MODELING FOR THREATENED AND ENDANGERED SPECIES MANAGEMENT: THE COLUMBIA BASIN PYGMY RABBIT AND THE GREATER SAGE GROUSE IN WASHINGTON

By

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The amount of support and encouragement I have received from friends, family and professors is enormous. I would like to mention two who are of particular importance by name. My wife, Christine, is partner to all my endeavors in ways only a spouse can be. She provided a loving home life, good food, and a perspective born of her own perseverance in life. My friendship with a colleague, Allyson Beall, grew from acquaintance to office mate to trusted collaborator and friend. Her encouragement and example are without equal.

The Washington Department of Fish and Wildlife supported my Ph.D. by funding two years of my graduate work. They provided me with the unique and exciting opportunity to be the field biologist at the first reintroduction of an endangered species, the Columbia Basin pygmy rabbit. They have graciously listened to the results of my analysis and expressed gratitude for the perspective it gives to the recovery effort.

The former Program in Environmental Science and Regional Planning at WSU supported me with TA positions and better office space than most graduate students ever see. Dr. Bill Budd, then chair, had enough faith in me (and Allyson) to send us to a conference where we, were able to network with sage-grouse working groups and get involved with a local conservation district modeling age-grouse and land use. The manager of that district, Britt Dudek, is forward looking and was eager to put the best technology to work to help his district maintain viability as a rural and agricultural society for the next several decades.

I trust that those who have made this dissertation possible are glad they have worked with me and find what I have done for their projects both worthwhile and useful.

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Abstract

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Threatened and endangered species are the hallmark of the biodiversity crisis of our times. The listing of species by governments prompts research and management to prevent further declines and to conserve and restore populations at sustainable levels. The shrub-steppe of eastern Washington hosts two species at risk, the Columbia Basin pygmy rabbit (*Brachylagus idahoensis*) and the Greater sage-grouse (*Centrocercus urophasianus*). Conservation and restoration requires tools to assess risk of population decline or extinction for species and to strengthen restoration plans that must integrate many forms of knowledge from science to expert opinion to local ecological knowledge. Computer models are powerful tools for these purposes. Software for population viability analysis has been specifically developed to make risk assessments. Other computer modeling programs such as system dynamics are adaptable to the task of integrating knowledge, simulating systems and providing a method for testing and supporting management decisions. As well, many general statistical methods and models can be used to analyze raw data on species and systems of concern. The Columbia Basin pygmy rabbit exists

only in a captive breeding program, which was unable to produce sufficient numbers of rabbits to support a reintroduction effort in 2007 and 2008. Population viability analysis was used to determine where the demographic bottleneck exists in the population and to explore where research efforts should be concentrated. It also defined a risk of extinction to the population if harvest for reintroduction was continuous over the several years most likely required to restore rabbits to the wild. Correlation and regression tree modeling was used to compare the survival of an experimental pygmy rabbit reintroduction that occurred in 2004 with the first actual release of captive reared animals back into a portion of their historical range. Population viability analysis was also performed for a remnant population of sage-grouse in eastern Washington. It was coupled with a system dynamics model that incorporated the land use complex and habitat suitability of remaining sage-grouse habitat in Washington. The system dynamics model was a participatory modeling exercise with a local conservation district designed to provide them with a land use planning and wildlife management tool.

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CO-AUTHORSHIP STATEMENT

Chapter 2 is largely my analysis of the captive breeding program for the Columbia Basin pygmy rabbit. It is co-authored with Rod Sayler and Rob Wielgus, members of my committee, who kept me on the straight and narrow of scientific investigation and without whom the work would not be as focused or accurate. Rob Wielgus has been my mentor for population analysis.

Chapter 3 is a paper that came about through a collaborative modeling project sponsored by the Foster Creek Conservation District, Waterville, Washington. The effort included a fellow Ph.D. student, Allyson Beall, and several members of the District. The report to the District was titled "The Foster Creek Sage-grouse and Human Systems Model" (2005), reflecting their focus on the interaction between human land use and the needs of wildlife. The report has two main features, a system dynamics model and a population viability analysis. Allyson Beall was the primary author of the system dynamics model. I was the primary author of the population viability analysis of this chapter. Our vision was, and still is, to combine system dynamics modeling with other established model types to enlarge the scope of investigations as well as to engage a wide audience of stakeholders. We use models as learning, management and planning tools for conservation. This portion of the dissertation would not have been possible without Allyson's expertise in systems modeling and communication with stakeholders of the District. Rod Sayler is co-author for his guidance in analysis and with the finished product as well as being a sounding board for me as I developed the population viability analysis.

Chapters 2 and 3 are in the format of journal articles as required by the peer reviewed journals to which they have been submitted.

Dedication

To all those who love life in its many manifestations and seek to preserve it.

To all my relatives.

PROLOGUE

What began for me as an exercise in system dynamics modeling under Professor Andy Ford and a class in population biology under Professor Rob Wielgus, turned into a box of tools for investigation and problem solving. While engaged in those classroom exercises, I often wondered at the distance between academia and the rest of the world, the world where the problems exist that we as students are supposed to be learning to understand and attempting to solve. I became aware early on in my studies that bridges between academia and practical management, between knowledge and application, were a vital part of improving human performance in the world and in reaching towards societal goals related to preservation of species and conservation of biodiversity.

Tools are often developed and refined in academia because of the emphasis on theory in that arena and because academics have time to work on such things, and in all fairness to them they are the part of our cultural system so charged. We could not do it without them. However, if academic methods cannot be put to work "on the ground" their value is limited to dusty papers. Without practical application, our theoretical work in ecology and conservation biology is, to me, of little value because theory can only makes progress when we get our hands dirty, test the theories and use the tools. As well, the feedback from these practical efforts is essential for academia to do its job. So I took the tools of systems and population modeling that I was taught and put them to work to address important and pressing issues in the area of threatened and endangered species management, one of the main prongs of conservation biology and indeed the reason the discipline was founded.

My intent in university has been to learn and through that learning gain insight into the workings of our amazing natural world and our relationships to it while at the same time providing tools for more effective land and species conservation. The papers herein are the result of practical problem solving using the information at hand or data collected from scientific investigation for two species of concern in Washington State, the Columbia Basin pygmy rabbit and the Greater sage-grouse. Problem solving has taken the form of computer modeling by which a wide range of data types can be synthesized and a system can be simulated under varying conditions. At the end of the day, I want to be able to say that I have not only loved life but also invested myself in its integrity.

Work with the Columbia Basin pygmy rabbits was conducted under animal care protocol 3097 of Washington State University. Pygmy rabbit research was supported by the Washington Department of Fish and Wildlife, the Washington Cooperative Fish and Wildlife Research Unit, and The Nature Conservancy. The Sage-grouse and Human Systems Model was funded by the Foster Creek Conservation District, Waterville, Washington.

CHAPTER ONE

INTRODUCTION

1 Introduction

1.1 Threatened and endangered species

We like to think that we are different than our predecessors, and indeed we are. Those of us alive in the 21st century are witness to the greatest loss of species that has occurred in the Earth's history in 65 million years. Leakey & Lewin (1995) call it the "sixth extinction" equivalent to the other five mass extinctions evident in the geological record. Environmental change and degradation in some degree have always accompanied human settlement (Diamond 1992). However, in our times, as a consequence of human population growth and corresponding demands upon the living systems of the earth for space, food and goods, populations of other living things are being exploited as well as pushed into rarity and extinction. Rates of extinction now exceed the expected rate typical in the fossil record by 5,000-25,000 times (Lawton & May 1995).

The loss of biodiversity has many proximal anthropogenic causes including land conversion and habitat loss, pollution and toxins released into the waters, soils and air, and over harvest. The process of decline for any one species may not be noticed until it is suddenly absent from its usual haunts. For many species, the process and the loss will never be noticed as an individual event. Yet we know from a biological perspective that every one of them has functions and relationships in its environment and when one goes missing adjustments and changes must and do occur. Ecosystem change may be what Dan Janzen (1986) called a "blurry catastrophe", a process that goes unnoticed until a threshold level of change is reached and a sudden catastrophic shift occurs (Scheffer et al. 2001; Walker &

Meyers 2004). In general, the result is a shift from an ecosystem that is more productive to one that is less productive (Rapport & Whitford 1999). To return a biological system back across that threshold may be physically difficult or impossible, not to mention politically difficult or prohibitively expensive. As biological beings, we are dependent on biological processes for many of the goods and services that make our lives both possible and meaningful. Clean water, clean air, productive soils and productive ecosystems have been called the "commons" (Hardin 1968) and generally taken for granted. We now know they are not immune to abuse nor are they "free" in the economic sense that no one has to account for their existence or condition. Much contemporary human endeavor is driven by an economic system that has externalized, i.e. not accounted for, the effects of human activity on biodiversity and natural processes, also known as non-market goods (Pearce & Moran 1998). Yet we are fundamentally dependent on this one planet in a direct manner for foods, fibers, medicines and recreation and indirectly for functional benefits such as flood control, carbon sinks, weather regulation and human culture.

The depth of the biodiversity crisis became "painfully obvious" to scientists and ecologists in the 1960's and 1970's (Meffe & Carroll 1997). The new synthetic science of conservation biology came into existence with the founding of the Society for Conservation Biology in 1985. Michael Soulé (1985) called it the "crisis discipline" and its purpose is to head upstream against the trend to extinction. Knowing that many species are already extinct, many are close to extinction, and that humanity will continue to press the stability of the biological world, conservation biology addresses the question of minimums and of how much or how little is enough (Soulé 1987). The discipline addresses questions of minimum size for populations to persist in evolutionary time, for the long term, and what conditions of habitat and environment are necessary for that persistence. Although conservation biology is overtly biological with scientific roots in community and ecosystem ecology, it is also cross-disciplinary and interfaces with areas of law and policy and society. In other words, conservation biology recognizes that the loss of biodiversity and risks to life as we know it is a human problem in both source and solution. Focus at the scientific level is on viable populations based on population dynamics and genetics and on how populations at risk can be maintained or their extinction prevented in fragmented and changing landscapes. Focus at the societal level is on law, policy and cooperation.

