. To address this potential bias, the population growth rate (λ) was also estimated via non-linear regression of the form

$$\frac{N_i}{N_I} = \lambda^{(i-I)},$$

using the most current 3, 5, and all years of data. The resulting projection models w

$$M_{\lambda\ NL-3}: N_{t+1} = N_t * \hat{\lambda}, (\hat{\lambda} \rightarrow t, \dots t - 2),$$

$$M_{\lambda\ NL-5}: N_{t+1} = N_t * \hat{\lambda}, (\hat{\lambda} \rightarrow t, \dots t - 4),$$

$$M_{\lambda\ NL-Y}: N_{t+1} = N_t * \hat{\lambda}, (\hat{\lambda} \rightarrow t, \dots 1) .$$

The final model considered was an auto regressive integrated moving average (ARIMA) model,
which selects a random walk model with appropriate degrees of autocorrelation and drift, that
best fit the data (M_{ARIMA}) (Box and Jenkins 1970). The ARIMA model was evaluated with a
minimum of 10 years of historical data. The ARIMA model was fit using the auto.arima function
in the R package forecast, with predictions made using the forecast function from the same R
package (www.r-project.org)

All abundance projections were a single year in advance. Projections were made for years
with direct observations only. In order to draw direct comparisons between projection models
requiring different levels of historical abundance, the years of projected abundance were
consistent across all models. Initially, all models began projections starting with the 11th year of
abundance, due to the 10-year data requirement for the ARIMA model. After the ARIMA model
was determined to be ineffective, the model evaluation was repeated, leaving out the ARIMA
model and using a minimum of 6 years of historical data. (i.e., the next highest data requirement
was 5 years for models $M_{A-5}, M_{REG-5}, M_{\lambda-5}, M_{\lambda\ NL-5}$)

For each projection, the absolute value of the relative deviance (RD) between the observed and projected abundance was recorded:

$$RD = \frac{\left|N_{projected} - N_{observed}\right|}{N_{observed}}$$

I used absolute RD in characterizing model performance because interest was in the percent error in the projections regardless of the positive or negative aspect of the error. I chose median RD for each model per population was chosen as the measure of precision because of the skewed distribution of RDs within each population. For each demographic class (Table 4.1, Figure 4.1-4), the alternative projection models were ranked based on the weighted average of median RD from each biological population within the class; with weights based on the number of projections made for each population.

4.1.2 **Projecting abundance with demographic data**

Output from statistical population reconstruction was also used to project abundance one year in advance. Nine statistical population reconstructions were available for examination; including 6 published and 3 unpublished population reconstructions (Table 4.2). With only 9 total data sets available, it was impractical to divide them into taxa and trend classes (Figure 4.5).

Table 4.2. Descriptions of the nine statistical population reconstruction data sets used to project time series of abundance with additional demographic data.

Taxa	Years of Abundance	Years of Projection	Sex	Number of Survival Parameters	Citation
Mule Deer, WA	24	19	Female	1	Skalski et al. (2007)
Mule Deer, CA	24	19	both	3	Unpublished
Cougar, OR	21	16	both	2	Unpublished
Elk, MI	18	13	both	1	Gast et al. (2013a)
Elk, ID	6	1	Female	1	Gove et al. (2002)
Marten, MI	12	7	both	9	Skalski et al. (2011)
Fisher, MI	8	3	both	10	Unpublished
Turkey, MO	15	10	Male	1	Gast et al. (2013k)
Greater sage-grouse, OR	14	9	Both	2	Broms et al. (2010)
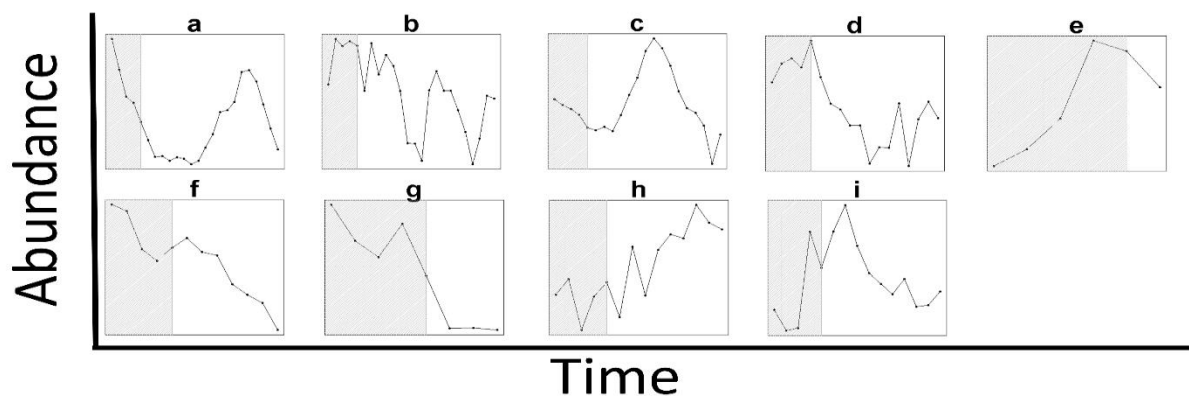
Figure 4.5. Time series of abundance from statistical population reconstructions of both birds and mammals, used to project abundance with additional demographic data. Species are indicated by letter as follows a) Mule Deer (*Odocoileus hemionus*), b) Mule Deer, c) Cougar (*Puma concolor*), d) Elk (*Cervus elaphus*), e) Elk, f) Fisher (*Martes pannanti*), g) Marten (*Martes americana*), h) Greater Sage-Grouse (*Centrocerus urophasians*), i) Eastern Wild Turkey (*Meleagris gallapovo*).

I evaluated 11 models which project future abundance using varying degrees of demographic and harvest data. The first model incorporates only harvest data, accounting for the annual known removals from the pre-harvest abundance estimates of the first year. The population growth rate (λ) was estimated using the following linear regression equation

$$N_{i+1} = \lambda * (N_i - H_i),$$

Projections were then of the form

$$MD_{reg-H}: N_{t+1} = \hat{\lambda} * (N_t - H_t)(\hat{\lambda} \rightarrow t, \dots 1)$$

In the remaining projection models, population growth rate (λ) is reparameterized into its two primary components, realized recruitment (R) and survival (S) (Skalski et al. 2005). The survival parameter was fixed at the estimate(s) from the associated statistical population reconstruction ($\dot{S}$). Five of the nine statistical population reconstructions used for this analysis had some degree of age-specific survival, in these cases $\dot{S}$ was fixed at the average of the age-specific survival estimates for non-age-specific projection. Given the re-parameterization and the independent estimates of survival, the remaining models estimate only the realized recruitment rate parameter (R). Realized recruitment rate (R) is a parameter that combines the per-capita fecundity rate (f), with the probability those neonates survive (S_0) to be recruited into the harvestable population (Skalski et al. 2005).

Non-age-specific projections for the models that estimated realized recruitment rate (R) were made using the equation $N_{t+1} = N_t * \hat{R} + N_t * \dot{S}$. Additionally, in order to take advantage of the age-specific survival and abundance estimates provided by SPR, models described in this

section were also projected using a Leslie matrix; assuming recruitment rate to be constant across

age classes (Leslie 1945), where

$$N_{t+1} = 1'M_R \overrightarrow{N_t},$$

$$
M_R =
\begin{bmatrix}
R & R & R & \cdots & R \\
S_0 & 0 & 0 & & 0 \\
& S_1 & 0 & & 0 \\
& & & & \\
0 & 0 & 0 & \cdots & S_A
\end{bmatrix}
\qquad
\overrightarrow{N_t} =
\begin{bmatrix}
N_t^1 - H_t^1 \\
N_t^2 - H_t^2 \\
N_t^3 - H_t^3 \\
\vdots \\
N_t^A - H_t^A
\end{bmatrix}
$$

The Leslie matrix method for age-specific projection is analogous to the non-age-specific

projection method for populations without age-specific survival.

The first eight models to estimate the realized recruitment rate (R) do so based on initial

age class abundance estimates from SPR (N^r). The first six of which (MD_R) estimated the

realized recruitment rate (R) as the ratio of the sum of the annual recruitment abundance (N_t^r) to

the sum of the corresponding previous year's abundance(s) (N_{t-1}), with 2, 3 or all years of data

$$\hat{R}_{MD_{R-2}} = \frac{N_t^r}{N_{t-1}}.$$

$$\hat{R}_{MD_{R-3}} = \frac{N_t^r + N_{t-1}^r + N_{t-2}^r}{N_{t-1} + N_{t-2} + N_{t-3}}.$$

$$\hat{R}_{MD_{R-Y}} = \frac{\sum_{i=2}^{t} N_i^r}{\sum_{i=2}^{t} N_{i-1}}.$$

Projections were then of the form

$$MD_{R-2}: N_{t+1} = N_t * \hat{R}_{MD_{R-2}} + (N_t - H_t) * \dot{S}$$

$$MD_{R-3}: N_{t+1} = N_t * \hat{R}_{MD_{R-3}} + (N_t - H_t) * \dot{S}$$

$$MD_{R-y}: N_{t+1} = N_t * \hat{R}_{MD_{R-Y}} + (N_t - H_t) * \dot{S}$$

for non-age-specific projection and

$$MD_{R-2}Les: N_{t+1} = 1' \boldsymbol{M}_{\hat{R}_{MD_{R-2}}} \overrightarrow{\boldsymbol{N_t}}$$

$$MD_{R-3}Les: N_{t+1} = 1' \boldsymbol{M}_{\hat{R}_{MD_{R-3}}} \overrightarrow{\boldsymbol{N_t}}$$

$$MD_{R-y}Les: N_{t+1} = 1' \boldsymbol{M}_{\hat{R}_{MD_{R-Y}}} \overrightarrow{\boldsymbol{N_t}}$$

for projections with age-specific parameterizations. In age-specific projections, each entry in the first row of the projection matrix M, is equal to the estimated realized recruitment rate for each model respectively. Model MD_{reg} estimated the average realized recruitment rate across all available years using the linear regression equation

$$N_{i+1}^r = N_i * R_{MD_{REG-R-Y}},$$

where N_{i+1}^r is the initial age class abundance estimated from SPR in year i+1 and N_i is the total abundance estimated from SPR in year i. Projections were then of the form

$$MD_{REG-R-Y}: N_{t+1} = N_t * \hat{R}_{MD_{REG-R-Y}} + (N_t - H_t) * \dot{S}$$

for non-age-specific projection and

$$MD_{REG-R-Y}Les: N_{t+1} = 1'M_{\hat{R}_{MD_{REG-R-Y}}}\overrightarrow{N_t}$$

for projections with age-specific parameterizations. In age-specific projections each entry in the

first row of the projection matrix M, is equal to the estimated realized recruitment rate for each

model respectively. The final model (MD_{REGS}) does not include recruitment class abundance

data, instead the realized recruitment rate parameter was estimated using the following

regression equation

$$N_{i+1} = N_i * R_{MD_{REGS-R-H-Y}} + (N_i - H_i) * \dot{S}.$$

Projections were then of the form

$$MD_{REGS-R-H-Y}: N_{t+1} = N_t * \hat{R}_{MD_{REGS-R-H-Y}} + (N_t - H_t) * \dot{S}$$

for non-age-specific projection and

$$MD_{REGS-R-H-Y}Les: N_{t+1} = 1'M_{\hat{R}_{MDREGS-R-H-Y}}\overrightarrow{N_t}$$

for projections with age-specific parameterizations. In age-specific projections each entry in the

first row of the projection matrix M, is equal to the estimated realized recruitment rate for this

model. These eleven projections which include additional demographic and harvest information

were then compared to the top 5 most accurate models for projecting time series of abundance

without demographic data based on the RD metric described previously. A minimum of 6 years

(5 years available to the model and one to compare to the projection made by the model) of data

were used to evaluate the top 5 previous projection models and 11 new methods based on demographic output from SPR.

4.2 RESULTS

4.2.1 Projecting abundance with only annual trend data

A minimum of 10 years of historical data was recommended with the use of annual ARIMA models (M_{ARIMA}) (Brockwell and Davis 1991). The M_{ARIMA} model did not outperform the base model (M_0) and was ranked 6$^{\text{th}}$ overall. Consequently, the ARIMA model was eliminated from consideration, and all remaining models were refit using a minimum of 5 years of historical data. The reanalysis increased the total number of annual projections by 37.3% (i.e., 355 additional projections).

When the only demographic data that exist are annual abundance values, the simple base model (M_0) that projects abundance next year equal to abundance in the previous year performed best overall (Table 4.1). Populations which exhibited a clear trend in abundance were projected more accurately than those with no clear trend (Table 4.3). Model $M_{\lambda-Y}$ produced the lowest relative error for both mammal and bird populations with a clear trend ($RD_{\text{mammal-trend}} = 0.100$; $RD_{\text{bird-trend}} = 0.144$) (Table 4.3). The base model (M_0) was only slightly less accurate than model $M_{\lambda-Y}$ when population trends existed (Table 4.3). The top model to project population abundance when no clear tend existed for either bird or mammal populations was the base model (M_0) ($RD_{\text{mammal-trend}} = 0.184$; $RD_{\text{bird-trend}} = 0.343$) (Table 4.3). Projections which incorporated

estimates of λ were the second and third ranked models when annual trends did not exist (Table 4.3).

4.2.2 **Projecting abundance when supplemental demographic data exists**

In the situation where supplemental information on harvest, recruitment, and survival exist, the base model (M_0) ranked fifth across the nine populations analyzed (Figure 4.5, Table 4.4). The most accurate projections were made using a simple demographic model that took into account known harvest and a localized estimate of recruitment (i.e., three-year average), model MD_{R-3}. The second and third ranked models were based on age-structured Leslie matrix models (i.e., MD_{R-3L} and MD_{R-2L}). The average size of the relative error was approximately 10% (i.e., 9.6%−10.6%), with the mule deer population in California being the exception (i.e., 16.3%− 21.7%) (Table 4.4). Here again, however, the accuracy of the base model (M_0), on average, was not appreciably lower than the more data-demanding models that adjusted for harvest and accounted for recruitment and/or survival (i.e., $RD = 11.1\%$). It should be noted, however, that the nine populations examined with complete demographic data (Figure 4.5) resembled more closely trended vs. non-trended populations. Our initial analyses of 71 populations indicated trended populations are more accurately projected than non-trended populations (Table 4.1).

Table 4.3. Median of the absolute deviance relative to the observed abundance of projections made with models to project abundance without additional demographic data, averaged across populations within taxa and trend class (Mammal, Bird, Trend, No Trend). Projected populations come from the Global Population Dynamics Database. Top 5 models within each taxa and trend class (Mammal Trend, Bird Trend, Mammal No Trend, Bird No Trend) are shown.

Rank	Mammal, Trend		Bird, Trend		Mammal, No Trend		Bird, No Trend	
1	$M_{\lambda-Y}$	0.100	$M_{\lambda-Y}$	0.144	M_0	0.183	M_0	0.343
2	$M_{\lambda-5}$	0.106	$M_{\lambda\,NL-Y}$	0.156	$M_{\lambda\,NL-Y}$	0.193	$M_{\lambda\,NL-Y}$	0.370
3	$M_{\lambda\,NL-5}$	0.108	M_0	0.168	$M_{\lambda-Y}$	0.203	$M_{\lambda-Y}$	0.371
4	M_0	0.112	$M_{\lambda-5}$	0.182	M_{A-3}	0.209	$M_{\lambda\,NL-5}$	0.381
5	$M_{\lambda-3}$	0.117	$M_{\lambda-3}$	0.189	$M_{\lambda-3}$	0.221	$M_{\lambda-5}$	0.396

Table 4.4. Median of the absolute deviance relative to the observed abundance of projections made with models to project abundance with additional demographic data. Projected populations come from available statistical population reconstructions. Models are ranked based on overall performance averaged across all populations (Overall). *Les* indicates the model was projected using a Leslie matrix.

Model	Mule Deer, WA	Mule Deer, CA	Cougar, OR	Elk, MI	Elk, ID	Marten, MI	Fisher, MI	Turkey, MO	Greater Sage-Grouse, OR	Overall	Rank
MD_{R-3}	0.071	0.217	0.036	0.046	0.087	0.071	0.106	0.100	0.091	0.096	1
$MD_{R-3}Les$	0.076	0.177	0.076	0.046	0.083	0.089	0.130	0.100	0.084	0.098	2
$MD_{R-2}Les$	0.068	0.163	0.069	0.112	0.027	0.117	0.027	0.124	0.133	0.106	3
MD_{R-Y}	0.134	0.228	0.039	0.060	0.090	0.070	0.076	0.088	0.091	0.111	4
M_0	0.070	0.267	0.067	0.074	0.035	0.094	0.008	0.086	0.089	0.111	5
$M_{\lambda-3}$	0.079	0.234	0.054	0.077	0.066	0.120	0.112	0.098	0.096	0.112	6
MD_{R-2}	0.067	0.215	0.043	0.112	0.031	0.106	0.052	0.124	0.144	0.113	7
$MD_{REG-R-Y}$	0.143	0.236	0.040	0.063	0.088	0.065	0.080	0.097	0.095	0.116	8
$MD_{REGS-R-H-Y}$	0.138	0.254	0.045	0.066	0.057	0.047	0.111	0.090	0.079	0.117	9
$M_{\lambda-5}$	0.092	0.273	0.056	0.103	0.063	0.064	0.074	0.089	0.073	0.118	10
$M_{\lambda\,NL-Y}$	0.123	0.245	0.077	0.088	0.067	0.040	0.058	0.096	0.076	0.119	11
$M_{\lambda-Y}$	0.123	0.260	0.071	0.100	0.063	0.041	0.074	0.086	0.079	0.122	12
$MD_{REGS-R-H-Y}Les$	0.145	0.251	0.096	0.066	0.054	0.038	0.132	0.090	0.074	0.126	13
$MD_{R-Y}Les$	0.132	0.303	0.092	0.060	0.086	0.088	0.109	0.088	0.086	0.136	14
$MD_{REG-R-Y}Les$	0.144	0.286	0.092	0.063	0.084	0.085	0.105	0.097	0.091	0.136	15
MD_{reg-H}	0.141	0.179	0.114	0.188	0.005	0.291	0.187	0.233	0.104	0.167	16
projections	19	19	16	13	1	7	3	10	9	97	

4.3 **DISCUSSION**

There has been very little formal evaluation of population projection methods which can be used with the data commonly available to game managers (Eberhardt 1987). The most common types of information available are population indices, assumed to have a constant proportional relationship to adult abundance. However, indices can be of limited value if the management goal is an abundance target or harvest quotas change over time (Anderson 2001). Justification of harvest policies or changes in harvest quotas is best accomplished with annual abundance estimates.

Our results suggest projections of annual game abundance can be accomplished with simple demographic models. The simplest of the projection models (M_0), i.e., $N_{t+1} = N_t$, proved to be among the best approaches when only abundance data were available. Meaning that current estimates of abundance are often the most accurate estimate of next year's abundance. Time series of abundance alone do not provide a substantial amount of information as to the cause of changes in abundance, thus this analysis favors the model that includes no additional information (i.e., model M_0). Additionally, the maximum relative deviance of model M_0 was constrained by the realized change in the populations from year to the next. Most of the observed populations on did not change drastically in abundance in a single year. Therefore, by not projecting any sort of trend, projections from model M_0 had a reduced probability of being highly inaccurate.

Projections of populations with no clear demographic trend using model M_0 had average relative errors of 18.3%–34.3% (Table 4.1). Trended populations had an average relative error using model M_0 between 11.2%–16.8% (Table 4.1). Robson and Regier (1964) suggested for

rough management, an accuracy of $\pm50\%$; for accurate management, $\pm25\%$; and for careful research into population dynamics, $\pm10\%$. Most of the projections from the abundance-based models fell within the range of accurate management, and some approached the careful research level (Table 4.1 and 4.3). In the datasets analyzed, reported abundance values were in reality abundance estimates with unspecified levels of measurement error. No projection model can have accuracy greater than the stochastic error in estimation. As such, the actual accuracy of the population projections would have likely been better than reported if actual abundance levels were known, not measured.

It should be noted that models which include density-dependent effects on survival or recruitment were not considered in this analysis. The time series of abundance data available to us were not well suited to fitting such relationships (Krebs 2002, Clark et al. 2010). In addition, we intentionally omitted populations with logistic growth most suited to such techniques (Figure 4.1-4).

It seems intuitive that increasing model complexity and, hence, realism would also increase the accuracy of model projections. In the small sample of nine populations we had at our disposal, incorporating harvest numbers, recruitment, and survival marginally improved population projections on average (Table 4.4). Adding age-structure information was only marginally better than models using a common growth rate (Table 4.2). Simpler models are often more robust to assumption violations (Eberhardt 1987), as well as less costly to implement and maintain. However, in order to use any of the models assessed here, annual estimates of abundance are still necessary. SPR provides both a framework for annual abundance estimation

and demographic parameter estimates needed to produce the most accurate abundance projections available.

Additional accuracy in population projections of terrestrial game populations may come from better data rather than better process models. Recruitment and mortality of game species can be heavily influenced by extrinsic factors such as weather, habitat loss, and forage availability (Connelly et al. 2005, Hewitt 2011). However, this review did not have the ability to examine the wide-scale value of using environmental covariates to help model survival or recruitment processes. It might be expected the performance of projection models that incorporate environmental covariate relationships would behave as well if not better than what was observed in these analyses. Collection of covariate data may be necessary to better understand and project population trends. Extrinsic factors will effect demographic processes differently across species and populations. Therefore, the best model for projecting abundance may be population specific. Adaptive harvest management proceeds under the assumption that there is one best model for each population and a pool of potential models is evaluated iteratively over many years to identify the best models (Smith et al. 2008). The models presented here represent a strong pool of candidate models with varying levels of simplicity for evaluation within an adaptive management framework. The best options will likely involve approaches that incorporate all available information, including abundance, demographics, environmental covariates, and index data.

4.4 MANAGEMENT IMPLICATIONS

The increase in referendums concerning harvest regulations from non-traditional stakeholders (Jacobson and Decker 2006) suggests harvest regulations should be set through

defensible and easily understood methods. Accurately projecting the future abundance of game populations will allow managers to set harvest regulations in a clear and defensible manner, which has the potential to decrease conflicts with stakeholders. Harvest managers with current abundance estimates would be well served to set next year's harvest regulations based on current abundance estimates, particularly in extrinsically controlled populations. However, it is both difficult and costly to directly estimate state or region wide abundance annually, using direct sampling methods (i.e, distance or sightability models). Alternatively, the use of statistical population reconstruction provides both a cost effective estimate of annual abundance at scales relevant to management and the most accurate projection models of those evaluated here. Additional improvements in projecting abundance should be explored that incorporate covariate relationships into the survival and recruitment processes. These efficient methods for projecting future abundance of game populations will allow for a fundamental paradigm shift, mangers can now set harvest regulations based on abundance and harvest rate goals rather than uncalibrated indices and hunter opinion surveys. Attaining accurate annual population projections has the potential to reduce management mistakes and increase public confidence in management agencies.

Chapter 5. RECOMMENDATIONS AND GUIDANCE FOR THE IMPLEMENTATION OF STATISTICAL POPULATION RECONSTRUCTION IN GAME MANAGEMENT

5.1 **INTRODUCTION**

Statistical population reconstruction has recently increased in popularity due to its efficient and robust estimation of abundance and other demographic parameters. Since 2007 there have been eight published SPR-type reconstructions that modeled seven species including large ungulates (Skalski et al. 2007, Gast et al. 2013a), game birds (Broms et al. 2010, Gast et al. 2013k), furbearers (Skalski et al. 2011) and carnivores (Conn et al. 2008, Clawson 2010, Fieberg et al. 2010). Accompanying the applications of SPR have been model evaluations and statistical advances, including the use of pooled age-class data in SPR (Skalski et al. 2012b), Bayesian analysis of SPR models (Conn et al. 2008), the use of random effect models in a maximum likelihood framework (Gast et al. 2013a) and models which offer more realistic variance estimates (Gast 2012). The previous chapters in this dissertation increased the utility of SPR and provide guidance on auxiliary data collection. Abundance and harvest auxiliary data sources were rigorously evaluated in Chapter 2 (Clawson et al. 2013). The ability of SPR output to augment existing long term data in order to perform meaningful analysis was highlighted in Chapter 3 (Clawson et al. 2015). Finally, methods to project future abundance of harvested populations were rigorously evaluated in Chapter 4. The result is a robust and flexible modeling platform that produces accurate parameter estimates and associated variance estimates. Despite

all of the evaluations and detailed examples which exist, guidance on using SPR for broad scale management is still sparse.

There are several reasons SPR has yet to be adopted for state wide monitoring programs. The primary reason is the lack of guidance for implementation at the state or game management region level. Previous applications have focused on model development and evaluation. Existing examples have modeled small scale, tightly monitored populations with simple harvest regulations. These examples served to illustrate many of the desirable qualities of SPR, however they fall short of providing a blue print which game managers can follow to apply these models on a broader geographic scale. Monitoring of species harvested over large geographic areas creates unique challenges, including how to representatively sample harvest, age composition and hunter effort data over large spatial scales and how to collect representative auxiliary data. Lack of guidance is not the only barrier to application. The broad adoption of new statistical methods is usually accompanied by the production of user-friendly software (Buckland et al. 2000). Unfortunately software to facilitate the application of basic SPR models is still under development (http://www.cbr.washington.edu/analysis/apps/PopRecon) or too cumbersome for general use (i.e., AD Model Builder, www.admb-project.org). Additionally, institutional inertia plays a role in delaying the adoption of new methodologies in harvest management. Wildlife management agencies are steeped in tradition and slow to change (Jacobson and Decker 2006). However, due to the undeniable efficiency and potential SPR models hold, there is substantial interest in management application of SPR models.

Several state and federal resource agencies have expressed interest in adopting SPR into their monitoring frameworks. The Missouri Department of Conservation is currently preparing to

use SPR as a primary component to monitor both their wild turkey (*Meleagris gallopovo*) and white-tailed deer (*Odocoileus virginianus*) populations. The applications of SPR in Missouri were made possible through my close collaboration, and initiated many of the topics covered in this dissertation. The Midwest Fish and Wildlife Association has invested in the development of user-friendly software to aid in the application of basic SPR models (http://www.cbr.washington.edu/analysis/apps/PopRecon). The Idaho Department of Fish and Game is currently collecting data with plans to construct SPR models to model Elk (*Cervus elaphus*) in north Idaho in the near future. There is also international interest in modeling big horn sheep (*Ovis Canadensis*) and polar bears (*Ursus maritimus*) in Canada, and Chamois (*Rupicapra rupicapra*) in Sweden. This strong interest from management agencies in SPR has created an urgent need for guidance and recommendations for the management application of SPR. This chapter will provide the much needed guidance for game managers.

The guidance provided in the chapter fulfills three primary objectives. The first objective is to increase understanding of model assumptions and data requirements. This will allow managers to critically evaluate model assumptions and existing data sources, leading to more effective collaboration with biometricians. The second objective is to answer the two primary remaining questions that are fundamental to planning new SPR modeling efforts (i.e., minimum harvest data requirements and relative utility of auxiliary data sources). The third objective is to increase the management utility and potential applications of statistical population reconstruction.

5.2 TYPES OF DATA REQUIRED FOR SPR ANALYSIS

There are three primary forms of data which are necessary for SPR; age-at-harvest, hunter effort and auxiliary data.

5.2.1 Age-at-harvest data

Quality age-at-harvest data are paramount to the successful application of statistical population reconstruction. Total harvest and age composition data are the primary forms of data that are sampled directly from the population and are used in the age-at-harvest likelihoods, which form the primary structure of the SPR analysis. The best age composition data arise from ageing all harvested animals. In practice completely censused age-at-harvest data often come from populations which are harvested in low numbers and which have tightly monitored harvest such as cougars (*Puma concolor*) in Oregon or elk (*Cervus elaphus)* in Michigan (Clawson 2010, Gast et al. 2013a). Conversely, age composition of the harvest may be cost prohibitive to census for species such as white-tailed deer (*Odocoileus virginianus*), which are harvested in large numbers and must be professionally aged.

In the event that the age composition of the harvest cannot be enumerated it can be subsampled. A representative sample of harvested animals can be aged and used to estimate the age composition of the total harvest. Inherent in characterizing the age composition of harvest data is the assumption that the sample of aged animals is representative of the overall harvest. The precision of age composition estimates will be related to the proportion of the harvest that is aged, unless the number of animals harvested is very large. If the number of animals harvested is very large, aging additional animals beyond a certain threshold will result in little additional precision (Cochran et al. 1965 p. 25). Age composition must be estimable within each harvest

region that will be modeled. Additionally, animals do not need to be aged to every individual age class; categorization into biologically important age-classes is sufficient (Skalski et al. 2012b). Older age classes can be pooled if they have the same harvest vulnerability and natural survival (Skalski et al. 2012b). Sampling of the age composition of the harvest and pooling mature age classes are common practice among management agencies for species with high harvest numbers (Rabe et al. 2002).