Categories of risk for animals and plants have been defined by the International Union for Conservation of Nature (IUCN 1996, 1997) that include critically endangered, threatened and vulnerable based on rate of population decline, restriction of habitat area, current population size and the probability of extinction over time frames ranging from 10 to 100 years. Many world governments have their own criteria as well, including the United States, which passed an Endangered Species Act (ESA) in 1973. The ESA has a single species focus that evaluates each species on an individual basis for listing as threatened or endangered. Protection is given to listed species which become special subjects of management and recovery plans. Quantification of population status and risk are critical considerations in listing, de-listing and management. Once a species is listed, hard questions and difficult decisions are the rule of the day running the gamut from habitat protection to captive breeding and reintroduction. How many animals in how many populations in how much habitat are the basic questions that require quantified assessments if not absolute answers. How many animals can be harvested for human use or relocation, where should they be placed and how can we account for catastrophe and uncertainty? Less quantifiable but equally difficult questions are social in nature. What constitutes an acceptable level of risk to a species or an ecosystem? How can local and regional communities be integrated into conservation and recovery plans, especially when critical elements in species survival mean changes to local land use, resource extraction and lifestyles?

Many kinds of knowledge and broad cooperation must be brought to bear on the task of recovery. Computer models provide a suite of tools for synthesis, learning and simulation of the numerous threatened and endangered species and systems that are now a common part of our world. The subject of this research is demographic modeling and risk assessment for two species in Washington (WA), USA, the Columbia Basin pygmy rabbit (*Brachylagus idahoensis*) and the greater sage-grouse (*Centrocercus urophasianus*). Both species are characterized by small population sizes with attendant losses in genetic diversity and risk of further decline and extinction.

1.2 The Columbia Basin pygmy rabbit (*Brachylagus idahoensis*)

1.2.1 Status of the pygmy rabbit in Washington

The Columbia Basin (CB) pygmy rabbit (*Brachylagus idahoensis*) is a shrub-steppe obligate that requires mature sage brush for both food and cover (Gahr 1993;

Green & Flinders 1980; Weiss & Verts 1984). It is a small lagomorph weighing ~450-600g at maturity, and one of only two species in North America that dig their own burrows; the other is the volcano rabbit (*Romerolagus diazi*) in Mexico (Nowak 1991). Consequently, deep loose soils are an important habitat element in areas used by the pygmy rabbit. Although widespread in the intermountain West, pygmy rabbit populations are patchily distributed in big sagebrush landscapes where sagebrush and soil requirements are met (Gabler 1997; Roberts 2001). Large scale loss of sagebrush to agriculture, especially areas with deeper soils, has restricted the range of the rabbit in Washington as well as across much of its historical range (Knick 1999; WDFW 1995). Threats to remaining areas of big sagebrush relative to pygmy rabbit habitat quality are fire, recreational use (WDFW, 1995) and possibly livestock management (Siegel 2002).

The CB population of pygmy rabbits found in central WA state is considered a distinct population segment due to its long dissociation for ≥10,000 years from other populations in the adjacent states of Oregon and Idaho (Lyman 1991). The pygmy rabbit was declared threatened in 1990 and endangered in 1993 by WA State. Emergency listing of the CB pygmy rabbit in 2001 under the ESA (Federal Register November 30, 2001) precipitated a series of management decisions that removed 16 individuals from the wild in that same year for a captive breeding program. All the rabbits were captured at the Sagebrush Flat Wildlife Management Area (SBF) in central Washington, the last known area of their occurrence in the state. No CB pygmy rabbits or active burrow sites have been found in the wild since 2004, and the pygmy rabbit is now considered extirpated in the state (USFWS, 2007). The captive population exhibited apparent inbreeding depression that resulted in low reproductive output, susceptibility to disease and a declining population size even under intensive management (USFWS 2007). Emergency genetic rescue was initiated in 2003 by intercrossing the captive CB rabbits with individuals from Idaho populations (USFWS 2007). The rescue was successful and the captive population exhibited increased reproductive success to the point that the first apparent surplus individuals were ready for reintroduction back into the wild in 2007.

1.2.2 Recovery objectives for the Columbia Basin pygmy rabbit

The goal of the pygmy rabbit reintroduction program is the recovery and maintenance of this ESA listed species to the level of a secure, self-sustaining population (USFWS 2007). The USFWS draft recovery plan (2007) states that management actions must " . . . sufficiently abate threats to free-ranging CB pygmy rabbits to ensure a high probability of the population's persistence within their historical distribution over the foreseeable future". Recovery goals are being pursued with a variety of actions in an adaptive management framework that include genetic rescue, habitat management and improvement, predator control, involvement of land owners both public and private, and the attempt to re-establish a number of local populations that will constitute a resilient metapopulation that can withstand long-term demographic threats.

Due to uncertainties in how recovery will progress and because of the need for more information on the ecology and life history of the pygmy rabbit, the USFWS (2007) has proposed a range of delisting criteria based on the 50/500 rule of Soulé (Soulé & Wilcox 1980). This rule provides an approximation of a minimum viable population that requires and effective population size (N_e) of 50 breeding individuals as a minimum to prevent inbreeding in the short term an N_e of 500 breeding individuals as a minimum for maintenance of long-term genetic variability and adaptability. The State of Washington also has specific recovery objectives and delisting criteria (WDFW 1995). Downlisting from endangered to threatened will require a 5-year average of at least 1,400 adult pygmy rabbits in six subpopulations. Delisting from state threatened status will require a 5-year average of at least 2800 adult pygmy rabbits in at least 12 subpopulations. Both changes in status also require habitat security for the recovered populations.

Within the larger recovery program, this study followed the first pygmy rabbits to be reintroduced into a portion of their former range at SBF on March 13, 2007, when 20 captive bred pygmy rabbits were brought "home."

1.2.3 Study Area

The primary reintroduction site designated by the Pygmy Rabbit Science Team is Sagebrush Flat Wildlife Management Area in central Washington. It consists of 1,311 ha of shrub-steppe landscape in south Douglas County. The term "shrub-steppe" as used by Daubenmire (1970) refers to plant communities with a conspicuous over story of shrubs with one or more layers of grasses and forbs underneath. SBF falls into his vegetation climax category of big sagebrush-bluebunch wheatgrass (*Artemisia tridentata, Psuedoregneria spicata*). The aspect is generally southern. Elevation ranges from 488-579 m. Average annual precipitation is 20 cm and temperatures range from -3° to 38°C. Soils are deep with a sandy loam texture (Kehne 1991).

Site preparations implemented by The Washington Department of Fish and Wildlife (WDFW) included the removal of obsolete structures and fences that could act as perches for raptors, a potential predator. Grazing by cattle was discontinued in 2001. Fire management plans are being developed and firebreaks surround and bisect the entire site. Predator removal was deemed unnecessary before reintroduction, but was initiated shortly after the release due to the observed level of predator induced mortality.

1.2.4 Reintroduction of the Columbia Basin pygmy rabbit to Sagebrush Flat, Washington in 2007

The USFWS (2007) has prepared a draft recovery plan in cooperation with WDFW and the Columbia Basin Pygmy Rabbit Recovery Team. There is also a Washington State Recovery Plan (WDFW 1995) with addenda (WDFW 2001, 2003). These provide the criteria for recovery and conservation of the pygmy rabbit in WA. Under guidance of these documents and the Recovery Team, the return to the wild of the first founder population of CB pygmy rabbits occurred in 2007. The overall goals and procedures for this specific release are outlined in a reintroduction plan (Sayler et al. (2006). Rabbits selected for release were those with at least 75% CB genetic makeup and considered non-essential for maintenance of the captive breeding program (USFWS 2007; K. Warheit, WDFW, pers. com.).

A pilot reintroduction study completed in Idaho (Westra 2004), coupled with results of ongoing studies of captive pygmy rabbits at the University of Idaho (Estes-Zumpf & Rachlow 2008; Sanchez 2007) and Washington State University (Sayler, pers. com.) provide a good background for planning reintroductions of CB pygmy rabbits in Washington. The pilot study released Idaho rabbits reared in captivity onto the Idaho National Laboratory (INL) in 2002-2004. This work demonstrated the feasibility and potential for success that could be expected from future reintroduction efforts in Washington. The experimental release utilized artificial burrows which have been successful with burrowing owls (*Athene cunicularia*) (Beltoff & Smith 2003), prairie dogs (*Cynomys parvidens*)and black-footed ferrets(*Mustela nigripes*). Methods similar to those developed for releasing Utah prairie dogs and black-footed ferrets (Biggins et al. 1999) were used to create artificial burrows to partially replicate natural burrows. Soft and hard release techniques were evaluated. Westra (2004) found that captive-reared pygmy rabbits traveled well for 10 hours to the release site. They also acclimated well to both artificial and natural burrows and made quick adjustment to natural foods, a large portion of which is basin big sagebrush (*Artemisia tridentata*). Month of release was important in the pilot study. Survival from release until the breeding season in early March ranged from 0% for July, 43% for August, 55% for September, to 71% for the last release group in February. Therefore, a late winter release close to the breeding season should limit mortality, which can be more carefully controlled in the captive rearing facilities than in the wild. The release date chosen for Washington (March 13, 2007) coincided with spring green-up at SBF and the start of the breeding season. The largest possible number of rabbits entering the breeding season in the wild will presumably provide the greatest potential for success.

Sites for installation of artificial burrows were located at SBF by a team of WDFW experts, Rod Sayler of the Pygmy Rabbit Recovery team and myself using visual cues and knowledge of former occupied burrow sites (Sayler et al. 2006). Burrows were located in two spatially distinct groupings to avoid a high density of burrows that could result in increased predation, as was the case in the pilot study in Idaho (Westra 2004). Having two clusters also provided opportunities to evaluate edge effects and other ecological variables potentially related to dispersal, habitat quality, and habitat use of released pygmy rabbits (Sayler et al. 2006). Forty locations were marked and artificial burrows were installed in November, 2006. Each was marked by hand-held GPS and the coordinates downloaded into GIS software. Natural burrows adopted by released rabbits were marked in the same way to provide a detailed record of burrow location and use over time.