Aging a random sample of harvested animals is the most statistically sound method for sampling age composition. However, without mandatory check stations or a system to mail in a portion of the animal which can be used to age the animal (i.e., jawbone, tooth or wing), random sampling may be difficult to achieve. Opportunistic sampling via meat locker checks or voluntary reporting are common practices. However, such non-random sampling techniques present the potential problem that animals sampled for age composition may not be representative of the overall harvest, leading to unknown bias. Hunters who use meat lockers may have differential harvest selectivity from those who process their own game (Hansen et al. 2006). Smaller animals that can be easily processed and stored at home may be underrepresented in meat locker checks (Hansen et al. 2006). If opportunistic sampling cannot be avoided, potential biases should be evaluated based on a simultaneous short-term random sample of the harvest.

If widespread professional ageing is not possible, hunter collected measurements paired with length frequency analysis is a potential strategy for augmenting limited age composition data. Additionally, if morphological measurement data can be collected from a large proportion of harvested animals, length frequency analysis may be able to correct the potential biases of

opportunistic sampling. However, size data are inherently less valuable then properly sampled

age data and augmentation of SPR with length frequency analysis is currently untested.

Finally, regardless of the type of age-at-harvest data collected, the data must be available

at the regional scale at which modeling occurs (see section on model scaling). State wide total

harvest and age composition are not enough to produce regional SPR models. Both total harvest

and age composition estimates must be available at the regional scale at which modeling occurs.

Therefore hunters must report in which region each animal is harvested.

5.2.2 **Hunter effort data**

In SPR models, hunter effort is used to estimate harvest probabilities. A harvest

vulnerability coefficient (c) is estimated that converts annual estimates of hunter effort (f_i) to

harvest probability (p_i) (Seber 1982). The relationship can include random effect parameters

(γ_i) allowing for interannual variation in the relationship between hunter effort and harvest

probability where

$$p_i = 1 - e^{-(c+\gamma_i)f_i}.$$

This parameterization of harvest probabilities can be sex and age-specific if supported by model

selection, assuming hunter effort and harvest data are detailed enough to accommodate such

parameterizations. Estimates of harvest probability and in turn hunter effort data are critical

components of the age-at-harvest likelihood, therefore it is crucial that hunter effort data be

representatively sampled.

Hunter effort can be recorded in many forms, from the number of permits sold to the

number of hours hunted. The most appropriate form of hunter effort depends on the specifics of

the harvest system. The number of permits sold would be a useful form of effort if participation

rates are at or near 100% and the harvest season has limited duration and limited take, (e.g. 9-

days in Wisconsin for white-tailed deer). In short duration harvest systems with high

participation rates, it could be assumed that all permitted hunters put forth the same average

amount of effort, making collection of more detailed forms of effort unnecessary. In order to use

permits sold as a measure of hunter effort, the permits would have to be region specific or the

number of hunters in each region would need to be estimated. In contrast, long duration harvests

with variable hunter participation rates and variable take require more detailed forms of hunter

effort to be collected. In systems where tags are inexpensive and easily obtained, hunters may

purchase tags and never actually hunt. Participation rate of licensed hunters is therefore an

important factor in choosing which form of hunter effort to use in SPR models. In long duration

harvest systems with variable participation rates, individual hunters can have great variability in

the amount of effort they put forth. This is particularly true in small game harvests with the

opportunity for multiple take. The issue is less important in single take harvests common to big

game species. In order to determine the proper level of detail for hunter effort data to be

collected by management region, initially the most detailed effort possible should be collected in

order to test assumptions and decide if a less refined measure of effort will suffice. In harvest

systems, time hunted in days or hours is the most detailed from of effort. Trap-nights, (i.e. the

number of traps set multiplied times the number of days each trap was set) is the most detailed

form of effort in trapping systems. Coarser forms of hunter or trapper effort can be used but the

assumption of additive effect may be violated i.e., $1 - e^{-c*f_i} \approx cf$ for p<10%.

Collecting hunter effort will require post-season hunter surveys. Surveys must include data on both successful and unsuccessful hunters, therefore a random sample of hunters via telephone, mail or internet survey rather than check station surveying is necessary. Surveys should be brief and to the point, in order to collect all necessary data and minimize non-response bias (Scott 1961). Most state agencies currently survey their hunter population (Roseberry and Woolf 1991). Existing hunter surveys can be adjusted to collect appropriate data with minimal additional cost. However the structure of state wide surveys is not always adequate to provide regional effort data. If managers can determine which region hunters visited before the survey is administered, a stratified random sampling design can better estimate hunter effort in each region and reduce the overall survey sample size. This opportunity exists in some states where big game permits are assigned by management region. Otherwise, a larger random sample of all state wide hunters must be taken and more detailed effort data collected.

Hunters must report in which game management region harvest occurred as well as all regions they hunted and the time spent in each region. Appropriate scaling of hunter effort by region is critical to SPR modeling efforts (see scaling section). The method of harvest (e.g. bow, muzzle loader, rifle) and type of tag used (male only, antlerless only etc.) must be reported along with effort and harvest success; these data are needed to model multi-season harvest regimes. Different forms of hunting will require different vulnerability harvest coefficients (c). For example, bow hunters are likely to harvest animals at different rates than rifle hunters. Additionally, tag specific data are used to apply the hunter effort data to the proper section of the population. For example, hunters with antlered only tags should not be included in hunter effort when modeling the female section of a deer population.

5.2.3 **Auxiliary data**

Age-at-harvest data are insufficient to reconstruct populations on their own, so additional data are necessary in order to fit SPR models (Gove et al. 2002). The auxiliary data can be any data, independent of age-at-harvest and hunter-effort data, which can be used to estimate abundance, harvest rate, or the probability of natural survival. Auxiliary data must be representative of the population being modeled. This means auxiliary data must be collected at the regional scale at which modeling occurs. The flexible nature of SPR allows multiple forms of auxiliary data to be included in a single model structure. Sampling considerations and the structure of the likelihood model will be unique to the type of auxiliary study (Brownie et al. 1978, Seber 1982, Millspaugh and Marzluff 2001, Skalski et al. 2005).

Auxiliary abundance data can be collected using any sort of large-scale abundance estimation strategy that provides an associated variance estimate; methods include mark-recapture (Seber 1982 p. 59), line transect (Seber 1982 p. 28), change-in-ratio (Skalski et al. 2005 p. 259), index removal (Skalski et al. 2005 p. 269) and DNA mark-recapture (DeYoung and Honeycutt 2005). Gast et al. (2013a) used independent abundance estimates from sightability corrected aerial surveys to aid in the reconstruction of an elk population in Michigan. For equal levels of precision of the auxiliary study, SPR models with abundance auxiliary data produce more precise and less biased parameter estimates than SPR models with harvest probability auxiliary data (Clawson et al. 2013). However, large-scale abundance studies can be expensive, labor intensive, and can pose untenable risks to management staff (Unsworth et al. 1990, Anderson et al. 1998, Sasse 2003, Jones et al. 2006). Due to cost and sampling considerations,

estimates of large-scale game population abundance are uncommon in practice and therefore infrequently used in SPR.

Harvest probabilities are commonly estimated via radio-telemetry (Millspaugh and Marzluff 2001) and band-recovery (Brownie et al. 1978) data . Radio-telemetry harvest probability auxiliary data better increase the stability of SPR models compared to abundance auxiliary data (Clawson et al. 2013). Band-recovery data are only useful as SPR auxiliary if reporting rates and harvest probabilities can be differentiated, either through mandatory reporting of all harvest or the use of an independent reporting rate study. The utility of band-recovery data auxiliary relative to radio-telemetry and abundance data in SPR models has yet to be evaluated.

Natural survival is generally estimated by radio tracking (VHF or GPS) a representative sample of the population (Millspaugh and Marzluff 2001). If total survival is estimated, it must be partitioned into natural and harvest components (i.e., $S_t = S_n * S_h$). In order to differentiate natural mortality from harvest mortality, radio-tagged animals must be checked for mortality before and after the harvest season, and cause specific mortality must be available during the harvest season. Estimating natural survival from radio-tagged animals can avoid problems of differential harvest of marked animals (Jacques et al. 2011). It can be expensive to obtain adequate sample sizes of radio-tagged animals to estimate natural survival within each modeling region of a state, especially if natural survival parameter estimates are necessary for different sex and age classes (Garton et al. 2001). However, the cost of large radio-telemetry studies can be justified if they serve multiple purposes, such as providing both natural survival and harvest probability auxiliary information for SPR models or non-SPR related purposes such as home range investigation (Dunn and Gipson 1977) or habitat utilization (Millspaugh et al. 2006).

The additional likelihoods that need to be added to the overall likelihood structure in order to estimate harvest and survival probability from radio-telemetry data depend on whether survival and harvest rate are modeled as concurrent or conditionally independent processes. If harvest and survival are modeled as conditionally independent processes, survival and harvest probability are estimated with two separate binomial likelihoods where the likelihood to estimate harvest probability is

$$\binom{T_i}{h_i} (P_i)^{h_i} (1 - P_i)^{T_i - h_i}$$

where T_i is the number of animals radio-tagged just prior to the harvest period in year i and h_i is the number of radio-tagged animals harvested in year i. The likelihood to estimate natural survival is then

$$\binom{T_i - h_i}{A_{i+1}} (S)^{A_{i+1}} (1 - S)^{T_i - h_i - A_{i+1}}$$

where $T_i - h_i$ is the number of radio-tagged animals still alive at the end of the harvest period in year i, and A_{i+1} is the number of animals alive at the beginning of the harvest period in the following year (i+1). If harvest and survival are modeled as concurrent processes, both natural survival and harvest probability are estimated in a single multinomial likelihood of the form

$$\binom{T_i}{h_i \ d_i^h \ d_i^o \ A_{i+1}} \left(\left(\frac{cf_i}{cf_i + \mu t_h} \right) (1 - e^{-cf + \mu t_h}) \right)^{h_i} \left(\left(\frac{\mu t_h}{cf_i + \mu t_h} \right) (1 - e^{-cf + \mu t_h}) \right)^{d_i^h}$$

$$\left((e^{-cf + \mu t_h})(1 - e^{-\mu t_o}) \right)^{d_i^o} \left(e^{-cf + \mu(t_h + t_o)} \right)^{A_{i+1}}$$

where T_i is the number of animals radio-tagged just prior to the harvest period in year i, h_i is the number of radio-tagged animals harvested in year i, d_i^h is the number of radio-tagged animals which died of non-harvest mortality during the harvest period in year i, d_i^o is the number of radio-tagged animals which died between harvest periods of years i and i+1, A_{i+1} is the number of radio-tagged animals alive at the beginning of the harvest season in year i+1. Additionally, t_h is the length of the harvest period and t_o is the length of time between annual harvest periods.

Indices of abundance are commonly collected and used in wildlife management, making them an attractive form of auxiliary data. Indices are typically a partial census or an indirect measure of animal abundance such as browse availability, scat, or nest counts making them inexpensive because they often do not involve direct counts of animals (Anderson 2003). Unfortunately, index data have been shown to be the least useful of all auxiliary data in SPR analysis (Skalski et al. 2007, Skalski et al. 2012a). The limited utility of indices is because the catch-effort data present in age-at-harvest analysis already provides information on population trends, which is the same role indices play. However, indices may be a cost effective form of data, which can be used to confirm the population trends estimated by SPR models (Skalski et al. 2007, Skalski et al. 2012a).

5.3 EVALUATION OF SURVIVAL AND HARVEST PROBABILITY AUXILIARY DATA IN SPR MODELS.

Reliable auxiliary data are extremely important to successfully implement SPR modeling (Gove et al. 2002, Clawson et al. 2013). Increasing the precision with which the auxiliary data estimate the individual parameter will increase the precision of the abundance parameters estimated within the SPR model (Clawson et al. 2013). However, the relationship between the

precision of auxiliary parameter estimates and abundance estimates from SPR is not direct and depends on the type of auxiliary data and the amount of harvest data available. While abundance auxiliary data have previously been shown to increase precision of SPR output better than harvest probability auxiliary of equal precision, it is difficult and expensive to collect at the scale necessary for SPR modeling. Harvest and survival auxiliary data are therefore of primary interest in SPR modeling efforts.

In order to assess the utility of various forms of auxiliary data for potential use in future SPR models, Monte Carlo simulations based on a stochastic Leslie matrix model (Caswell 1989) were performed. Harvest, hunter effort and auxiliary data were simulated and SPR models were fit using AD Model Builder (www.ADMB-project.org). The measurement error associated with population reconstruction was estimated from the empirical variance among replicate simulations. This simulation approach provides a model-independent means of estimating measurement error.

In order to assess the relative utility of harvest auxiliary and natural survival auxiliary data in SPR models, 8 sets of simulations were run. The simulations compared SPR output using 4 different levels of precision for harvest probability and 4 levels of precision for natural survival probability using sample sizes of 20, 40, 60, and 80 radio-tagged animals. Each sample size and auxiliary type combination was tested with 6 years of harvest data and 13 age classes (Table 5.1). All auxiliary data were simulated as being collected in a single year, starting in the first year of the population reconstruction. Each set of simulations was run 7,000 times using full age-class SPR models. Survival auxiliary data outperformed harvest probability auxiliary data for equal sample size (Table 5.1). SPR models with survival auxiliary data produced more precise

estimates of abundance, natural survival, and even harvest rate than models with harvest auxiliary data, for equal sample sizes of auxiliary data Table 5.1, Figure 5.1-3. Bias was less than 2% for all parameters in all scenarios tested (Table 5.1). Therefore radio-telemetry studies to augment SPR models should be designed to estimate natural survival rather than harvest probability if the sole purpose is to maximize the precision of SPR output. However it is often necessary to plan auxiliary studies with the greatest overall utility, bearing in mind budget constraints and multiple management objectives. Either auxiliary type will provide quality data for SPR modeling.

Table 5.1. Table of simulations performed to assess the relative utility of harvest probability and natural survival auxiliary studies in SPR, at varying sample sizes with 6 years of age-at-harvest and hunter effort data with 13 age classes.

Auxiliary Type	Auxiliary Sample Size	CV of Abundance	CV of Harvest Probability	CV of Survival	Bias of Abundance	Bias of Harvest Probability	Bias of Survival
Harvest	20	0.497	0.290	0.099	0.013	-0.014	-0.004
Harvest	40	0.385	0.245	0.084	0.013	-0.012	-0.004
Harvest	60	0.309	0.213	0.074	0.010	-0.009	-0.003
Harvest	80	0.262	0.192	0.066	0.006	-0.007	-0.002
Survival	20	0.460	0.247	0.083	-0.007	0.007	0.002
Survival	40	0.355	0.193	0.063	-0.004	0.004	0.001
Survival	60	0.288	0.163	0.054	-0.002	0.002	0.000
Survival	80	0.238	0.143	0.047	-0.002	0.001	0.000
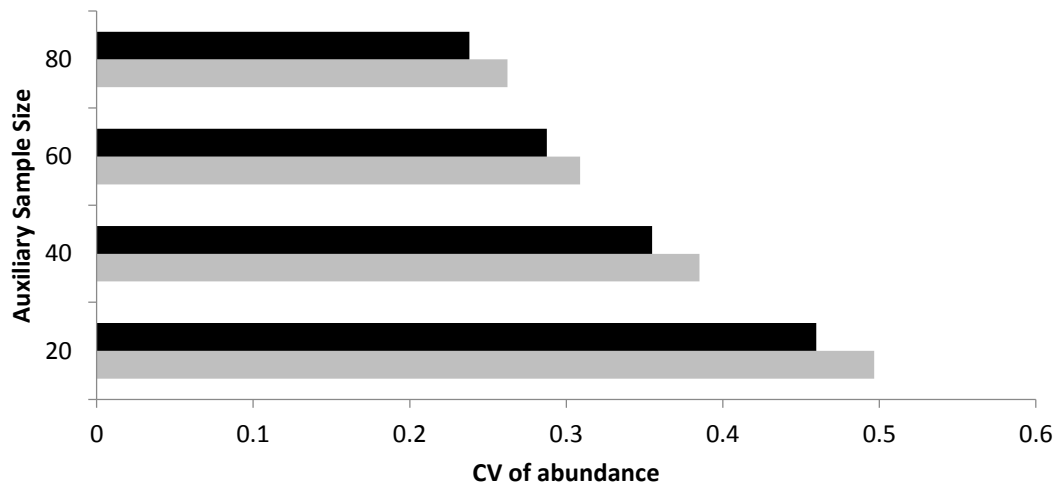
Figure 5.1 Precision (coefficient of variation, CV) of abundance estimates from an SPR model (horizontal axis), with survival (black) or harvest (grey) auxiliary data, by auxiliary sample sizes (vertical axis). The SPR model used in this analysis has 13 age classes with 6 years of harvest and hunter effort data.
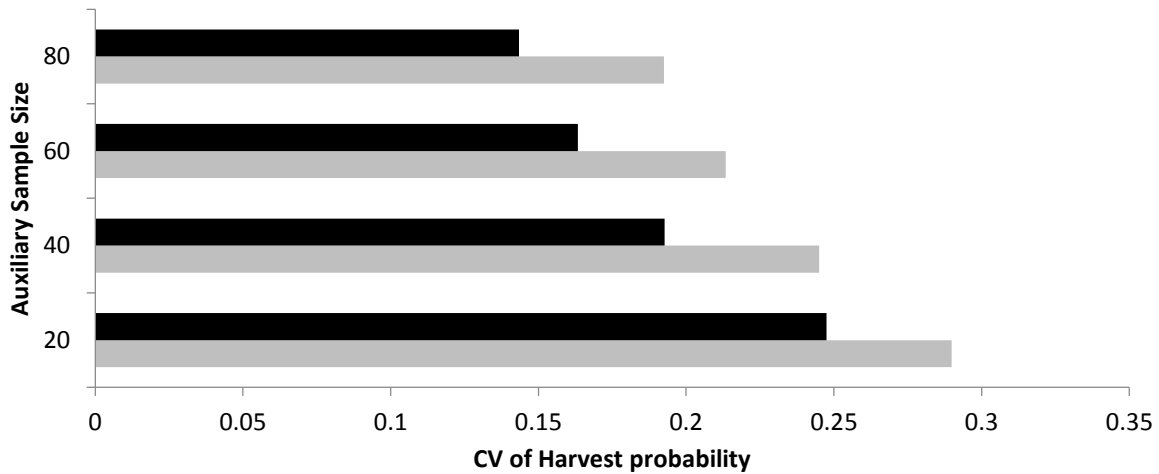
Figure 5.2. Precision (coefficient of variation, CV) of harvest probability estimates from an SPR model (horizontal axis), with survival (black) or harvest (grey) auxiliary data, by auxiliary sample sizes (vertical axis). The SPR model used in this analysis has13 age classes with 6 years of harvest and hunter effort data.
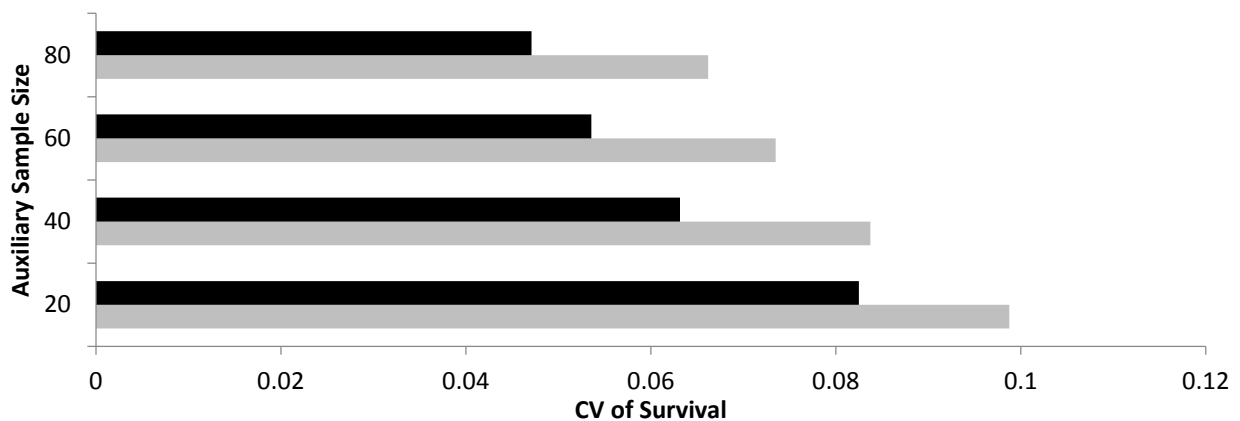
Figure 5.3. Precision (coefficient of variation, CV) of survival probability estimates from an SPR model (horizontal axis), with survival (black) or harvest (grey) auxiliary data, by auxiliary sample sizes (vertical axis). The SPR model used in this analysis has 13 age classes with 6 years of harvest and hunter effort data.

5.4 BAND-RECOVERY AUXILIARY DATA

Although radio-telemetry data are commonly collected by management agencies, they are

not the only way to estimate harvest rates and survival of harvested species. Another common

method to estimate harvest rate and survival is through band-recovery methods, commonly

known as Brownie models (Brownie et al. 1978, Nichols et al. 1991, Otis 2006, Conn et al.

2008). Band-recovery models represent a lower cost alternative to radio-tag studies because

marked animals do not have to be monitored after release. In band-recovery studies, animals are

marked and released with individually identifiable tags over multiple years. Bands are recovered

from harvested animals over subsequent years and the recovery histories are modeled based on

the probability of survival, harvest and reporting (Brownie et al. 1978). Models can range in

complexity from estimating a single total survival parameter, and single recovery rate for all

animals and years (Model 3 in Brownie et al. 1978), to year specific total survival and recovery

parameters (Model 1 in Brownie et al. 1978).

Including band-recovery data as auxiliary in SPR is not as straight forward as including

radio-telemetry data. The parameters estimated in band-recovery models (Brownie et al. 1978)

are martingales of SPR parameters. The survival parameter (S) estimated in the Brownie model

is the total annual probability of surviving both natural and harvest mortality. In SPR models, the

Brownie survival parameter is parameterized as $S_{Brownie} = S(1 - p)$. Similarly the recovery

rate (f) estimated in the Brownie model is the combined probability of being harvested (p) and

reported (R), which in an SPR model is parameterized as $f_{Brownie} = R * p$, where R is the

probability a band is reported given it is harvested. These two confounded parameterizations

severely limit the utility of banding-recovery studies as auxiliary data for SPR.

The utility of band-recovery studies as auxiliary data for SPR based on Model 1 from

Brownie et al. (1978) were evaluated using Monte Carlo simulations analogous to Gast (2012).

Simulations were parameterized to reflect the harvest of a banded turkey population. Simulations

were done with 10,000 banded animals annually. Even with the astronomical sample size of banded birds simulated, SPR models were not able to converge to meaningful abundance estimates with either the Model 0 or Model 1 of Brownie et al. (1978). The lack of identifiability of SPR parameters in the Brownie model simply does not allow band-recovery models without separately estimated reporting rates to be used as useful SPR auxiliary data.

There are two primary methods to address this problem of identifiability between harvest rate and reporting rate in band recovery models. Mandatory reporting of all harvested animals is the first method, the reporting rate is then assumed to be 100% (for both marked and unmarked animals). Conn et al. (2008) successfully used band-recovery auxiliary data in a population reconstruction of black bears (*Ursus americana*) in Pennsylvania where 100% reporting was assumed. However, Conn et al. (2008) used the band-recovery data in a Bayesian context so it remains to be evaluated in the context of unconstrained SPR models. The second option is to include reward bands in the banded population. The return rate of reward bands is typically assumed to be 100%. Nichols et al. (1991) reported 100% return rates when bands earned a $100 reward, for Mallards (*Anas platyrhynchos*) in the central North America. The use of rewards then allows the non-reward band reporting rate to be estimated independent of the harvest rate. Reward band-recovery data have not yet been evaluated as an auxiliary data source for SPR but are a good candidate for future evaluation of potential SPR auxiliary sources.

5.5 MINIMUM HARVEST DATA REQUIREMENTS FOR STATISTICAL POPULATION RECONSTRUCTION

In order to assess the minimum harvest and hunter effort data requirements for SPR models, Monte Carlo simulations based on a stochastic Leslie matrix model (Caswell 1989 p. 8) were performed. Populations were simulated with 13 age classes and 10, 8, 6, or 4 years of harvest data. The simulations included auxiliary radio-telemetry data simulated as being collected in a single year to estimate natural survival using either, 40 or 80 radio-tagged animals. Each scenario was simulated 7,000 times using the full age-class SPR model.

Based on these simulations, statistical population reconstruction can be performed with as little as 4 years of harvest and hunter effort data with very low bias (<1% in all cases), although such reconstructions generally have relatively poor precision (Figure 5.4 and Figure 5.5). Reconstructions that used 10 years of age-at-harvest and hunter effort data had CV's of abundance that were 7-10% lower than population reconstructions with 4 years of data. The impact of additional harvest and effort data was most pronounced in low quality auxiliary scenarios (Figure 5.4). The precision of abundance estimates from SPR, in the first ten years of data collection, depend more on the quality of auxiliary data used than on the number of years of harvest data available (Figure 5.4).

These simulations give a general sense of the expected relationship between precision and bias of abundance estimates relative to the amount of harvest data available. However, there are additional factors that may affect the precision of abundance estimates resulting from SPR. These simulations assume total harvest and hunter effort are known and that the age composition of the harvest is enumerated. This level of detail in harvest and hunter effort data is generally

achieved in highly monitored small scale harvest regimes. Many states estimate hunter effort, age composition of the harvest and even total harvest for species like deer and turkey, to save cost and effort. It would be expected that the added uncertainty of the harvest and effort input would degrade the precision of reconstructed abundance estimates.
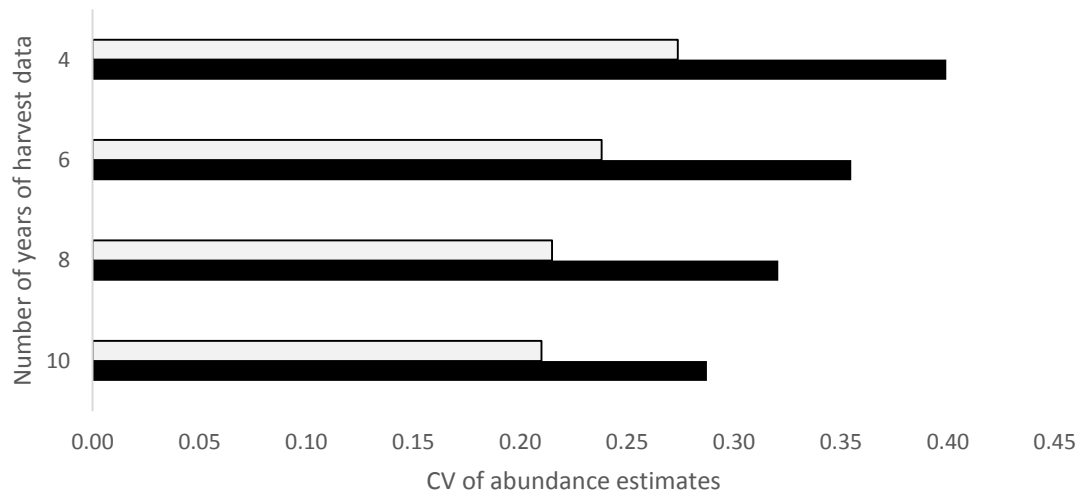
Figure 5.4. Coefficient of variation of abundance estimates resulting from simulations of statistical population reconstruction models with varying levels of harvest data and two levels of auxiliary, 40 radio-tagged animals (black bars) or 80 radio-tagged animals (grey bars) to estimate natural survival.
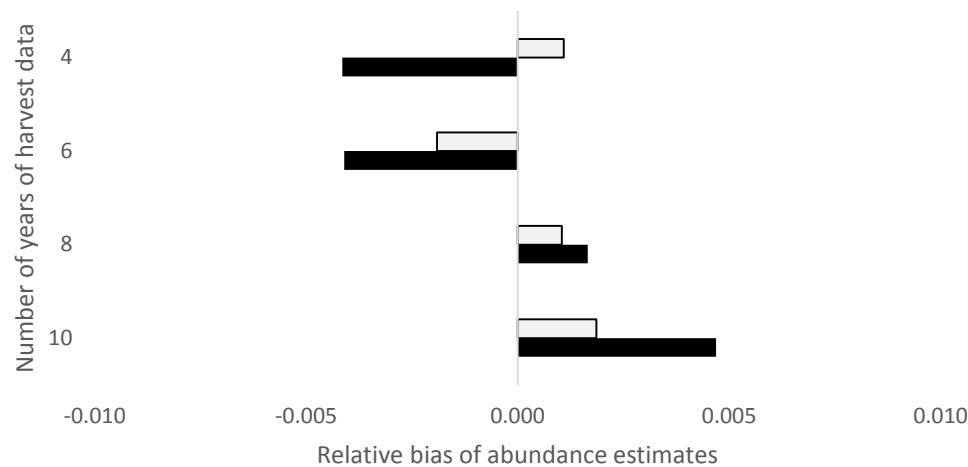
Figure 5.5. Relative bias of abundance estimates resulting from simulations of statistical population reconstruction models with varying levels of harvest data and two levels of auxiliary, 40 radio-tagged animals (black bars) or 80 radio-tagged animals (grey bars) to estimate natural survival.