Each artificial burrow was constructed from a 3 m length of perforated, corrugated plastic drainage tubing (10 cm diameter). The pipe was buried in a shallow, v-shaped trench approximately 0.75 m deep at the bottom center and sloped gradually upwards at both ends. Openings were configured to come out under sagebrush plants as a means of hiding them and mimicking natural burrow entrance locations. Both ends of the pipe were open. Soil disturbance was kept to a minimum and the fill over the burrow was packed in by the weight of the workers. Additionally, dead sticks of sagebrush were dropped on top of the fresh soil. It is known that pygmy rabbits build and use extensive burrow systems (Wilde 1978). Therefore, in the center of each tube, an 8cm x 8cm opening was cut to provide a means for a rabbit to dig out sideways and begin construction of alarger burrow system.

The Idaho study (Westra 2004) did not conclusively demonstrate the benefits or detriments to survival of providing artificial burrows for released pygmy rabbits. It is possible that artificial burrows provide initial hiding cover from predators and may also minimize translocation stress until natural burrows can be dug or located by the released animals. It is a high priority objective to continue to evaluate and improve the techniques related to provisioning of artificial burrows to determine whether their use will be desirable in future releases, whether initial or supplemental (Sayler et al. 2006). A late winter release on frozen ground would limit, if not prevent, natural burrowing activity. Therefore, artificial burrows may provide a necessary initial safety factor at that time of year.

Unfortunately, the first release was not successful and the field portion of this study was largely terminated at the end of June, 2007, when only two rabbits remained alive (Utapau, field ID M6, and Impala, field ID F4). Impala was taken by a raptor on August 13, 2007, and Utapau's empty collar was found on October 27, 2007, officially terminating the first reintroduction effort. The plan had been to gain demographic and behavioral data that could be used to analyze distributional patterns and habitat use, but it turned out that sample size was too small when only four rabbits remained alive in the wild after three weeks (Appendix A). A planned habitat use and relationship study was not feasible due to small sample size although burrow use and radio telemetry locations were recorded. Research efforts were turned to population viability analysis (PVA) of the captive pygmy rabbit population to investigate its potential to provide surplus rabbits for continued reintroduction efforts. Chapter 2 is a PVA produced for the CB pygmy rabbit breeding and reintroduction program. These analyses are based on the demographics of the breeding program (Appendices B, C, D, E). The unsuccessful first attempt to reintroduce captive pygmy rabbits limited the expansion of the PVA to include a reintroduced/wild population dynamic because the released rabbits did not survive long enough for the calculation of meaningful demographic rates.

1.3 The Greater sage-grouse (*Centrocercus urophasianus*)

1.3.1 Status of the Greater sage-grouse in Washington

The Greater sage-grouse (*Centrocercus urophasianus*) is a unique gallinaceous bird found in the sage brush habitats of Western North America. The males perform a dramatic and characteristic display dance on leks that are often traditional places for ritual spring mating. Large population declines across the entire range of the species beginning in the 1970's, including Washington, have made it a candidate for possible listing under the ESA (Federal Register December 6, 2007).

The sage-grouse is a sage brush obligate species, meaning that it depends on sage brush for food, cover and nesting. Historically, sage-grouse were found throughout the shrub-steppe and meadow-steppe of eastern WA, but are now restricted to two isolated populations, one in Douglas County of about 650 birds and one in Kittitas-Yakima County of about 350 birds (M. Schroeder, WDFW, pers. com.). Sage-grouse in WA are habitat limited due to a lack of good quality shrub-steppe vegetation (Stinson et al. 2004). Causes of habitat loss, fragmentation and degradation in WA as well as across the range of the species are the result of anthropogenic activities and include land conversion, grazing, sage brush removal, invasion by exotics, changes in fire regimes, development, roads, power lines and noise (Connelly et al. 2004; Schroeder et al. 1999). The greater sage-grouse was listed as state threatened in WA in 1998.

1.3.2 Modeling sage-grouse and land use for the Foster Creek Conservation District

Loss of sage brush habitat affects many species besides pygmy rabbits and sage-grouse. The needs of a suite of sage brush obligates is being addressed in a Multiple Species Habitat Conservation Plan (MSHCP) developed by the Foster Creek Conservation District (FCCD), Douglas County, Washington. Much land in the county is privately owned and federal listings of endangered species have the potential to influence private land management (Langpap 2006). Wide spread benefits to both people and biodiversity could result from focusing on the conservation of sage-grouse because it is viewed as an umbrella species (Rich & Altman 2004; Rowland et al. 2006). Improving habitat for the sage-grouse should also assist efforts to improve conditions for many other species of concern. The MSHCP is developed around 20 species of concern in Douglas County with sage-grouse designated as the flagship species.

Creating practical conservation plans requires the involvement of multiple stakeholders and the incorporation of many kinds of information from hard science to local knowledge. The FCCD honors and engages all stakeholders, their needs and their knowledge. Douglas County has a large rural land base dependent on agriculture, thus conservation planning for the remaining shrub-steppe must incorporate various land uses and conditions. A collaborative model building process with the FCCD and its stakeholders produced two structurally different models that combined different information types and were intended for use as management support tools at the local level (Beall & Zeoli in press). Population viability analysis (PVA) was used to quantify the risk of extinction faced by sage-grouse in central Washington. System dynamics analysis (SDA) was used to form a system-wide perspective that synthesized sage-grouse biology with habitat suitability and with the socially and economically-driven uses of those habitat areas. Testing and comparison of model performance was done with the inherent capability for sensitivity analysis of both modeling methods. Similarity of results gave confidence that both models accurately represent important issues in threatened and endangered species management.

The collaborative modeling building process and the choice of model systems and modeling software is described in Beall and Zeoli (in press). A comparison of the two model types, SDA and PVA, and their outputs relative to sage-grouse life history parameters is described in Chapter 3.

1.4 Modeling as a tool for threatened and endangered species management

Computer models are widely used in addressing environmental issues (Costanza & Ruth 1998) ranging from landscape scale management (Jakeman et al. 2006) to the study of population dynamics (Akçakaya et al. 1999). They are an essential tool in conservation biology (Beissinger & McCullough 2002) and have multiple uses in the understanding and management of threatened and endangered species (Akçakaya & Sjögren-Gulve 2000). A main objective of modeling is to synthesize and formalize in a mathematical fashion what is known about a system, or a portion of a system, and what are perceived as its essential elements. A model, therefore, represents the current state of knowledge about a system without implying that knowledge is complete. On the contrary, models are necessarily incomplete, simplified (although not necessarily simple) representations of reality, not reality itself (Grimm 1999; Odum 1997). John Sterman (2002) stated it clearly: "all models are wrong". They are in fact small imitations of a larger reality, and they can never be otherwise. We are left with the indisputable fact that any model is a set of generalizations and assumptions about a real world situation (Meadows & Robinson 1985). This is just as true of our mental models. The computer age has provided the opportunity to take the mental models upon which we have traditionally based, and still base, our decisions, whether it is about how to feed the world or how best to save an endangered species, and place them in a constructed framework that allows us to evaluate the assumptions, synthesize the knowledge and explore the futures that our mental models encompass.

The purpose of computer modeling, above all else, is to gain understanding of a system (Grimm, 1999) and of the relationships within it (Ford 1999) to expand the boundaries of our own mental models and our limited ability to mentally simulate complex non-linear systems (Sterman 2002). A model is a research tool that can identify key system drivers, where more research is needed and where understanding and mental models are limited. Intervention or leverage points in a system can be identified where small change can lead to system shift, a very practical outcome of modeling that indicates how management can be most effective and result in optimal outcomes (Meadows 1999).

Simulation models such as SDA and PVA project system performance and trajectories into the future for the purpose of testing model and researcher assumptions about the dynamics of a system (Sterman 2002) and to discover how the state of a system changes over time (Grant et al. 1997). Projection models can also give specific information about the probability of an outcome such as risk of extinction or expected population growth in a particular time frame (Morris & Doak 2002). Sensitivity analysis can uncover critical values that meet performance criteria (see Chapters 2 and 3) and can address uncertainty in parameter estimates as well as in stochastic processes (Cariboni et al. 2007). Modeling approaches can improve the science of reintroduction by extending hypothetico-deductive methodology because they can be used to generate and test hypotheses (Seddon et al. 2007), especially important when it is not possible to run experiments on a real world system because it is too costly, results take too long to manifest due to time delays (Sterman 2002), and in the case of endangered species, experiments would increase the risk to a species or system that is already at an unacceptably high risk.

Ralls et al. (2002) encouraged the use of multiple models and models with different structures to lend rigor and credibility to results. Varley and Boyce (2006) clearly stated that different models, even if they produce different predictions, do not pose an insoluble dilemma but should be viewed as helpful in resolving key system features. They also emphasize the need for models in the planning stages of threatened and endangered species recovery to predict outcomes and to provide a framework for evaluation in the adaptive management paradigm. Models are tools for both and teaching and learning (Brook et al. 2002a) because they incorporate available information, make us think about a system in new ways and provide a means of communicating with principles and stakeholders in conservation projects (Stave 2002; van den Belt 2004).

Two different types of models were constructed to explore and evaluate issues relevant to the pygmy rabbit and the Greater sage-grouse. The first was a formal population viability analysis (PVA) for the CB pygmy rabbit, a risk assessment based on demographics (Chapter 2). PVA was applied to demographic data from the captive breeding program for the CB pygmy rabbit to determine the growth rate and population trajectory of the captive population, and to find critical values for demographic rates that would reduce risk of extinction under harvest scenarios (i.e., the removal of rabbits for reintroductions). The second model type was system dynamics analysis (SDA), a broader model format through which local land use and management were explicitly related to the population dynamic of a species of concern, the greater sage-grouse in Douglas County. SDA was combined with PVA for the sage-grouse population to form a complementary pair of models that can be used for cross validation and to provide a more comprehensive management tool for conservation planning and adaptive management than either model could by itself (see Chapter 3).

1.4.1 Population viability analysis (PVA)

PVA is a quantitative modeling tool that synthesizes species-specific demographic parameters and life stage information to simulate population performance over time and to evaluate the risk of decline or extinction as well as probability of recovery and persistence (Burgman et al. 1993; Ralls et al. 2002).

PVA arose out of the awareness that populations of many birds and other species were dwindling and that understanding both genetics and demographics were vital to deciding on minimums for conservation of species and their habitats. As Michael Gilpin (Gilpin 1996) put it, a common methodology was needed to treat cases of low population size (e.g., are 48 parrots enough?), and loss and fragmentation of habitat (e.g., how many thousands of acres of intact old growth habitat should be preserved to prevent the Northern spotted owl (*Strix occidentalis caurina*) population from dropping below 2000) with the consequent impacts preservation would have on local communities (Lamberson et al. 1992; Thomas et al. 1990). PVA has since become recognized as a useful tool for conservation planning and decision making (Beissinger 2002; Morris & Doak 2002) in regards to the maintenance of biodiversity and species recovery programs (Clark et al. 2002). PVA's have been conducted for many life forms including plants, insects, mammals, birds, fish and amphibians (Akçakaya et al. 2004; Westley & Miller 2003) illustrating its broad application and increasing acceptance. PVA is most useful when approached as a long-term iterative process that improves our understanding of a system (Boyce 1992), when it is coupled with adaptive management (Ralls et al. 2002) and when it is updated with new data from monitoring and other studies (Maehr et al. 2002).

The following is a list of questions that can be explored with PVA:

- What is the risk of extinction faced by a species over a specified time?
- Will a population persist if conditions remain the same as they are now?
- What are the most likely causes of extinction (e.g., large fluctuations in population size or growth rate, low juvenile recruitment or shrinking habitat?

- Is the growth rate of the population positive, negative or neutral?
- How variable is the growth rate and how does variability affect expected population size?
- How do the demographics of a population operate in time and space?
- How is a population affected by environmental and demographic stochasticity?
- What is the average expected size of a population over a period of time (trajectory and confidence interval)?
- What is the expected loss of genetic variation over time?
- To which model parameter(s) is a population most sensitive, e.g., juvenile versus

  adult survival, or habitat quality and quantity?
- Is a population likely to persist given a plausible range of change in parameters?
- What are critical values for model parameters (e.g. survival rate of juveniles, maternity rate?)
- What is the minimum population size needed for population persistence?
- What is the stable age distribution?
- Is harvest possible and how many from each age class?
- Is a metapopulation dynamic at work?
- What is the rate of immigration and emigration ?
- What is the risk involved in dispersal and emigration?
- Is a metapopulation more stable than a single population and how many

subpopulations of what size are required to limit risk to an acceptable level?

- At what size should a captive population be maintained to prevent risk of extinction?
- Can a captive population sustain harvest for reintroduction?
- What factors most influence establishment of new populations?
- What are scientifically defensible and measurable recovery criteria?
- Where is more research needed?
- What is the best approach to monitoring?
- What is the amount of uncertainty in parameters and predictions and how does it affect management objectives and decisions?
- Can management affect any of the sensitive parameters?
- What can management actually hope to achieve?

Two software packages were used for the pygmy rabbit PVA, Vortex 9.5, available from the Chicago Zoological Society (Lacy et al. 2005) and RAMAS Metapop 4.0 (Akçakaya & Root 2002). The sage-grouse PVA used only Vortex 9.5. Vortex is an individual-based simulation model that follows the fates of each animal in a population and simulates the events of its life history such as birth, death and catastrophe as discrete events that happen according to defined probabilities (specified distributions). RAMAS is a stage-based matrix projection model that follows cohorts through their life-cycle based on the demographic structure of the population. Brook et al. (2002a) demonstrated the ability of different PVA packages, to produce consistently similar results if data are specified correctly. Beissinger and

Westphal (1998) encouraged the use of multiple PVA models to increase the scope of an investigation. As well, Brook et al. (2002b) conducted a test of PVA's based on 21 long-term studies and found them to produce surprisingly accurate representations of population trajectories and risk assessments for endangered species. Using two different modeling systems allowed us to take advantage of a wider range of graphical and numerical outputs and to check for differing results that would indicate problems with data, input parameters, or model structure. Both modeling systems simulate demographic and environmental stochastic processes (Lacy 2000) that reflect expected change and uncertainty in model parameters.

1.4.2 System dynamics analysis (SDA)

Forrester (1961, 1969) developed system dynamics methodology to define systems in terms of their underlying structural relationships. A primary use has been the study of business dynamics (Sterman 2000), however, system dynamics modeling has been applied to a whole range of ecological issues (Cavana & Ford 2004), from the Limits to Growth study for the Club of Rome (Meadows et al. 1972) to the building of consensus among participants in environmental problem solving (Costanza & Ruth 1998; Vennix 1996). Several kinds of software make it possible to build models from scratch that can include a spectrum of information types ranging from hard science to intuition (Ford 1999). The software used for the Foster Creek Conservation District Integrated Sage-grouse and Human Systems Model (Beall & Zeoli 2005) was PLE Plus 5.3 and PLE Plus DSS32 v5.4b(Ventana Systems, Incorporated 2003).

According to Faust et al. (2004) only a few wildlife models have been developed in system dynamics. Yet, this approach is especially suited to the task because of its ability to represent complex systems as formalized mathematical models that can be used to investigate and simulate those systems (Grant et al. 1997). System dynamics can represent a population in terms of its demographic structure and relate it to other model structures such as land use, habitat fragmentation and any other important influence on a population. Model structures are main elements of a systems model that are built as visual stock and flow diagrams to define and clarify relationships between model parameters. These structures are mathematically connected in the model, but can be presented to stakeholders in an easily readable format that does not require specialized skills of interpretation. A user interface can be tailored to the concerns of the stakeholders with options for modifying parameters of concern and for viewing outputs as either graphs or tables.

System Dynamics Analysis (SDA) is a term coined by Beall and Zeoli (Beall & Zeoli in press) to describe the use of system dynamics methodology applied to the synthesis and analysis of the many kinds of information deemed significant to the future of the Douglas County sage-grouse population. It was our belief that an SDA model would be more readily accessible to and useable by the many kinds of people who have a stake in the outcome of conservation planning at the FCCD than a stand-alone PVA model type. Because of this accessibility, SDA lends itself to participatory, long range planning and optimizing the use of available agency resources for planning (Beall and Zeoli, in press).

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CHAPTER 2

POPULATION VIABILITY ANALYSIS FOR CAPTIVE BREEDING AND REINTRODUCTION OF THE ENDANGERED COLUMBIA BASIN PYGMY RABBIT

2 Population viability analysis for captive breeding and reintroduction of the endangered Columbia Basin pygmy rabbit

2.1 Abstract

We studied survival and population dynamics of a captive population of endangered Columbia Basin pygmy rabbits *(Brachylagus idahoensis)* from 2003-2007, to evaluate its potential for supporting reintroduction and recovery of wild extirpated populations in shrub-steppe ecosystems of eastern Washington, USA. We developed stochastic PVA models in Vortex and RAMAS to assess viability, performance and surplus production of the captive population. This pygmy rabbit population has characteristics of an r-selected species exhibiting low adult survival beyond one year and dependency on high juvenile recruitment for population growth. Low juvenile survival and high variability in stochastic growth rates result in high variability in annual productivity. Our analysis showed that the captive population at N=100 cannot sustain a steady annual harvest of ≥ 30 rabbits for reintroduction and supplementation without increasing the risk of quasi-extinction (n=30) to 59%. We then conducted sensitivity analysis on maternity, carrying capacity and survival rates to identify critical values for model parameters that would lower risk of extinction to the captive population when used as a source of rabbits for reintroduction. Increasing juvenile survival and recruitment into the first breeding class was the most effective method for enhancing the breeding program. Our population model suggests that captive breeding and recovery programs for r-selected lagomorphs present significant conservation

challenges because of the need to rapidly grow such populations to overcome demographic and genetic challenges faced by a short-lived prey species.

Key Words

Washington, endangered species, RAMAS, Vortex, reintroduction, population modeling

2.2 Introduction

The pygmy rabbit *Brachylagus idahoensis* is a small, burrowing lagomorph that inhabits the sagebrush steppe biome of the intermountain west, USA, with an historical distribution that included eight western states. The population in Washington (WA), known as the Columbia Basin distinct population segment (USFWS, 2007), went into steep decline beginning in the 1990's. This population was considered distinct because of its long isolation from other populations in Oregon and Idaho for ≥10,000 years (Lyman, 1991). The pygmy rabbit was declared threatened in 1990 and endangered in 1993 by WA State. The U. S. Fish and Wildlife Service listed the population as endangered under an emergency rule in 2001 (Federal Register, November 30, 2001), which precipitated a series of management decisions resulting in establishment of a captive breeding program for conservation of the remaining population. No pygmy rabbits have been found in the wild in Washington since 2004, and it is considered extirpated from the state (USFWS, 2007).

Sixteen wild rabbits captured to establish the captive breeding program exhibited apparent inbreeding depression that resulted in low reproductive output, susceptibility to disease, and a declining population size even under intensive management (Elias, 2004). Emergency genetic rescue (Tallmon, Luikhart & Waples, 2004) was initiated in 2003 by intercrossing Columbia Basin pygmy rabbits with individuals from a larger pygmy rabbit population in Idaho to produce individuals with a nominal 75% Columbia Basin and 25% Idaho genetic representation. The genetic rescue resulted in renewed reproductive vigor to the point that the breeding facilities were at capacity (~ 100) in the autumn of 2005 and plans were made to harvest surplus rabbits from the captive population to begin a reintroduction program.

We used population viability analysis (PVA) and stochastic population modeling to determine if the improved breeding success of the captive intercross rabbit population post genetic rescue can produce a consistent surplus of rabbits over several years to support recovery efforts in the wild. In this paper we investigate the growth and stability of the captive pygmy rabbit population based on demographic data from the captive breeding program and recent studies of wild pygmy rabbits in Idaho (Sanchez, 2007). Sensitivity analysis of model inputs allowed us to evaluate which demographic parameters drive the population and where management efforts might be best applied to achieve recovery of pygmy rabbits in the wild in eastern Washington.