5.6 SPATIAL SCALING FOR STATISTICAL POPULATION RECONSTRUCTION MODELS.

One of the first considerations when building an SPR based monitoring framework is the spatial extent of the population being reconstructed. SPR modeling regions must be appropriately scaled to support model assumptions, provide adequate data and achieve management objectives. Statistical population reconstruction models assume that within an age and sex class, animals have homogeneous natural (non-harvest) survival probability. Therefore, regions for SPR modeling must be chosen which support this assumption. Large ungulate populations generally have consistently high adult survival (Hewitt 2011), which is mainly dependent on the habitat quality, predator assemblages and large scale environmental conditions (Hewitt 2011, Brodie et al. 2013) which may allow for larger regions to be modeled. In contrast, small game species, such as upland game birds, have high fecundity and comparatively low natural survival which is

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highly variable and can depend on localized weather and habitat (Vangilder 1996). The susceptibility of game populations to local environmental and habitat conditions may require smaller regions to be modeled in order to satisfy the assumption of homogeneous survival probability.

Harvest vulnerability within an age and sex class is also assumed to be homogeneous in statistical population reconstruction models. Harvest vulnerability is affected by land access, dominant cover type, terrain, road density, proximity to urban centers, and most notably harvest regulations. In Montana it was shown that elk use private farm land closed to hunting as refuge (Burcham et al. 1999). In Pennsylvania, deer hunters were found to hunt in easily accessible areas (Stedman et al. 2004). In Missouri, turkey hunters exerted more harvest pressure on populations in close proximity to urban centers (Clawson et al. 2015). Therefore, the distribution of public and private lands and hunter access are considerations when defining SPR modeling regions with regard to harvest vulnerability. Most importantly, harvest regulations must be the same across an entire SPR modeling region in order for the assumption of homogeneous harvest vulnerability to be valid. Harvest regulations include bag limits, timing of the hunt, regulations pertaining to form of take as well as regulations pertaining to which age and sex of animal can be harvested (e.g., antler point restrictions).

Finally SPR assumes that immigration and emigration are negligible in the region being reconstructed. The relative effects of immigration and emigration on SPR modeling decrease with the size of the area being modeled. An SPR modeling region should therefore be scaled by the biology of the game species and its hunting regulations. If animals are migratory they must exhibit a high degree of interannual site fidelity during the harvest. In large enough regions this

may hold true for many species. In the case the assumption of closure to immigration and emigration is violated, data must be collected to estimate immigration and emigration rates between adjacent SPR modeling regions.

A separate SPR model will be constructed for each modeling region defined. Harvest, hunter effort and auxiliary data will need to be collected in each region. The size of the region being modeled should be inversely related to total harvest numbers. Low harvest mortality requires larger regions to ensure animals are harvested from each age and sex class being modeled. This requirement is usually only a concern in populations with low abundance and/or harvest rates. Total number of animals aged within a region is another important data consideration. For most game species, not all harvested animals are aged (Rabe et al. 2002, Hansen et al. 2006). In cases when harvest is not entirely aged, the total number of animals aged within a given region will determine the precision of the estimates of age composition of the harvest. Without increasing the total number of animals aged in a state, larger regions will result in more precise estimates of regional age composition of the harvest. Conversely smaller regions will require more animals to be aged to maintain the precision of age composition estimates.

Auxiliary studies need to be conducted in each region where SPR is to be performed. Larger regions will result in fewer overall regions within a state, therefore the total number of animals tagged in auxiliary studies and thus cost of auxiliary data will be lower. Thus, larger modeling regions reduce overall cost of SPR modeling. However, representative sampling of the game population for auxiliary studies becomes more difficult at large spatial scales.

In summary, scaling of SPR modeling regions must balance assumptions of demographic homogeneity, harvest regulation consistency and data needs. Regions should be as large as

possible without violating the assumptions of demographic homogeneity. Larger modeled regions provide larger harvest numbers and the probability for more age-at-harvest data leading to improved model precision. Too many modeling regions within a state will result in onerous and possibly cost-prohibitive sampling requirements for multiple age-at-harvest and auxiliary data sources. Too few regions will result in unacceptable violations of assumptions and difficulty attaining representative auxiliary data. A balance must therefore be found between upholding the validity of assumptions and resources available for monitoring.

5.7 POOLED AGE CLASS STATISTICAL POPULATION RECONSTRUCTION

Categorizing animals into biologically relevant age classes is common practice in game bird and ungulate management. The age classes of game birds are generally indistinguishable past 2 years of age (Giles 1971). Accuracy in ageing ungulates based on tooth eruption and wear can be as low as 16% for elk (*Cervus elaphus*)older than five years old (Hamlin et al. 2000). More accurate ageing methods, such as counting cementum annuli can be cost prohibitive to apply to large numbers of animals annually. The common collection of pooled age class data has prompted the development of pooled age class SPR models, where older adult age class data are pooled (Skalski et al. 2012b). Within the pooled adult age classes animals are assumed to have homogeneous natural survival and harvest parameters (Skalski et al. 2012b).

Pooled age class SPR was first used to model a greater sage-grouse (*Centrocercus urophasianus*) population in Idaho where animals were aged as young-of-the-year and adults (Broms et al. 2010). A formal evaluation of pooled age class SPR models with three age classes based on data from a Columbian black-tailed deer (*Odocoileus hemionus columbianus*)

population in Washington and Monte Carlo simulations found parameters from pooled age class

SPR models had no reduction in precision or increase in bias compared to full age class SPR

models (Skalski et al. 2012b). Gast et al. (2013k) found no loss of precision or increase in bias

between parameters from pooled age class SPR models relative to those resulting from full age

class SPR models, when random effects were included in the catch-effort relationship. Clawson

et al. (2013) illustrated that auxiliary data had the same effects on pooled and full age class SPR

models.

In order to perform SPR with pooled age-at-harvest data among adult age classes, the

pooled age classes must have the same vulnerability to harvest. Harvest vulnerability as it relates

to pooling age classes is primarily governed by animal behavior and hunter selectivity.

Therefore, equal hunter selectivity is a necessary condition of pooling age classes. For most

game birds, animals 2 years old and older are likely indistinguishable to hunters pre-harvest

(Giles 1971). Female ungulates may be differentially selected up to age 2.5 years based on body

size (Hewitt 2011). If hunters heavily select for antler size in male ungulate populations, animals

may need to be aged to 3.5 years old or older. Differential harvest vulnerability is also due to

animal behavior, in addition to hunter selectivity (Noyce and Garshelis 1997). Subsequently,

animals of pooled age classes must also exhibit similar movement rates and wariness of hunters,

during the hunting season. Gast et al. (2013a) found the first 5 age classes of both male and

female elk to have differential harvest vulnerability, which was likely due to a combination of

animal behavior and hunter selectivity.

In order to pool age classes for SPR analysis, animals must also have homogeneous

natural survival. The age at which survival becomes homogeneous can be determined based on

direct observations and life table analysis (Skalski et al. 2005 p. 150). Senescence is rarely a

problem in an SPR context. Most deer in the United States are harvested before the age of 6

(Hewitt 2011) and small game populations have generally low survival and high harvest rates

which rarely allow for animals to reach an age of senescence (Alpizar-Jara et al. 2001).

Additionally, modeling efforts to account for senescence were not shown to improve parameter

estimates from SPR (Clawson 2010). Moreover, if senescence does occur in a harvested

population, it is likely to affect so few individuals as to have a negligible effect on abundance

estimation (Clawson 2010).

If the assumptions of homogeneous harvest vulnerability and natural survival rate are met,

pooled age class SPR is recommended over full age class SPR. Pooled population reconstruction

can save costs without any loss of precision. Pooling adult age classes prevents zero counts from

showing up in the age-at-harvest matrix. Abundance is estimated as the observed harvest

escalated by the estimated harvest rate, and as such, no observed harvest in a particular year and

age class results in an estimate of zero abundance in that age class. Additionally, pooled age

class SPR results in no loss of precision or increase in bias (Skalski et al. 2012b, Clawson et al.

2013, Gast et al. 2013k). Further, cost savings associated with collecting pooled age-at-harvest

data could be reinvested in the collection of quality auxiliary data, which would have a

substantial impact on the precision of SPR (Clawson et al. 2013).

5.8 USE OF MORPHOLOGICAL DATA AS A SURROGATE FOR
AGING

Age composition of the harvest must be accurately estimated in order to apply SPR.

Fortunately, age composition only needs to be obtained for biologically relevant age classes

(Skalski et al. 2012b). Game birds, such as grouse, pheasant and turkey can be accurately aged by hunters based on plumage characteristics (Giles 1971), thus allowing hunters to directly report age-at-harvest data (Hansen et al. 2006). Carnivore and furbearer species must be aged based on cementum annuli. Many furbearer and carnivore harvest systems have mandatory reporting, therefore a random sample of teeth for ageing is readily attainable. Widely harvested ungulates, such as white-tailed deer, present a unique challenge in terms of representatively sampling age-at-harvest data, because they often do not have mandatory reporting and are difficult for hunters to age. Harvested ungulates traditionally require trained professionals to handle each animal that is to be aged. Even labor efficient methods of aging, such as tooth eruption and wear become costly when thousands of animals must be aged annually across a state, even if a random sample can be obtained (Rupp et al. 2000). Therefore managers may seek less expensive ways to age widely harvested ungulate populations if states are unwilling or unable to invest resources into collecting large amounts of age data directly.

Hunter reported information is the least costly form of data that can be collected by management agencies. However, they can also be the least reliable form of data as well. If trained professionals cannot reliably age deer based on visual assessment alone, it can be assumed the general hunting public cannot as well (Gee et al. 2014). Alternatively, determining morphological measurements that can be used to age harvested ungulates, would allow for hunter reported age-at-harvest data. If morphological measurements can be used to accurately age animals, the measurement data collected by hunters could be directly used to estimate the age composition of the harvest. If distributions of morphological measurements overlap between age classes, length frequency analysis can be used to incorporate the associated ageing error into the

likelihood structure. For morphological measurement data to be useful in SPR, a means of evaluating the data is necessary and a way to incorporate the data into SPR must be developed..

5.8.1 Evaluating morphological measurements

In order for a method to effectively evaluate morphological measurement data it must objectively classify harvested animals into age classes and evaluate the classification error. Evaluations of morphological data, which can be reported by hunters, in order to age harvested animals are scarce (Hellickson et al. 2008, McDonald 2009). Hellickson et al. (2008) used a regression model to evaluate antler characteristics of male white-tailed deer (*Odocoileus virginianus*) in Texas, finding a combination of antler characteristics to be highly correlated with age. McDonald (2009) performed a graphical analysis of morphological measurements from both male and female white-tailed deer harvested in Illinois. McDonald (2009) suggest a combination of eye to nose measurements and antler characteristics to differentiate 1.5 year old male deer from 2.5+ year old male deer. Neither analysis provides an objective procedure to classify animals into age classes based on morphological measurements or how to evaluate the error associated with such a method. Alternatively, discriminant analysis offers both an objective method of classification and the potential to evaluate model performance.

Using the morphological measurement and age data for male white-tailed reported by McDonald (2009), discriminant analysis was applied to create a model for ageing male deer based on physical characteristics. Discriminant analysis uses characteristics of a sampled population to categorize individual samples into one or more classes (Press and Wilson 1978). There are several options as to the structure of the discriminant function; two widely used options are linear discriminant analysis and logistic regression with maximum likelihood

estimators (Press and Wilson 1978). Here, a logistic regression model with maximum likelihood estimators was used to estimate a discriminant function for classifying male deer into one of two age classes (i.e., 1.5 or 2.5+) based on sampled physical characteristics. The best discriminant function was chosen based on likelihood-ratio test (Kutner et al. 2004). Once a discriminant model was chosen, a cutoff rule was selected that minimized misspecification of the two age classes (i.e., 1.5 and 2.5+). In order to both fit and test the discriminant model, two independent data sets were necessary, one to fit the discriminant model and another to evaluate model performance. The complete data set ($n = 3025$) was randomly split into two data sets using the sample function in R (www.R-project.org). One data set was used to fit the model ($n = 2025$); the other, smaller, data set was used to evaluate the model ($n = 1000$). Data were collected in a chronic wasting disease management area in Illinois from 2005-2007 by the Illinois Department of Natural Resources. For each deer harvested, distance from eye to nose, antler beam circumference, and number of antler points were collected. Data were collected for both male and female deer; however, only data for males are available in this analysis.