2.3 Methods

2.3.1 PVA software

We conducted PVA's using Vortex 9.72 (Lacy, Borbat & Pollak, 2005) and RAMAS Metapop 4.0 (Akçakaya and Root, 2002). Vortex is an individual-based simulation model that follows the fate of each animal in the population and simulates the events of its life history such as birth, death and catastrophe as discrete events that happen according to defined probabilities. RAMAS is a stage-based matrix projection model that follows cohorts through their life-cycle based on the demographic structure of the population. Both modeling systems simulate demographic and environmental stochastic processes (Lacy, 2000). Using two different modeling systems allowed us to take advantage of a wider range of outputs and to check for differing results that would indicate problems with data, input parameters, or model structure. Brook et al. (2000) demonstrated the ability of different PVA packages to produce similar results and Beissinger and Westphal (1998) encouraged the use of multiple PVA models to increase the scope of an investigation. All scenarios were run in both software systems and their outputs compared for similarity.

2.3.2 Captive breeding model

The captive breeding program provided complete reproductive and survival data for 2003-2007 from the three facilities housing the captive population (i.e., Northwest Trek Animal Park, Oregon Zoo, Washington State University). We used 1,000 iterations for each stochastic population growth scenario, but we modeled only a short time horizon of 10 years. We took this approach because the recovery program is driven by urgent short-term needs to recover the Columbia Basin pygmy rabbit from a genetic and demographic bottleneck. Pygmy rabbits are short-lived and have a short generation time, and such an approach helps prevent propagation of errors that occur when long time frames are used (Beissinger and Westphal, 1998).

We set a demographically based quasi-extinction threshold at 30 animals (Boyce, 1992; Morris and Doak, 2002) below which demographic stochasticity tends to drive a population to extinction (Gotelli, 1998). The reported probability of extinction (PE) is relative to the quasi-extinction threshold of 30, and is not an absolute prediction but a way to evaluate the consequences of potential changes in management and demographic rates (Reed et al., 1999). The risk of terminal extinction (PE_T), i.e., risk that the population will be below the quasi-extinction threshold at the end of the 10 year simulation, and the risk of interval extinction (PE_I), i.e., risk that the population will be below the threshold at any time during the simulation, are both reported.

Demographic rates for survival were calculated using the Mayfield method (Mayfield, 1975). Our model only included data for the intercross population of captive pygmy rabbits after genetic rescue was initiated because purebred Columbia Basin pygmy rabbits are functionally extinct in the captive breeding program and because reintroduction in the wild will be accomplished by releasing only intercross rabbits (USFWS, 2007). Maternity data are from the captive population only. No survival or fecundity estimates are available from the extirpated wild Washington population; however, some data on adult survival are available from recent studies of pygmy rabbits in Idaho (Sanchez, 2007) and were included for comparison.

There were four age classes in the model, juvenile (0-12 months), one year olds (12-24 months), two year olds (25-36 months) and three year olds (37-48 months). The initial size of the modeled captive model population was 75 adult rabbits at stable age distribution, 38 males and 37 females, which was the approximate condition and size of the captive breeding population. For baseline model testing, carrying capacity (K) was set at 500 to obtain an experimental growth rate and population trajectory unaffected by density dependence until K is reached. Ceiling density dependence was used in both model systems so that Vortex and RAMAS outputs would be comparable and so that the population would not experience reduction in birth rates as it approached K.

Baseline models of the captive population were tested for equality in the deterministic growth rate (λ) and therefore underlying deterministic processes (Brook et al., 2000) before proceeding with stochastic analyses. The quantitative performance of the models was validated by randomizing the data set then splitting it in half and building two demographic models which were then compared for similar output. The models were also qualitatively validated by testing the predicted growth of the model population against the observed growth of the captive population from 2003-2007. The models met both validation procedures.

2.3.3 Harvest model

The future of the Columbia Basin pygmy rabbit in the wild is completely dependent on performance of the captive breeding population. Therefore, it is critical that the captive population not only maintains itself, but also has the potential to support restoration efforts through a continuous and sustainable harvest of individuals for several years to both initiate and supplement new wild populations. The potential number of surplus rabbits that could be available in any given year was investigated based on the 95% confidence interval of the stochastic growth rate. The effect on the captive population of continued harvest for reintroductions was investigated by constructing a harvest model. Six consecutive harvests of 30 rabbits, 15 males and 15 females, were taken from a captive breeding population of N=100, the current K of the breeding program. Harvest was simulated by removing only one year olds and by removing both one and two year olds in proportion to the stable age distribution. Harvest occurred in model years two through seven to determine if the population could sustain a consistent annual harvest most likely required to support a reintroduction program in the wild.

2.3.4 Sensitivity analysis

The vital rates in the baseline RAMAS matrix model were tested for proportional sensitivity using elasticity analysis (Caswell, 2001), and in both

RAMAS and Vortex models for sensitivity to survival by age class and maternity. Current knowledge indicates that high mortality results in most pygmy rabbits breeding only during their first year under wild conditions (Sanchez, 2007). We ran population growth scenarios with rabbits breeding for three years, as they do in the captive breeding program, two years, and one year using maternity and survival data from the breeding program as well as recently calculated mortality rates from wild pygmy rabbits in Idaho (Sanchez, 2007). Several different K's between 100 and 500 were modeled to test population response to K. The model was investigated to find critical values in maternity, survival, and size of the captive population that would support sustained annual harvest and result in a captive population with a $PE_T < 10\%$.

2.4 Results

2.4.1 Captive breeding model

A Kaplan-Meier product limit survival curve (JMP/SAS 6.0, 2005) was used to define three distinct periods in captive juvenile survival, which are the first four days, the next 24 days and the remainder of the year (Figure 2.1). Age classes were distinguished so that harvest could be targeted to one and two year olds. Sex ratio was assumed to be one-to-one at birth and for all modeled populations. Adult male and female survival rates did not differ significantly in captivity (χ^2 =0.1873, d.f.=1, p> 0.6652) nor between one and two year olds (χ^2=0.2643, d.f.=1 p>0.6072), and the data set was too small to test for a difference for three year old adults (n=9). Therefore, we combined survival rates for sex and age class for adults one-three years of age in our analysis, but survival rates were kept separate for juveniles. Although they are based on the same vital rates, Vortex and RAMAS require different input forms for demographic variables, particularly maternity (Table 2.1).

The deterministic growth rate (λ) was the same for baseline models of the captive breeding population in both RAMAS and Vortex ($\lambda = 1.30$). Although the stochastic growth rate (R_s) of the captive population was also positive, it was characterized by high variability (R_s=1.25, 95%CI=0.67–2.32). Sensitivity analysis showed that the growth rate was unaffected by changes in K. The large variation was due to high elasticity and high variability in juvenile fecundity and survival rates, which together explained 62% of the proportional variability in the model (Table 2.2). The model produced a demographic structure with a stable age distribution of 72% juveniles, 18% one-year adults, 7% two-year adults, and 3% three-year adults. Consequently, this short-lived species has a high proportion of individuals in the juvenile age class and high reliance on them for population persistence, giving it characteristics of an r-selected species. The greatest risk to survival for juveniles occured in their first 28 days of life (Figure 2.1).

2.4.2 Harvest model

We investigated the ability of the pre-breeding captive population (N = 75) to support the reintroduction effort in eastern Washington by determining the number of rabbits potentially available for reintroduction on an annual basis. We used the 95% confidence interval for the stochastic growth rate of the captive population model to predict what size the population could attain after one annual breeding cycle and how many animals might be available for harvest in any given year for different pre-breeding captive population sizes ranging from 75 to 300. Although K for the breeding program is ~100 because of limitations in facilities, the prebreeding population is maintained at about 75. For example, the size of the ending population that could result from a pre-breeding population of 75 rabbits ranges from 48 to 188. The lower population bound is always less than the prebreeding population size because at the end of the annual cycle there could be fewer rabbits than the pre-breeding number (i.e., the 95% CI for the stochastic growth rate includes the negative). When considering potential harvest from the captive population, a pre-breeding population of 75 that is allowed to grow to K=100 before harvest, could produce a surplus of 113 rabbits or show a deficit of 27 rabbits with a mean of +20 (Figure 2.2). The empirical evidence is illustrative. The actual pre-breeding captive population in 2006 was 67 and the surplus for release in 2007 was 20. The pre-breeding population in 2007 was 74 and the surplus for release in 2008 is zero. Both surpluses are within the range of model predictions.

We simulated a harvest of 30 rabbits per year, half male and half female, for six years to evaluate the possibility of a continued supply of rabbits needed to support reintroduction. The captive population at N=100, when used as a source population with annual harvest of 30 rabbits showed a reduced stochastic r, from (R_s=1.25, 95% CI=0.67 – 2.32) to 1.05 (95% CI = 0.49 - 2.25), and faced a substantial risk of terminal extinction to < 30 animals (PE_T = 59 %, 95% CI=56-61). RAMAS produced slightly lower PE_T than Vortex (e.g., RAMAS reported 59% PE_T and Vortex reported 68% PE_T for the model with harvest) and we report RAMAS results. The PE_T for a population without harvest was 0%. The increased extinction risk is significant because the captive population is the foundation of pygmy rabbit restoration in eastern Washington and the sole source of genetic management for the unique population segment of the Columbia Basin pygmy rabbit.

Harvesting both one and two year olds produced slightly greater PE_T and PE_I values than harvesting only one year olds, therefore the reported results are for harvest of only one year olds. The captive population model with N=100 could not support the attempted harvest of 30 animals/year for six years (Figure 2.3). A constant harvest number is more meaningful than a proportional harvest because a lot of animals usually are needed to create successful reintroductions (Fischer and Lindenmayer, 2000). The average surplus for the first three years was about 17 (SD=7) rabbits and then declined to 8 (SD=8) by year six (Figure 2.3, see also Figure 2.2). Testing showed that the current captive population can only sustain a repeated harvest of 8 animals per year to maintain $PE_T \leq 10\%$. Without changes in demographic rates, a captive population of K=300 is required for the mean annual harvest to be sustainable near 30 animals (28, SD=5) with a $PE_T \leq 10\%$ because of variability in the stochastic growth rate and the effect of removing adults of breeding age. Regardless of any likely management approach, harvest from the captive population is still unpredictable from year to year, and any year can include zero surplus animals.

2.4.3 Sensitivity analysis

Sensitivity analysis was explored in the model that simulated annual harvest of rabbits from the captive population for reintroduction. Population growth scenarios independently increased survival, maternity, and the size of the breeding population. Increasing adult survival alone by as much as 50% to 0.81, had a limited positive effect on PE_T, lowering it from 59% (95% CI=56-61) to 53% (95% CI=50-55). Increasing population size alone was not an effective strategy because the size required, K=300, is potentially cost prohibitive by itself and does not decrease variability in R_S (Table 2.3). However, critical threshold values for juvenile survival and maternity were identified that produced positive growth rates, and a terminal PE $\leq$ 10%. Sensitivity testing demonstrated that either an 85% increase in juvenile survival from 0.30 to 0.54 or a 76% increase in maternity from 6.61 kits/female to 11.61 kits/female was required to reduce the PE_T below 10% (Table 2.3). A simultaneous increase in juvenile survival of 50% to 0.44 and a doubling of the population to 150 also met the criteria for reduction of extinction probabilities. A surprising result was that high variability in R_S did not decline in the captive population with harvest even when maternity and survival rates were increased, however, variability in R_S did decline in a population with vital rate increases when it was not subjected to harvest. Harvest appeared to keep R_S

and resulting potential surplus derived from the captive population in a highly variable state.

Growth of the captive pygmy rabbit population was largely dependent on breeding by one and two year olds because of the limited number of three-year-old females. By comparison, there is some indication that wild populations may be limited primarily to breeding as one year olds because of low and widely varying survival rates (Sanchez, 2007). Although the protected captive population was not dependent on only one-year olds for breeding; we also ran models with rabbits breeding for three years, two years and one year using maternity and mortality data from the breeding program as well as mortality rates from wild populations in Idaho (Sanchez, 2007). Without exception, if females bred only during their first year, all such models produced negative deterministic growth rates (λ) and high probabilities of extinction (PE_T). It did not matter if adult female survival was raised to 100%. Model populations with females breeding for only one year cannot overcome high juvenile mortality when coupled with the maternity values observed in the captive breeding population. Information available on pygmy rabbit productivity in the wild is scant, i.e., average litter size, number of kits/female/year, and % females breeding successfully (Table 2.4), and therefore a comparison between maternity rates observed in captive and wild populations is not possible and represents the most significant gap in our knowledge of their population ecology at this time.

2.5 Discussion

The survival and recovery of Columbia Basin pygmy rabbits in the wild in eastern Washington is now completely reliant on the success of the captive breeding program. The nearly complete records on reproduction and survival of the captive population allowed us to model and test captive demographics and the potential of this remnant population to grow and to provide surplus animals for reintroduction into the wild. The captive population has a positive stochastic growth rate, yet shows very high variability in that rate and resulting population trajectories such that the captive population is at high risk of extinction from repeated harvests that would likely be required to initiate and support new wild populations. Intrinsic factors that result in large population fluctuations create instability and overcome the seeming positive nature of a high growth rate (Miller & Lacy, 2005). Sanchez (2007) found that survival of individuals in wild pygmy rabbit populations in Idaho can be highly variable at relatively fine spatial and temporal scales. High variability in local wild populations suggests the need for a metapopulation to provide a rescue effect by emigration among small, and possibly segregated individual populations.

Although the population dynamics of wild pygmy rabbit populations on large unfragmented shrub-steppe landscapes are poorly known, our limited empirical data and high variability in the captive stochastic growth rate suggest that pygmy rabbits might exhibit a stable metapopulation composed of unstable local populations. A strong juvenile dispersal urge and the relatively large distances they can travel (0.1 – 12.1 km) (Estes-Zumpf and Rachlow, in review) may reflect an evolutionary adaptation for recolonization and a metapopulation structure. We suggest that the pygmy rabbit appears to be a species dependent on landscape-scale patch dynamics and one that cannot easily persist in small isolated populations whether captive or wild. Because pygmy rabbits are short-lived, with seldom more than two years of adult life, annual productivity must be high for populations to persist. The relatively low adult survival rate even in captivity complicates achieving larger numbers of rabbits for release, because rabbits cannot be easily stockpiled for a release event for more than one year.

The biggest gap in our knowledge of wild pygmy rabbit population dynamics is the limited information on fecundity. There is no vital reproductive rate measured in the wild to compare to the rate observed in captivity. If most females breed only 1 year because of high mortality, and if captive maternity rates are also obtained in the wild, current estimates of survival from both wild (Sanchez, 2007) and our captive studies show all modeled populations in deterministic decline. Therefore, we do not yet have a clear picture of how pygmy rabbits demographically persist in the wild.

The wide estimated variability in the number of surplus rabbits potentially available for release in the wild, even if positive changes can be made in juvenile survival, highlights a significant level of uncertainty about the future of the Columbia Basin pygmy rabbit. The implications of this finding for the recovery of the pygmy rabbit are broad. The immediate problem is that the captive-breeding program does not seem to be a consistent and reliable source of rabbits for recovery efforts, especially at its present pre-breeding size of ~75 adults. Surplus rabbits are not assured every year and the population model shows that a continuous annual harvest of as few as 30 rabbits over six years for recovery purposes puts this captive population at considerable predicted risk of extinction. After new wild populations are initiated, they will most likely require additional supplementation before being considered at low risk of extinction, however, additional surplus rabbits to augment a new population may not be available the year following an initial reintroduction event when they would be most needed.

A robust recovery program, particularly for a short-lived, r-selected prey species, needs to produce more than 30 individuals each year to initiate new populations just to overcome the demographic stochasticity that threatens small populations (Lacy, 2000). We used 30 as a minimum estimated number of surplus rabbits available from the captive-breeding program for modeling purposes only, but not because this is a desirable number for a pygmy rabbit reintroduction program. In addition to staying above the quasi-extinction threshold, a numerical buffer needs to be provided for expected losses in translocation due to stress and its associated effects (Letty et al., 2003: Teixeira et al., 2007) and possible high initial mortality as experienced with wild European rabbits *Oryctolagus cuniculus* (Letty et al., 2003) and grey squirrels *Sciurus carolinensis* (Adams, Hadidian & Flyger, 2004). Wolf et al. (1996) and Fischer and Lindenmayer (2000) have shown clearly that success in translocation is related to the number of animals released. Low success for small reintroduced populations of threatened and endangered species, even in good habitat, also has been documented (Griffith et al., 1989; Osterman, Deforge & Edge, 2001).

Several factors could help stabilize the captive population and make it a more reliable source of pygmy rabbits for release: 1) increased maternity, i.e., kits/female, 2) increased adult survival, 3) increased the size of the captive population, and 4) increased juvenile survival. Maternity has been relatively constant in the breeding program or even showing a slight positive increase, but may not be subject to manipulation unless it is discovered that maternity rates in the wild are consistently higher and provide a better benchmark for attainable fecundity rates. Adult survival in captivity is better than the survival rates observed in the wild in Idaho (Sanchez, 2007). In addition, because maternity and adult survival are carefully monitored in captivity and animals receive excellent veterinary care, these rates may be at their relative maximum in the captive situation. These two factors, maternity and adult survival, have their most positive effects on model outcomes when coupled with a simultaneous increase in juvenile recruitment. Increasing the size of the captive population to 300 can reduce the risk of PE_T to 3% (95% CI=0-5), but as a single management action, it provides little benefit in production of surplus rabbits because of high variability in the potential surplus produced at even large population sizes. Therefore, kit survival seems to be the major leverage point in the system amenable to management intervention at this time.

The major problem facing pygmy rabbit recovery in Washington is low recruitment of juveniles into the breeding age class in captivity. Our analysis shows that efforts to improve the population dynamic need to be concentrated on improving survival in the juvenile age class, which experiences its greatest mortality in the first 28 days of life. We also found that doubling the size of the captive population means that increases in juvenile survival can be smaller to achieve the specified harvest level than if juvenile survival were the sole focus of management efforts. However, if surplus rabbits are not available for reintroduction, neither are they available to reinvest in the captive-breeding program to increase its size, as empirically illustrated by the 0 – 20 "surplus" rabbits produced in 2006 - 2007.

There are several reasons why our population modeling might project more optimistic growth rates than occur in captive pygmy rabbit populations over the long term. Our models are strictly demographic and do not incorporate inbreeding depression, a known problem with small populations of pygmy rabbits (Elias 2004). Even though Columbia Basin founders with inbreeding depression were interbred with Idaho pygmy rabbits to effect a genetic rescue beginning in 2003, the remaining intercross rabbits are still in a genetic bottleneck. An estimated Ne (< 35) based on the demographics of the captive population (Lande and Barrowclough, 1987) subjects it to ongoing genetic drift, even with managed breeding. Captive populations of wild animals can lose productivity and desirable body traits in as few as 3 generations in captivity (Araki, Cooper & Blouin, 2007) and may also develop maladaptive behaviors (Mathews et al., 2005). Columbia Basin pygmy rabbits have been bred in captivity since 2001 and time is of the essence to achieve population growth and remove the population from the demographic and genetic bottleneck in which it still resides. In addition, we may be underestimating demographic variability because of the short time line of the data set (Beissinger, 2002).

Another major factor that might make our pygmy rabbit population models optimistic is that catastrophes such as disease in captivity or fire in the wild were not included. The dynamics of disease in wild populations of pygmy rabbits are not well known, but animals in the captive population are subject to high mortality rates from several common disease vectors (Elias, 2004). One of the three separate captive populations experienced a disease event in 2007 and produced no young. Sagebrush landscapes are subject to periodic fires that destroy their suitability for pygmy rabbits and other sagebrush obligates (Wambolt et al., 2002). At some point, the remaining habitat fragments of shrub-steppe will burn; for example, fires have occurred at two pygmy rabbit habitat fragments within the last 10 years (i.e., Coyote Canyon, Hanford National Monument). The spread of invasive plants coupled with alteration of fire regimes poses an enormous challenge in the shrub-steppe of the Western U.S. (Brooks et al., 2004; D'Antonio & Vitousek, 1992; Young & Evans, 1978).