The best discriminant model to differentiate 1.5-year-old male deer from 2.5+ year-old male deer included antler beam circumference and number of antler points (Figure 5.6). Eye-to-nose measurements did not reliably differentiate 1.5-year-old male deer from 2.5+ year-old male deer (Figure 5.7). The antler beam circumference and antler point model successfully differentiated 89.1 % of 1.5-year-old male deer and 89.3% of 2.5+year-old male deer for the data set used in model fitting. When the same model was used to age the independent data, 88.0% of 1.5-year-olds and 88.5% of 2.5+ year-old-male deer were correctly aged.
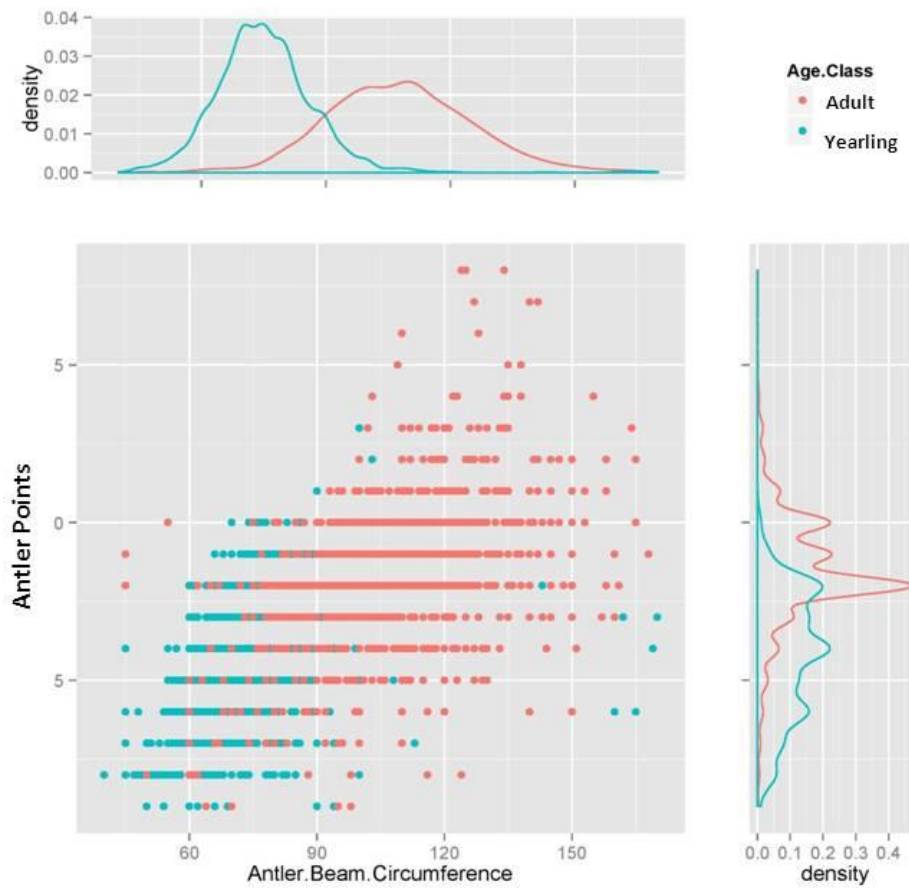
Figure 5.6. Harvested adult (orange) and yearling (green) male white tailed deer from Illinois plotted by antler point count (vertical axis) and antler beam circumference (horizontal axis).
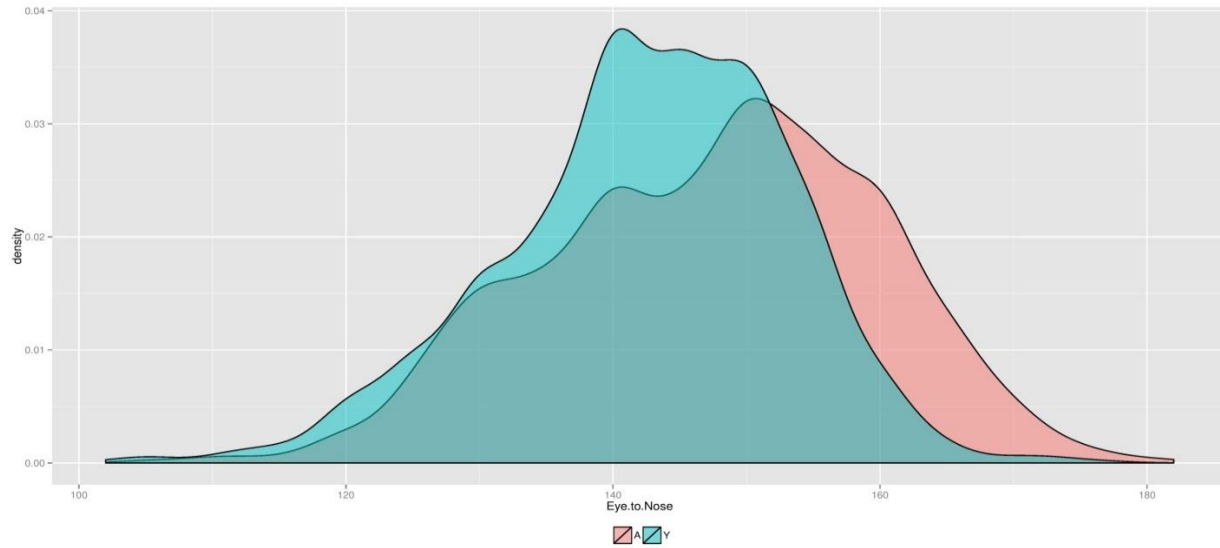
Figure 5.7. The distribution of eye-to-nose distances (horizontal axis) of harvested adult (orange) and yearling (green) male white-tailed deer from Illinois.

The discriminant analysis of antler beam circumference is consistent with the graphical analysis done by McDonald (2009) on this same data set. In contrast, McDonald also recommends using eye-to-nose measurements in conjunction with antler beam circumference to differentiate adult and yearling male deer, despite eye-to-nose measurements only having 55.3% and 57.7% success rates for adult and yearling deer, respectively.

In the case of female white-tailed deer, McDonald (2009) was able to differentiate female fawns from older female deer with a 90% success rate for both age classes, based on a graphical evaluation of eye to nose measurements. The ability to differentiate yearling females from adult females using eye-to-nose measurements was greatly reduced, with success rates of 65.57% and 63.49%, respectively (McDonald 2009). Unfortunately, raw data were not available for additional analysis of female morphological measurements.

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This discriminant analysis offers a starting point for further research into morphological metrics suitable for differentiating age classes of white-tailed deer. However, animal condition, including antler characteristics is related to local resource availability as well as age (Hewitt 2011). Determining which, if any, measurements will be generally appropriate for aging deer will require site specific data. Discriminant analysis that uses one data set to fit the model and another to test the fitted model is recommended for future evaluations of potential morphological measurements to age harvested ungulates, rather than the use of correlation metrics or graphical analysis previously used in the literature (Hellickson et al. 2008, McDonald 2009).

5.8.2 Length frequency analysis

Despite the high probability of success in predicting male deer age based on number of antler points and antler beam circumference, classification is imperfect, and there is overlap in the distributions of the age classes for both measurements. When aging criteria based on morphological measurements are imperfect, length frequency analysis should be directly incorporated into SPR. The use of length frequency distributions allows for the propagation of the additional variance associated with imperfect aging into the variance estimate of population abundance.

SPR uses a maximum likelihood framework to simultaneously estimate vital rates and abundances of a harvested population. If both size-at-harvest and age-at-harvest data are collected, length frequency analysis can be incorporated into SPR models. A representative sample of the population must be both aged and measured, while size data must be collected from a much larger portion of the population. Adding length frequency analysis to SPR requires two additional likelihood components be added to the joint likelihood model. First, a likelihood

component relating the observed age and size data is needed to estimate size-age distributions

(Equation 1). Assuming size-at-age is distributed normally, the likelihood would take the form

$$L_{\text{Age-Size}} = \prod_{i=1}^{Y}\prod_{a}\prod_{k=1}^{h_{a,i}} \frac{1}{\sqrt{2\pi\sigma_{a,i}^{2}}}\, e^{-\frac{1}{2}\left(\frac{\left(l'_{a,k,i}-\mu_{a,i}\right)^{2}}{\sigma_{a,i}^{2}}\right)} \qquad (1)$$

where

$h_{a,i}$ = number of individuals aged and measured for size at age a, in year i,

$l'_{a,k,i}$ = the observed size measurement for individual k, of age a, in year i,

$\mu_{a,i}$ = average size at age a, in year i, and

$\sigma_{a,i}^{2}$ = variance of size measurements at age a, in year i.

The second likelihood that must be added is the multinomial frequency likelihood (Equation 2)

(Quinn and Deriso 1999). The frequency likelihood estimates the probability a harvested animal

is in size class l (Q_l) and is of the form

$$\text{Likelihood}_{\text{Frequency}} = \left(\frac{L}{L_1' L_2'...L_J'}\right)\prod_{l=1}^{J} Q_l^{L_l'} \qquad (2)$$

where

L = number of individuals measured for size only,

J = the number of size intervals,

L_l = observed frequency in size class l, and

Q_l = proportion in size class l ($l = 1, ..., J$).

Q_l is parameterized as the probability of being in a certain size class, given an animal is of a

certain age $\left(\psi_{l,a}\right)$, multiplied times the probability of being in that age class $\left(\Theta_a\right)$, and summed

over all possible age classes:

$$Q_l = \sum_a \psi_{l,a} \cdot \Theta_a$$

where

$\psi_{l,a}$ is the probability that an animal is in size class l, given it is an age class a, and

Θ_a is the probability that an animal is in age class a.

$\psi_{l,a}$ can then be approximated based on the parameters estimated from the age-size likelihood

(1), with a discrete probability mass function of the form

$$\psi_{l,a} = \frac{1}{\sqrt{2\pi\sigma_a^2}} e^{-\frac{1}{2}\left(\frac{(l-\mu_a)^2}{\sigma_a^2}\right)} \tag{3}$$

where l is the midpoint of the size category; if the size categories are necessarily small in relation to σ_a^2 (Hasselblad 1966). Equation 3 approximates the continuous probability density function of the age-size relationship with a discrete probability mass function. Narrow categories of size range assure the discrete distribution is an adequate approximation of the continuous distribution (Hasselblad 1966). The probability that an animal is in age class a can be parameterized in terms of expected age-specific (H_a) and total (H) harvest as

$$\Theta_a = \frac{E(h_a)}{E(H)} = \frac{N_a \cdot P_a}{\sum\limits_a N_a \cdot P_a}$$

where, the abundance (N) and harvest probability (P) parameters are estimates from the remainder of the SPR modeling framework, providing the primary link between the length frequency analysis and the rest of the SPR model. With the above parameterization of length frequency analysis, age-specific annual mean and variances of the measured size characteristic of the harvested animals are the only additional parameters estimated $\left(\mu_{a,i}, \sigma_{a,i}\right)$. Parameters are then estimated through the maximization of the joint likelihood

$$L_{\text{Obj}} = L_{\text{Age-at-harvest}} \cdot L_{\text{Aux}} \cdot L_{\text{Aging}} \cdot L_{\text{Age-Size}} \cdot L_{\text{Frequency}}.$$

The proposed model structure detailed above was evaluated using Monte Carlo simulations analogous to Gast et al. (2013a) representing a deer population with 2 age (1.5, 2.5+) classes and 20 years of data, including data on juvenile and adult antler beam circumference. Age-and-size and age-only SPR models both estimated all of the demographic and size parameters accurately. This evaluation confirms that in principle, SPR models can be augmented

with morphological data. What has yet to be studied is the extent to which morphological data improve SPR model output, over the use of limited age data alone. If the addition of morphological data is shown to improve model performance, future evaluations should then explore maximizing precision for fixed cost by optimizing the proportion of animals which are aged versus measured in the annual harvest.

Morphological data will only be applicable under a limited set of conditions. First, there must be a size-age relationship estimable with known age data. Second, size-at-harvest data generally represent a loss in information from age-at-harvest data, therefore, the collection of large amounts of age data must be cost prohibitive. The amount of information loss will depend on how well the discriminant function performs. Third, the collection of large amounts of accurate, randomly sampled, size data must be feasible and inexpensive. Finally, morphological data in full-age-class SPR models may be of limited usefulness, as size-age relationships generally break down in mature age classes. If age classes are to be pooled, they must have homogeneous survival and harvest probability. Therefore, if morphological measurements cannot differentiate age classes with different harvest vulnerability and natural survival rates, additional age data will be necessary. More analysis of LFA is needed before full implementation.

5.9 THE IMPACTS OF ANTLER POINT RESTRICTIONS ON STATISTICAL POPULATION RECONSTRUCTION

Antler point restrictions are commonly used in the management of ungulate species as a means to control the age and sex composition of harvest (Hewitt 2014). Antler point restrictions can increase the recruitment of young males and produce older males for harvest, reduce overall

harvest pressure, and/or shift harvest pressure from antlered to antlerless animals depending on the severity of the restrictions and the harvest system to which they are applied (Hewitt 2011). The protected age classes are usually 1.5-2.5 year old males depending on the regulation and species. In order to apply SPR to a harvested population with antler point restrictions, the restrictions need to be consistent across the entire region to be modeled (see spatial scaling section).

There are two options for SPR modeling of male ungulate populations where harvest is subject to antler point restrictions. One option is for the proportion of each age class that is exempt from harvest due to antler point restrictions can be estimated based on independent data, which allows modeling of all harvested age classes. Alternatively, an SPR model can be used to model only age classes that are completely vulnerable to harvest. Such a model would begin at the lowest age class in which all animals are fully vulnerable to harvest for the remainder of their life (i.e., 2.5+ or 3.5+). Harvest of partially vulnerable age classes and age classes younger than the partially vulnerable classes would not be modeled. Female only SPR models and the female portion of 2-sex models are unaffected by antler point restrictions.

5.9.1 Estimating antler point-age relationship

A regionally representative sample of the antler point-age relationship is necessary in order to estimate the proportion of males in each age class that are eligible for harvest under antler point restrictions. An antler point-age relationship derived from harvest data may not be representative of the live population, therefore an evaluation of live animals is necessary. Antler point-age relationships must be evaluated at the regional scale at which model occurs because antler growth rates are often site specific (Hewitt 2011).

In order to estimate the probability that an animal of a given age is legal for harvest based on data from an antler point-age study, a binomial likelihood for each age class is added to the overall SPR joint likelihood model. In traditional SPR models abundance (N) is estimated as

$$N = \frac{h}{\hat{p}}$$

where h is the observed harvest, and $\hat{p}$ is the estimated harvest probability (Gast 2012). An SPR model augmented with data from an antler point-age study would estimate abundance in a partially closed age classes as

$$N = \frac{h}{\hat{p} \times \hat{v}}$$

where $\hat{v}$ is the estimated probability a male in the age class is eligible for legal harvest.

The effect of the partial closure of age classes on SPR models has yet to be evaluated. Before a full antler point-age study is undertaken, a small scale preliminary study is advisable. A preliminary study of the site specific antler point-age relationship would allow the variability in the antler point-age relationship to be estimated. Also, data from a preliminary study would be helpful in assessing the effect partially closed age classes may have on SPR model performance. A full study could then be designed with appropriate sample size and study design to ensure adequate precision of the partial closure parameter(s).

5.9.2 Modeling only the portion of the population vulnerable to harvest

The alternative to estimating the proportion of each age class that is vulnerable to harvest, is to only model age classes that are completely vulnerable to harvest. The youngest age class that is fully vulnerable to harvest would need to be determined. If harvest probability is constant

across fully vulnerable age classes a catch-curve analysis can be used to determine the youngest fully vulnerable age class (Robson and Chapman 1961). Otherwise, the youngest fully vulnerable age class must be determined based on a representative sample of live animals from the population being modeled. Alternatively, the minimum fully vulnerable age class could be assumed, however this untested assumption could bias model estimates. The structure of the model would be analogous to standard SPR models, however only age-at-harvest data for animals greater than or equal to the youngest age that is completely vulnerable to harvest would be used in the model. Many management agencies age harvested ungulates to only the first few age classes based on tooth eruption and wear (Hamlin et al. 2000). This is done because aging based on tooth eruption and wear is inaccurate for mature age classes, and alternatives, such as counting cementum annuli are expensive (Hamlin et al. 2000). A pooled age class SPR model of a population subject to antler point restrictions would require animals to be aged to at least 2 age classes, starting with the first fully vulnerable age class. This would require using aging procedures more advanced than tooth eruption and wear, thus increasing the cost of aging data. Additionally, "recruitment" would be into the youngest fully vulnerable age class. No information would be provided on younger age classes, which are generally the focus of many management questions.