The future holds much uncertainty for the recovery of the endangered Columbia Basin pygmy rabbit. Our models have outlined the immediate demographic issues faced by the recovery program and identified key research needs (i.e., juvenile survival). A major implication for success of the recovery program is that several additional populations need to be established as soon as possible to overcome an ongoing demographic and genetic bottleneck and to produce greater population stability that may be characteristic of a pygmy rabbit metapopulation on a large, unfragmented shrub-steppe landscape. We suggest that the ecology of this r-selected, endangered mammal argues for efforts to increase the size of the captive population as much and as quickly as possible to stabilize it for sustained harvest and to overcome the genetic and demographic challenges faced by a short-lived prey species.

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Table 2.1. Annual rates for demographic variables used in baseline population models of the Columbia Basin pygmy rabbit (mean and SD).

Juvenile Survival S_j $\bar{X}$ (SD)	**Adult Survival** S_a $\bar{X}$ (SD)	**Maternity: RAMAS** M_{xR}[a] $\bar{X}$ (SD)	**Juvenile Fecundity: RAMAS** F_{jR}[b] $\bar{X}$ (SD)	**Adult Fecundity: RAMAS** F_{aR}[c] $\bar{X}$ (SD)	**Maternity: Vortex** M_{xV}[d] $\bar{X}$ (SD)	**% Successful Females: Vortex** $\bar{X}$ (SD)
0.30 (0.11)	0.54 (0.08)	5.58 (1.07)	0.76 (0.35)	1.48 (0.21)	6.61 (0.95)	83 (7)

[a] M_{xR} = #Kits Yr_x/#Adult Females Yr_x

[b] $F_{jR} = S_j * M_{xR+1}$

[c] $F_{aR} = S_a * M_{xR+1}$

[d] M_{xV} = #kits Yr_x/#Successful Females (i.e., with litters) Yr_x

Table 2.2. Elasticity analysis of demographic rates for the Columbia Basin pygmy rabbit baseline population model.

	Juvenile	**Adult 1**	**Adult 2**	**Adult 3**
Fecundity	0.36	0.16	0.07	0.03
Survival Juveniles	0.26			
Survival Adult 1		0.10		
Survival Adult 2			0.03	
Survival Adult 3				
Totals	0.62	0.26	0.10	0.03

Table 2.3. Tested values for juvenile survival, captive population size and maternity in a model of the captive Columbia Basin pygmy rabbit population with attempted annual harvest of 30 rabbits for 6 years.

Juvenile Survival $\bar{x}$(SD)	% Change in Juvenile Survival	K	Maternity: Kits/Successful Female[b] $\bar{x}$(SD)	% Change in Maternity	PE Terminal % (SD)	PE Interval % (SD)	Stochastic Growth Rate[c] $\bar{x}$(SD)
0.30 (0.11)	-	100	6.61 (0.95)	-	59 (56-61)	86 (2)	0.01 (0.37)
-[a]	-	-	11.61 (1.67)	+76	3 (1-6)	30 (2)	0.47 (0.41)
-	-	300	-	-	3 (0-5)	17 (3)	0.16 (0.33)
0.54 (0.23)	+85	-	-	-	4 (1-7)	19 (3)	0.49 (0.44)
0.44 (0.20)	+50	150	-	-	2 (0-5)	22 (3)	0.37 (0.44)

[a] Hyphen denotes no change from baseline value as given in the first row

[b] Input for Vortex modeling software (see Table 1.1)

[c]Output from Vortex modeling software

Table 2.4. Comparison of reproductive data available for the pygmy rabbit (adapted from Fisher, 1979).

Source	State	Sample size	Mean litter size $\bar{X}$ (Range)	Kits/Fem/Yr	Litters/season
Janson 1946	UT	14	5.93 (4-8)		
Bailey 1936	OR				2
Hall 1946	NV	1	6 (5-8)		
Davis 1939	ID	2	6		
Fisher 1979	ID	10	6 (5.2-6.1)	13-13.7	2.2-2.3
Captive Breeding 2003-2007	WA	84	3.2 (3.0-3.5)	5.65-7.55	1.36-2.16

Figure 2.1. Kaplan-Meier product-limit 322 day survivorship curve for juvenile captive Columbia Basin pygmy rabbits.

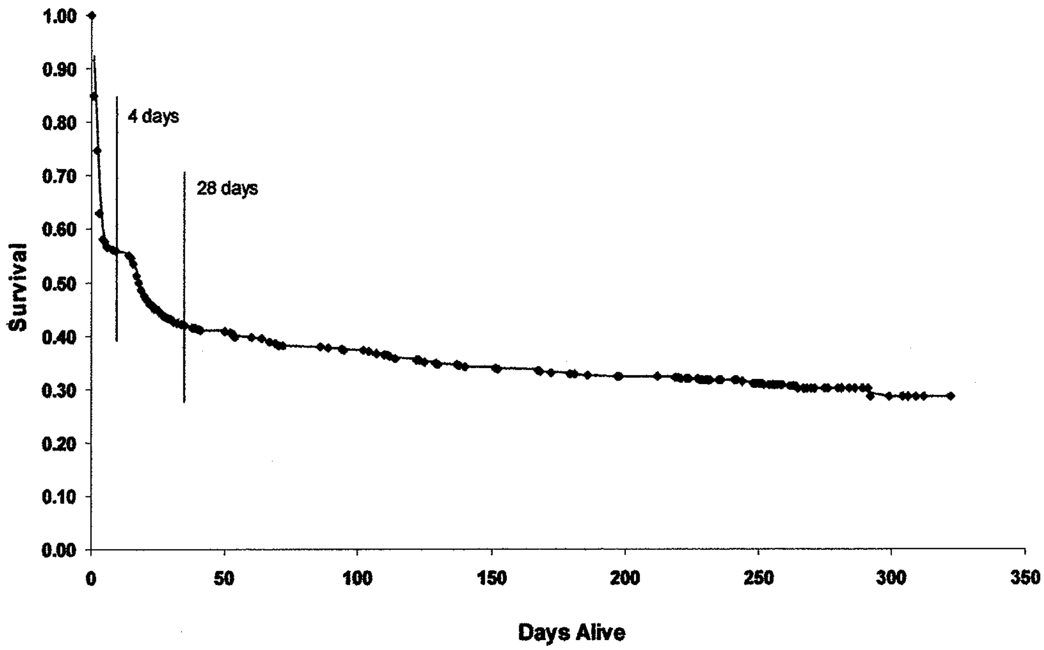


Figure 2.2. Potential annual surplus for harvest from the captive breeding population of the Columbia Basin pygmy rabbit for populations ranging from 75 to 300 animals (mean and 95% CI).

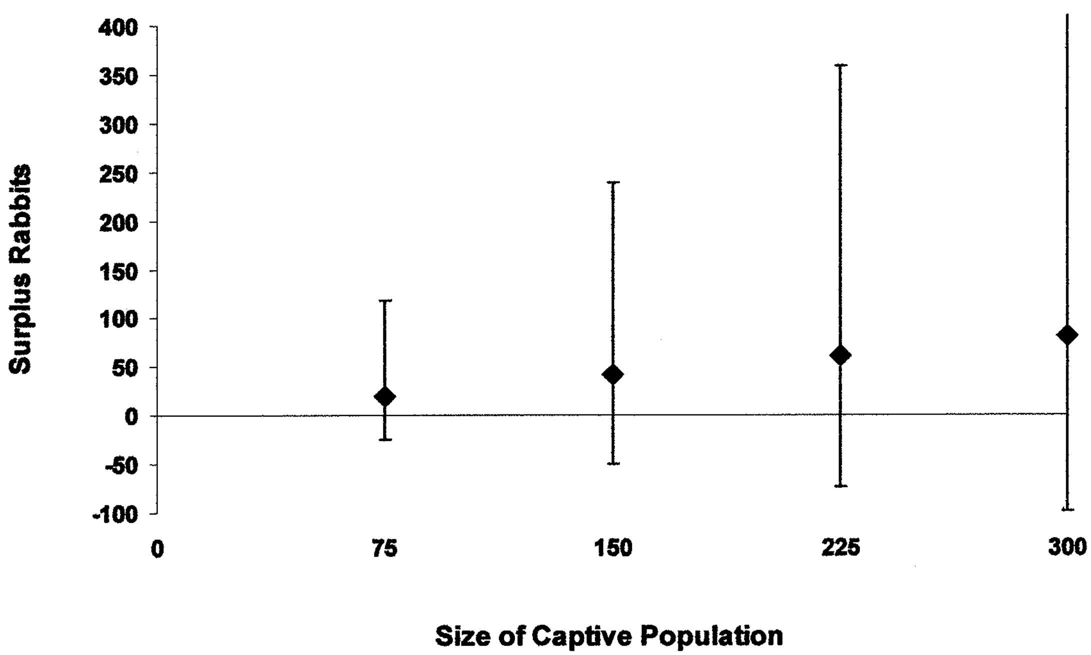
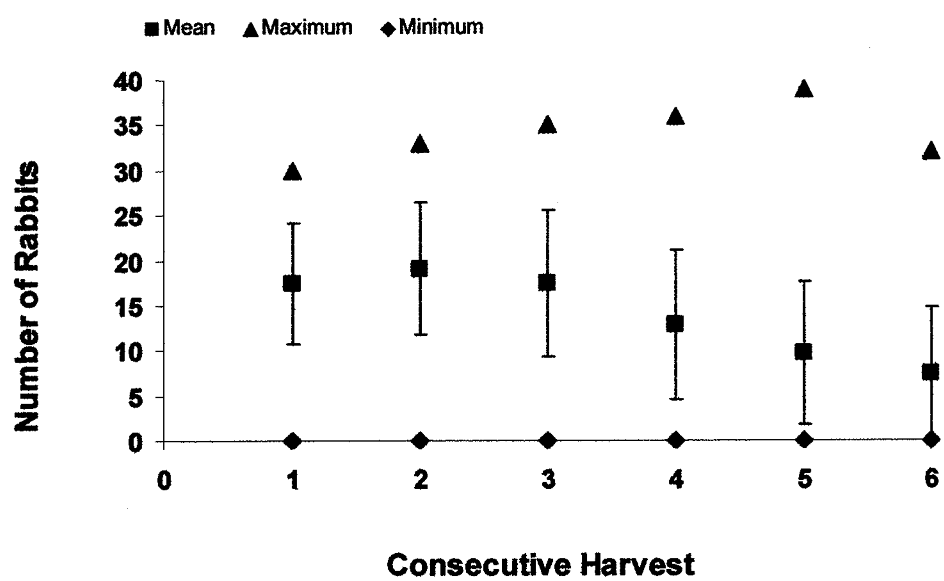


Figure 2.3. Number of rabbits that can be harvested from the existing captive breeding program for the Columbia Basin pygmy rabbit (n = 75). Attempted harvest is 30 rabbits for 6 years.