5.9.3 Conclusion

Both analysis options for SPR modeling of populations subject to antler point restrictions require an investment in data not traditionally collected by management agencies. If aging data are currently available for mature age classes and the youngest fully vulnerable age class can be easily identified, modeling only fully vulnerable age classes is an appealing modeling option.

However, if detailed age-at-harvest data are unavailable for mature age classes, the additional resources required to improve ageing data may be better spent acquiring data necessary to estimate the antler point-age relationship of the population in order to model all harvested age classes (i,e, section 5.11.1). In addition to allowing more complete modeling, data on the antler-point age relationship of a harvested ungulate population could be used to refine antler point restrictions to ensure they have the desired effect. Also, data from tagged animals in an antler point-age study could potentially be used to directly estimate harvest rate, abundance or survival, providing a source of auxiliary data for SPR models.

5.10 SEASON STRUCTURE

In statistical population reconstruction, harvest is the primary sampling process. In order to draw statistical inference from the harvest data, SPR models must accurately model the harvest process. Thus, complex harvest regimes often require equally complex SPR models. In basic statistical population reconstruction, a single harvest season with a single form of take and short duration is modeled (Gove et al. 2002, Broms et al. 2010, Skalski et al. 2011). Breaking the harvest into multiple events, harvesting animals with multiple forms of take (hunting and trapping or archery rifle and muzzle loader seasons) and long duration harvest periods all complicate the modeling process.

If the hunting season is relatively short, natural mortality can be assumed negligible during the hunting season. In which case, harvest mortality and natural mortality can be modeled as conditionally independent processes (Clawson 2010). If harvest mortality (p) and natural survival (S) are conditionally independent, the probability an animal survives both mortality sources can be modeled as $(1 - p)S$. However, if the harvest period encompasses a biologically

significant period of natural mortality, harvest mortality and natural mortality should be modeled

as concurrent processes. When both harvest and natural mortality are modeled concurrently the

probability an animal dies due to harvest can be modeled as

$$\left(\frac{cf}{cf + \mu t}\right)\left(1 - e^{-(cf+\mu t)}\right)$$

where c is the harvest vulnerability coefficient, f is hunter effort, t is the duration of the harvest

season and μ is the instantaneous natural mortality rate (Clawson 2010). The probability an

animal dies from natural causes during the harvest season is then

$$\left(\frac{\mu t}{cf + \mu t}\right)\left(1 - e^{-(cf+\mu t)}\right).$$

The probability an animal survives both sources of mortality for an entire year is then $e^{-(cf+\mu T)}$,

where T is the entire annual time period (i.e, 365 days, 12months etc). This change in the

survival and harvest probability modeling allows for both mortality processes to occur at the

same time, thus accommodating long term harvest regimes.

If harvest is broken into multiple short non-sequential events, harvest and survival can be

modeled as conditionally independent processes. However an additional survival parameter is

necessary to account for natural mortality between harvests. For example, with a spring and fall

harvest system, the probability an animal is harvested in spring is parameterized p_{spring}. The

probability an animal is alive at the beginning of the fall harvest period is $\left(1 - p_{spring}\right) * S_1$

where S_1 is the probability an animal survives the natural mortality period between harvests. The

probability an animal is harvested in fall is parameterized p_{fall}, and finally the probability an

animal survives an entire year is $(1 - p_{spring}) * S_1 * (1 - p_{fall}) * S_2$, where S_2 is the probability an animal survives the natural mortality period after fall harvest. SPR can therefore be modified to accommodate multiple short harvest events that are broken up by discrete periods of natural mortality.

Alternatively animals are often harvested in a single, reasonably short period, which is broken up into discrete sequential sections by form of take. An example of such a harvest regime would be deer in most states that are subject to early archery harvest, muzzle loader harvest and then rifle harvest. If this is the case, the probability of harvest in each season section can be modeled as conditionally independent processes, analogous to the turkey example without the interim survival parameter. The probability of an animal alive at the beginning of the harvest season being harvested in any of the three season sections would be

$$p_{archery} + (1 - p_{archery}) * p_{loader} + (1 - p_{archery})(1 - p_{loader})p_{rifle}$$

It is necessary to model sequential forms of harvest as conditionally independent discrete sections if they can be reasonably assumed to have differential harvest vulnerability.

If animals are simultaneously vulnerable to harvest from multiple forms of take with differential harvest vulnerability, the multiple forms of take must be modeled concurrently. The overall probability of harvest in the season would then be parameterized

$$p = (1 - e^{-(c_1 f_1 + c_2 f_2 + c_3 f_3)})$$

where c_k is the harvest vulnerability coefficient for a form of take and f_k is the corresponding measure of hunter effort for that form of take. Wolf harvest in Montana is an example of a

harvest system which could be modeled this way. In Montana, archer, rifle and trapping harvest

seasons for wolves all overlap, but each form of take would need to be modeled with a different

harvest vulnerability coefficient.

Availability of effort and harvest data may constrain how the harvest processes can be

modeled. In order to model the harvest probability of a specific form of take, total harvest, age

composition of the harvest and hunter effort data must be take specific. When data are

unavailable to model minor forms of take, it is advisable at a minimum to accurately model the

most substantial forms of take first. Misspecifications of harvest vulnerability will contribute

bias to the model commensurate with the proportion of harvest for which they account. If only

5% of the harvest comes from a certain from of take, misspecification of its associated harvest

vulnerability coefficient will have little impact on the resulting parameter estimates. The priority

of resource agencies should be to provide quality data to model all substantial forms of take. If

only harvest data, but not hunter effort data, are available for minor forms of harvest, these minor

forms of take should be incorporated as known removals in the SPR model structure. Gast et al.

(2013k) modeled a wild turkey population in Missouri using landowner harvest as a known

source of take because no effort information was available. Known removals are incorporated

either before or after the probabilistic harvest takes place. If the known removals happen in a

discrete period before or after the probabilistic harvest, the impact of known removal modeling

will be minimal. However, if the known removals happen concurrent with a probabilistic source

of harvest the process will be improperly modeled and thus caution should be exercised. Failure

to model significant forms of mortality may have substantial consequences in terms of the bias

and precision associated with parameter estimates of SPR, the magnitude of which has not been evaluated.

5.11 **TWO SEX SPR MODELING**

Most harvested species are polygynous and therefore harvest focuses on the male portion of the population. In polygynous mating systems, females are the primary drivers of population demographics (Morris & Doak 2002), therefore most management concerns center around demographics of females and young animals (Lukacs et al. 2009). If only one sex is harvested, a single sex SPR analysis can be paired with annual sex ratio data in order to provide estimates of total abundance. Additionally, many harvested populations have at least limited harvest of females, providing the opportunity for two sex SPR modeling. Two sex SPR models exist on a continuum between a single SPR model with pooled sex data, if all parameters are shared, to two separate SPR models if no parameters are shared. Pooling sex data is possible when there is no sex specific selection in harvest, such as in some upland game bird species, or for some species which are harvested via trapping. Conversely, when survival or harvest vulnerability are not homogeneous between sexes a sex-specific SPR model is necessary. A sex-specific SPR model may be appropriate in species like elk, deer, and turkey where there is sex specific selection in the harvest. Differential harvest vulnerability between the sexes can arise because of animal behavior, hunter preference, regulatory restrictions or some combination thereof.

Sex-specific SPR modeling begins with two separate SPR models, one for each sex. Total harvest and harvest age composition data are necessary for each sex separately. If both sexes are eligible for harvest at the same time by all hunters, hunter effort data are not sex specific, otherwise hunter surveys must indicate sex specific effort. The male and female models can

share natural survival parameter(s), or if harvest is not sex selective, males and females can share harvest vulnerability parameters. Model selection procedures are used to determine which parameters can be shared between the two models (Gast et al. 2013a). Models are written and optimized together to allow for this sharing of parameters. Gast et al. (2013a) modeled male and female elk in Michigan with a 2 sex SPR model where each of the first 5 age classes had sex and age-specific harvest vulnerability coefficients, but males and females shared the same natural survival rate.

There are three options for auxiliary data to augment 2-sex SPR modeling. Each sex can have its own separate auxiliary to estimate sex specific abundance, natural survival or harvest vulnerability. Alternatively, a single auxiliary can be used which estimates a shared parameter, either survival or harvest vulnerability. Finally, total abundance (male and female combined) with no demarcation of sex, can be used as auxiliary data for a sex-specific SPR model. Total abundance is likely the least helpful form of auxiliary for sex-specific SPR models because total abundance is a convolution of male and female abundance (i.e., $N_t = N_m + N_f$). However, no formal evaluation of auxiliary data for 2 sex SPR models has yet been done.

5.12 DEMOGRAPHIC SPECIFICITY AND ROBUSTNESS OF SPR MODELS

In statistical population reconstruction models, abundance in a particular year and age class ($N_{a+1,t+1}$) is linked to the abundance in the previous year and age class ($N_{a,t}$) through natural survival (S_a) and harvest parameters ($p_{a,t}$)

$$N_{a+1,t+1} = N_{a,t}(1 - p_{a,t})S_a.$$

Initial age class abundance in a year (recruitment) is generally estimated independent from any of the previous year's abundance estimates. Previous attempts to model the relationship between recruitment and the previous year's abundance in SPR models produced accurate estimates of the stock-recruit relationship, but the resulting annual abundance estimates were biased (Gast 2012). The lack of specificity in the recruitment process of SPR models allows for robust and accurate estimation of age-specific abundance as well as natural survival and harvest rate parameters. These models are applicable to a myriad of species with substantially different reproductive biology, including greater sage-grouse (*Centrocercus urophasianus*), marten (*Martes americana*), black bear (*Ursus americana*), elk (*Cervus elaphus*) and deer (*Odocoileus* spp.) (Gove et al. 2002, Skalski et al. 2007, Conn et al. 2008, Broms et al. 2010, Skalski et al. 2011). Unfortunately, the lack of demographic specificity also means that little information is provided on the processes governing the recruitment process.

SPR models provide no information on animals that are not eligible for harvest. For many species the pre-harvest age period encompasses the first year of life, from birth to one year of age. The first year of life is a time period that has traditionally been a primary focus of monitoring efforts for harvested populations (Healy and Nenno 1985, Vangilder and Kurzejeski 1995, Miller et al. 1998, Ricca et al. 2002, Gilbert and Raedeke 2004, Robinson et al. 2014). The frequent estimation of detailed metrics of the recruitment process has traditionally been driven by a lack of abundance estimates. Without being able to monitor the state of the population abundance, managers have been forced to focus on studying demographic parameters that can be more readily measured.

Detailed metrics of juvenile recruitment are often studied with the assumption that changes in the recruitment process translate to commensurate changes in the number of animals recruited into the harvestable populaiton. For example, turkey poult survival and nest success are the focus of many studies of wild turkey demographics (Norman et al. 2001, Lehman et al. 2008, Fuller et al. 2013). Managers often assume that low nest success or high poult mortality will subsequently result in declines in the number of juvenile turkeys available for harvest in the following year. However, turkey poults are generally only monitored for the first 4 weeks of life, because after that time hens form brood flocks and poult mortality is difficult to monitor (Vangilder and Kurzejeski 1995). The assumption of a correlational relationship between early recruitment metrics and realized recruitment may often hold, however it is rarely tested in practice. SPR estimates of realized recruitment offer the opportunity to test the relationship between commonly collected recruitment metrics and realized recruitment (Clawson et al 2015). In this way, the broad viewpoint of SPR allows data to drive the prioritization of future field projects rather than relying on traditional assumptions. Additionally, the robust demographic structure of SPR provides a better understanding of the demographic process and allows for accurate future abundance estimates.

5.13 COVARIATES IN SPR ANALYSIS

The demographic processes of almost all animals depend to some degree on environmental conditions. Avian game populations have been shown to be highly vulnerable to spring weather conditions (Vangilder and Kurzejeski 1995, Roberts and Porter 1998a;b, Lowrey et al. 2001). Ungulate populations are generally less vulnerable to environmental perturbations, but have been shown to be affected by extreme weather conditions and habitat quality (Gilbert

and Raedeke 2004, Brodie et al. 2013). Gilbert and Raedeke (2004) found high rainfall paired with cold temperatures reduced fall recruitment of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in Washington. Brodie et al. (2013) found deep snow can negatively affect elk (*Cervus elaphus*) survival in systems where wolves (*Canis lupus*) are present. Additionally, environmental covariates can influence animals through food availability, which in turn can affect game abundance (Noyce and Garshelis 1997). In addition, high food availability can reduce animal movements and have negative effects on harvest rates (Ryan et al. 2004).

Given environmental covariates can affect the survival, harvest and recruitment of game species, their inclusion in population dynamics and harvest models, such as SPR, may be advantageous. Fieberg et al. (2010) modeled harvest probability as a function of both hunter effort and food availability within an SPR type model of black bears. Gast (2012) attempted to model elk harvest vulnerability as a function of extreme weather covariates thought to effect hunter efficiency. The specific environmental covariates included by Gast (2012) were found to be non-significant during the model selection process, however his work provides a framework for using environmental covariates in SPR.

The primary consideration, when including environmental covariates to estimate interannual variation in SPR parameters, is knowing which parameters they effect based on prior biological knowledge. If covariates are thought to effect harvest vulnerability they could be modeled in the form

$$p_i = \left(1 - e^{-\left(c + \gamma_i + \underline{\beta}\underline{X}'\right)f_i}\right)$$

where $\underline{X}'$ is a matrix of environmental covariates and $\underline{\beta}$ is a vector of estimated regression coefficients modeling harvest vulnerability (c).

Analogously, if covariates are thought to effect natural survival (S_i), survival can be parameterized

$$S_i = \frac{1}{\left(1 + e^{\left(\beta_0 + \underline{\beta}\underline{y}' + \epsilon_i\right)}\right)}$$

Where β_0 is the estimated base survival rate, $\underline{y}'$ is a matrix of environmental covariates and $\underline{\beta}$ is a vector of estimated regression coefficients modeling natural survival.

Traditional SPR model structure purposefully does not model a relationship between recruitment and previous abundance in order to increase the robustness of the model. However, if recruitment is highly dependent on an environmental covariate, it may be appropriate to add additional structure to the recruitment process being modeled. A stock-recruit relationship with environmental covariates could be modeled as

$$N_{i,1} = \left(e^{\rho + \underline{\beta}\underline{X}' + \epsilon_i}\right) \sum_{j=b}^{A} N_{i-1,j}$$

where ρ is a base recruitment rate, $\underline{X}'$ is a matrix of environmental covariates $\underline{\beta}$ is a vector of estimated regression coefficients modeling recruitment, and $\sum_{j=b}^{A} N_{i-1,j}$ is the total breeding abundance in year in the previous year..

By their very nature, environmental covariates model interannual variation in the demographic process to which they are applied. Modeling multiple sources of interannual variability simultaneously can cause instability in the numerical optimization process due to a lack of identifiability between sources of variation. Therefore, environmental covariates should be included within only a single demographic process, to avoid difficulty in numerical optimization and over-fitting the model (Gast 2012). Likelihood-ratio tests (Kutner et al. 2004) and AIC (Burnham and Anderson 2004) can be used to test the significance of regression coefficients and assess model support for the inclusion of environmental covariates.

Covariate modeling in SPR is not limited to environmental covariates. Skalski et al. (2011) modeled survival of Martens in Michigan as a function of the age where

$$S_i = \frac{1}{\left(1 + e^{(\beta_0 + \beta_1 age + \beta_2 age^2)}\right)}$$

Similarly annual survival (S_i) could be modeled as a function of abundance $\left(\sum_{j=a}^{A} N_{i,j}\right)$ to account for density dependent effects on survival

$$S_i = \frac{1}{\left(1 + e^{\left(\beta_0 + \beta_1 \sum_{j=a}^{A} N_{i,j}\right)}\right)}$$

where β_0 is the estimated base survival rate and β_1 is the estimated coefficient relating abundance to natural survival.

Modeling SPR parameters as functions of covariates has had limited application to date (Fieberg et al. 2010, Skalski et al. 2011). Further testing of the effects of including covariates on

SPR model outcomes is needed. Including environmental covariates may have little discernable effect on the precision or point estimates of parameters, however they may contribute substantially to the understanding of the biological processes driving the variation in model parameters. The covariate's relationship may also be helpful in projecting future abundance based on observed demographic and environmental conditions.

5.14 MODEL FITTING, SELECTION AND EVALUATION IN STATISTICAL POPULATION RECONSTRUCTION

Since the initiation of statistical population reconstruction (SPR) modeling (Gove et al. 2002), models have been repeatedly evaluated, modified and improved (Ryding et al. 2007, Broms et al. 2010, Skalski et al. 2011, Skalski et al. 2012b). The models proposed by Gast (2012) significantly change the previous SPR model structure, deriving abundance estimates based on a Horvitz-Thompson type estimator

$$\widehat{N}_{i,j} = \frac{h_{i,j}}{\widehat{P}_{i,j}}$$

where $\widehat{N}_{i,j}$ is the abundance estimate, $\widehat{P}_{i,j}$ is the harvest probability estimate and $h_{i,j}$ is the observed harvest count all in year i age class j, rather than estimating abundance of the age classes present in the first year, and the initial age class in each subsequent year directly (Gove et al. 2002). This change in model structure reduces parametrization, increases stability of numerical optimization and produces more accurate variance estimates. Gast (2012) also provided guidance for the inclusion of random effects into the SPR model structure, allowing demographic processes (i.e., harvest and survival) to be modeled with interannual variation.

Based on these substantial improvements in variance estimation and model realism the models offered by Gast (2012) are preferable for future application of SPR.

Regardless of the SPR model structure used, model selection and evaluation are closely related endeavors that are fundamental to the successful application of SPR. A model which best fits the data but produces unreasonable parameter estimates is not useful, and equally as problematic is a model which produces reasonable parameter estimates but is not supported by the data. Therefore, while model selection and evaluation are different processes they are inherently dependent on one another. Model selection and evaluation must then be used in concert in order to choose the "best" modeling option from both perspectives simultaneously.

5.14.1 **Model selection and evaluation**

Model selection should begin with a strong pool of candidate models based on preliminary data evaluation as well as detailed knowledge of the harvest system and biology of the population being modeled. For fixed-effects SPR models, likelihood ratio tests (Hogg and Craig 1978 p. 413-422) can then be used to select between nested candidate models. Information-theoretic approaches such as AIC offer a method of selecting between non-nested fixed-effects models (Burnham and Anderson 2004). Model selection for mixed-effects SPR model, and non-linear mixed-effects models in general, is both complex and without a widely accepted methodology (Gast 2012). The selection of mixed-effects models is complicated by the choice of whether to first select for which fixed effects are to be included and then select random effects or vice versa. Additionally, modelers must choose whether to evaluate models based on marginal or conditional likelihood values and how to determine the "effective" number of parameters (Bolker et al. 2009). The details of these choices are beyond the scope of this chapter

and are well summarized be Gast (2012). The best guidance for mixed-effects SPR model selection is as follows:

1. Fit the most complex model which is biologically plausible with only fixed effects parameters.

2. Select random effects for inclusion using sequential modified likelihood-ratio tests (Self and Liang 1987), based on the conditional likelihood values.

3. Use marginal AIC to sequentially remove fixed effects parameters which do not significantly improve the fit of the model.

By initially including all plausible fixed effects parameters in the model, potential random effects are not constrained. Modified likelihood-ratio tests are used because selection for random effects violates the boundary assumption of traditional likelihood-ratio tests (Self and Liang 1987). While these procedures do not represent an iron clad method of model selection, because one does not exist, they do represent the best available knowledge. The area of model selection for nonlinear mixed-effects models is an important area of future research.

The model selection procedures detailed above should be used in conjunction with model evaluation procedures to choose the best overall model. The primary model evaluation strategy for SPR models is to evaluate parameter estimates for biological realism and compare them to independent data sources (Clawson et al. 2013). For instance, natural survival estimates above 1 may be an indication of model misspecification depending on the magnitude of the point estimate and its associated variance. Estimates of natural survival very near 1 with confidence intervals which span 1 and encompass probable values may arise due to sampling error. However, estimates drastically larger than 1 with no possible values contained in the associated confidence interval may indicate serious model misspecification. Therefore I do not recommend

reparametrizing natural survival so that it is bounded between 0 and 1 (i.e., logistic transformation) as it will hide potential model misspecification. Comparisons for biological realism can be based on estimates from the literature from similar population or more preferably from independent data from the population being modeled. Indices are a good candidate for this type of confirmatory data because they are not useful as auxiliary data in SPR models and are inexpensive to collect. Skalski et al. (2007) compared trends in mule deer abundance resulting from an SPR model to an index of browse damage, finding the very similar trends in both. If trusted indices do not compare favorably with trends estimated from SPR models, additional evaluation of both the model structure and indices are necessary.

Point deletion methods offer an additional form of model evaluation for SPR models and should be used in conjunction with checks for model realism (Clawson et al. 2013). In point deletion evaluations successive years of data are removed from the front or back of the time series of data, new SPR models are then fit to the truncated data sets. High sensitivity of parameter estimates to minor degrees of point deletion is cause for concern and may indicate data are insufficient for SPR modeling (Clawson et al. 2013).

Finally, SPR models using the original parameterization (Gove et al. 2002) should also be evaluated using Anscombe residuals (Anscombe 1953) of observed vs expected harvest counts plotted against both age and year (Clawson et al. 2013). Trends in residuals across ages or years as well as large numbers of residual points outside of +/-2 indicate a lack of model fit. SPR models which use the Horvitz-Thompson type estimator of abundance (Gast 2012) cannot be evaluated using residuals because the observed and expected harvest counts are the same.

5.14.2 **Model fitting**

Due to the complexity of the SPR likelihood structure, calculation of closed form parameter estimates are intractable. Numerical optimization is therefore required to derive maximum likelihood estimates of parameters. Numerical optimization is a complex process, often referred to as more of an art than a science. Diligence is therefore required to assure any optimization routine converges to a global maximum. Users should use multiple different sets of starting parameter values and if available, different optimizers with varying step size and convergence criteria to assure the global maximum is found. Quality initial parameter values and properly scaled data inputs can greatly aid in the optimization process. Specifically for SPR models, hunter effort should be scaled to be on the order of 1 or 0.1 in order to aid in stable optimization. The program chosen for analysis will determine the optimizers which are available. The Solver function in Microsoft excel is inadequate to reliably fit SPR models. R (www.r-project.org) and USER (http://www.cbr.washington.edu/analysis/apps/user) offer traditional newton-rhapson and simplex optimizers, that with diligence can be used to fit SPR models. Automatic differentiation based optimization routines (i.e., AD Model builder (www.ADMB-project.org) and PopRecon (http://www.cbr.washington.edu/analysis/apps/PopRecon)) offer a more stable alternative to traditional optimization routines (i.e, SIMPLEX and Netwon-Rhapson) when fitting SPR models.

5.15 CONCLUSION

The complexity of harvest systems and equal flexibility of SPR offer a seemingly infinite number of possible model structures, each with its own opportunities and challenges. This dissertation offers guidance to game managers seeking to use SPR as part of their management strategy. Given the almost unlimited scenarios that are possible, each application of SPR will need to be tailored to the specific biology, geography and harvest policies of the game population being modeled.

Throughout this chapter the need for representative data, collected at appropriate spatial scales, is highlighted repeatedly. Managers need to collect data through statistically rigorous sampling methods, avoiding convenience sampling, if at all possible (Anderson 2001). Additionally, it is important to realize that population reconstruction models must be constructed to accurately reflect the harvest process. Harvest and hunter effort data need to be collected at the geographic and regulatory scale at which SPR will occur. Successful implementation of SPR will require close coordination between game managers, field biologists, and biometricians to produce realistic and accurate reconstructions of population abundance and trends. Armed with information on abundance, recruitment, natural survival and harvest rate, game managers should be better equipped to manager wild populations into the 21st century.

Chapter 6. MANAGEMENT IMPLICATIONS OF THIS RESEARCH

Currently, most state management agencies use uncalibrated indices to monitor harvested populations (Rupp et al. 2000, Sands and Pope 2010, Collier et al. 2013). This was an acceptable method of management during a period when the main goal was to increase game abundance and recover depleted game populations (Schmidt 1980). However, today's changing priorities of management agencies and increased scrutiny from non-consumptive stakeholders (Jacobson and Decker 2006) is causing management agencies to reevaluate how game populations should be monitored (Mason et al. 2006). Statistical population reconstruction offers a cost effective alternative to the use of indices or conducting annual abundance estimates as a primary monitoring tool.

Statistical population reconstruction (SPR) has the potential to be a powerful monitoring tool for game management agencies. Prior to the work done in this dissertation there were two primary barriers to wide spread management application of SPR. First, there was no information on the relative utility of using auxiliary data sources in SPR. In Chapters 2 and 5 of this dissertation, the relative utility of abundance, survival, and harvest rate auxiliary data were comprehensively evaluated. Estimating natural survival was shown to have the highest utility in improving the precision of SPR abundance estimates. In addition, Chapters 2 and 5 also provide general sample size requirements for auxiliary studies. Based on this research managers can now efficiently implement SPR by identifying existing data sources that can be used as auxiliary data. More importantly, managers can now design effective SPR auxiliary field studies, balancing their utility to SPR models with other management objectives.

The second barrier to SPR implementation I addressed in this dissertation was the lack of information available on minimum harvest and hunter effort data requirements. Rigorous evaluation via simulation showed that, with quality auxiliary data, statistical population reconstruction can be applied with as little as 4 years of age-at-harvest and hunter effort data. Further evaluation revealed that the precision of SPR parameter estimates was more dependent on the precision of auxiliary data, than the number of years of harvest and hunter effort data, over the period examined (e.g., 10 years). Based on this information, managers do not need to wait for decades to start implementing SPR. This means more populations can being SPR analysis sooner with less cost. The guidance on planning horizons and sample size recommendations is important when proposing major changes in harvest data collection and auxiliary field studies to support SPR.

The parameter estimates provided by statistical population reconstruction models can be used for more than simply supplanting indices for trend monitoring. Chapter 3 illustrates the use of output from SPR to model an extensive historical data set, which otherwise was almost completely ignored. The result was a spatially explicit view of 50 years of population growth and hunter response to an emerging game population. The slow response of hunters to an emerging game population, observed in this study, can serve as a point of reference for future game bird reintroduction planning. Furthermore, empirical evidence that hunters historically value convenience at the expense of higher game abundance may affect how agencies choose to allocate management efforts. Finally, the 50 year time series of realized recruitment estimates, provided a unique opportunity to test some of the long held beliefs regarding turkey recruitment and weather, reinforcing some and challenging others. The utility of SPR model output clearly

goes well beyond simply monitoring the trends of harvested populations and setting next year's harvest regulations. Further, this approach offers managers a unique ability to answer questions which were previously intractable.

Another important management implication is the projection of future abundance in order to set harvest regulations in a proactive manner. Chapter 4 provides a rigorous evaluation of methods to project the simple time series of abundance and reconstructed populations into the future. $N_{t+1} = N_t$ was a surprisingly adequate projection model for many populations. Expectedly, models which included survival and recruitment data from SPR models were shown to produce the most accurate projections of future abundance. From these results game managers have quantitative guidance on projecting next year's abundance, allowing them to set purposeful harvest policies and reduce potential conflicts with a variety of stakeholders.

This dissertation provides the information and guidance necessary to increase the potential management applications of SPR. Detailed guidance on model scaling and data sampling considerations will help managers critically evaluate model assumptions and allow for effective collaboration with biometricians when designing SPR modeling frameworks. Additionally, managers understanding the fundamental assumptions which underlie the modeling process will increase their confidence in the method, leading to broader acceptance of SPR in the resource management community. Further, solutions for modeling populations, with two-sex harvest, pooled age class data and those subject to antler point restrictions, increase the potential management applications of SPR. This dissertation also explored the use of morphological measurements in order to supplant or augment age composition data for widely harvested ungulate species. Incorporating morphological data in SPR has the potential of expanding its use

to more populations which need rigorous management and at the same time reduce costs when state budgets for game agencies are being reduced.

Statistical population reconstruction is a flexible, powerful and efficient monitoring framework that takes advantage of commonly collected data to estimate age-specific abundance, natural survival and harvest rates. Management application of SPR has the potential to improve inference from and/or reduce the cost of annual monitoring of game populations, thus providing management agencies additional resources and data to accommodate the additional scrutiny and mandates associated with increasingly diverse stakeholder groups. The information contained in this dissertation will facilitate the broad scale management application of SPR, a process which has the potential to fundamentally change how harvested wildlife are monitored in the United States.

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