CHAPTER 3

SYSTEMS MODELING FOR ENDANGERED SPECIES MANAGEMENT: COMBINING SYSTEM DYNAMICS ANALYSIS AND POPULATION VIABILITY ANALYSIS FOR CONSERVATION PLANNING FOR SAGE-GROUSE

3 Systems modeling in endangered species management: combining system dynamics analysis and population viability analysis in sage-grouse conservation planning

3.1 Abstract:

The Greater sage-grouse (*Centrocercus urophasianus*) is a large gallinaceous bird found in sage-brush habitats of Western North America. Large population declines since 1970 have made it a candidate for listing under the Endangered Species Act. The creation of long-term conservation plans is bringing together multiple stakeholders in local working groups who need tools to predict how management plans may affect sage-grouse populations Working with a local group in Douglas County, Washington, we developed and compared two structurally different models to assess sage-grouse issues in central Washington. System dynamics analysis (SDA) with Vensim software was used in a participatory framework with stakeholders to develop a comprehensive model that synthesized sage-grouse biology, habitat suitability, and social and economic concerns. Population viability analysis (PVA) with Vortex software was used to simulate demographic rates and quantify the risk of extinction for sage-grouse. We compared the performance of the models by using sensitivity analysis and statistical screening. Both models identified the same demographic parameters as critical to the sage-grouse population dynamic. We demonstrated that SDA with its ability to incorporate and model diverse information, and an external PVA performing risk analysis in a stochastic model, augment and support each other. The parallel modeling integrates science with the visual and interactive nature of systems-

dynamics to facilitate the engagement of a wide audience in ecological and land-use management decisions for endangered species.

Key words: Greater sage-grouse, endangered species, system dynamics, population viability analysis, sensitivity analysis, participatory modelling, statistical screening.

3.2 Introduction.

The Greater sage-grouse (*Centrocercus urophasianus*) is the largest of several North American grouse species and is endemic to sagebrush (*Artemisia spp.*) habitats of the western United States and Canada (Schroeder et al., 2004). Concerns over the long-term decline of sage-grouse that began in the 1970's, plus the absence of population recovery in most areas, have resulted in petitions to list Greater sage-grouse as a U.S. federally threatened or endangered species under the Endangered Species Act (ESA) of 1973. Anthropogenic change at the landscape scale and fragmentation of sagebrush dominated areas are major driving forces of the population decline (Schroeder et al., 1999; Connelly et al., 2004). These changes include habitat conversion to agriculture, inappropriate livestock management, changes in fire regimes, invasion of exotic annual plants (e.g., cheat grass, B*romus tectorum*), energy development and urbanization. Changes in management of sagebrush lands that would likely follow a listing could potentially affect the livelihoods of ranchers, farmers and others who are dependent on these lands (Wambolt et al., 2002) and is a frequently expressed concern of landowners. A recent decision by the U.S. Fish and Wildlife Service (USFWS) that a listing was "not warranted" (Federal Register, January 12, 2005) was conditioned by the formation of over 64 local working groups across 11 states whose task is to join with federal and state management agencies to develop long-range management plans for local sage-grouse management (Western Governors' Association, 2005). These groups are involved in large-scale cooperative conservation partnerships that are bringing farmers, ranchers, tribes, environmental organizations, industry groups and government agencies together to develop plans to conserve and manage sagebrush ecosystems to benefit sage-grouse and other sagebrush obligates (Connelly et al., 2004). Although coordinated by a Conservation Planning Framework Team formed by efforts of the Western Association of Fish and Wildlife Agencies, the important work of planning is focused at the local working group level. Groups are currently in various stages of the planning process and need analytical tools to bring together scientific information, practical land management considerations and diverse stakeholder interests (e.g., wildlife conservation, agricultural production, regulatory authorities and private land owners) to assess the effects of alternative plans on future sage-grouse populations.

We describe two population models for Greater sage-grouse, which were built in a collaborative model building process with the Foster Creek Conservation District (FCCD) in central Washington. FCCD has a planning team with representatives from state and federal agencies, non-governmental organizations, and local landowners. They are engaged in a holistic assessment of conservation strategies to reverse downward trends in key fish and wildlife species through the development of a Multi-species Habitat Conservation Plan (MSHCP). Their strategies also work to preserve local landscapes and lifestyles. The flagship conservation species for the district is the Greater sage-grouse, which experienced a population decline of over 77% from 1960 to 1999 and is now found on only 8% of historical range (Schroeder et al., 2000). Sage-grouse were listed as state threatened in 1998, based on biological assessments that acknowledge the risk faced by this isolated population in Washington (Stinson et al., 2004).

Ralls et al. (2002) and Beissinger and Westphal (1998) encourage the use of multiple models and models with different structures to lend rigor and credibility to assessments of endangered species status and management. However, different modeling systems have different strengths and weaknesses, particularly related to the communication of methodology and results to diverse user groups and the public. For models to be most successful in educating stakeholders and guiding management activities, they must be scientifically credible, integrate diverse knowledge, elucidate outcomes and consequences and be accessible to policy and decision makers. Integrated approaches to modeling human-ecological systems for the evaluation of management options are being used by the U.S. Geological Survey, the MIT-USGS Science Impact Collaborative (MUSIC, 2008) and also by the U.S. Army Corps of Engineers Shared Vision Planning which uses system dynamics software as one of their tools to assist with problem solving (USACE, 2008).

A conceptual model of the integrative process (Figure 3.1) shows system dynamics modeling at the center as a data and information archive and an analytical tool for the whole system of concern. Other models designed for specific analyses critical to system performance can be run externally, and their results used as inputs to, and as cross checking for, the integrated model. We used population viability analysis (PVA) modeling software designed specifically for risk assessment in endangered species management, as a parallel model to the system dynamics analysis, hereafter SDA. The PVA interfaced with the SDA in an iterative process that tested inputs and outputs of both models for consistency in analytical results. We developed and tested the two different models together to synthesize sage-grouse biology with options for land use to form a comprehensive, system-wide perspective of the issues surrounding sage-grouse management in Douglas County, Washington. The SDA integrated sage-grouse life history, habitat suitability and local land use. The strength of systems modeling is the ability to synthesize, integrate and convey diverse types of information (e.g., biology, economics, and land use alternatives) that are relevant to conservation issues. SDA software permits the creation of interfaces that present simulation results in readily accessible visually concise formats that may be tailored to a variety of interested groups. The strength of PVA is the ability to perform risk assessment and estimates of population persistence and stochastic growth from demographic data. We compared the performance of the two model systems by using sensitivity analysis to identify critical demographic values, to predict extinction risk and by using outputs of one model as inputs for the other to determine if they produced similar results. Our objective was to compare results from a PVA risk analysis frequently used in endangered species management with those of a systems dynamics model to determine if SDA and PVA can augment each other, and if demographic analysis in SDA is comparable to that of PVA. After results have been compared and shown to be similar, the comprehensive SDA model may be used as a management support tool with greater confidence. As well, management options simulated in the SDA that change population size or demographics can be analyzed in the PVA for contributions to risk of decline or extinction for the threatened or endangered species.

3.2.1 System dynamics analysis - SDA

Forrester (1961) initially developed system dynamics methodology to define systems in terms of their underlying structural relationships. Systems dynamics modeling has since found acceptance in a broad range of conservation and ecological issues (Cavana and Ford, 2004) including building consensus among participants (Costanza and Ruth, 1998; Stave, 2002), watershed management (Tidwell et al., 2004), fisheries management (Otto and Struben, 2004) and predicting invasive species movement (BenDor and Metcalf, 2006). Pedersen et al. (2003) developed a systems model to evaluate the effects of sheep grazing and fire on sage-grouse population dynamics. However, systems models have seldom been used in endangered species planning, despite their apparent suitability in combing diverse types of information and presenting results in visual formats. Several software packages now make it possible to build systems models that can include and organize the diverse types of knowledge about ecological and social systems (e.g., land use, economics, and population biology) that are necessary for effective conservation land use planning. These models can then be used to create "what if" scenarios that simulate potential future change.

A systems model is built by first choosing key variables, called stocks, which show the collection points (state variables) in a system. Chicks would be an example of a stock (Figure 3.2). The flows or movements in and out of those stocks (e.g., successful hatches) are then added, and finally, rates are assigned to the flows to complete a functioning quantitative model depicted in a visual format (Ford, 1999). In the context of wildlife population studies, flow rates may reflect a variety of ecological influences, such as habitat and seasonal changes in survival rates, or density dependent relationships. A systems model makes explicit the dynamic connections between individual components in the system. These connections are shown as the directional arrows forming loops that link stocks and flows together as in the model structure representing female sage-grouse life history (Figure 3.2). The entire structure of the sage-grouse systems model is visible to the user in such stock and flow diagrams. The equations linking the stocks and flows and related documentation referencing model inputs were written into the model as notes and are also accessible for user review. The ability of a systems model to incorporate multiple information types (Ford, 1999) is a positive aspect of SDA that allows simulations to include a variety of interactions, feedbacks and time delays, i.e., nonlinear dynamics. Inputs can range from demographic rates for sage-grouse, to local economic data and social concerns of land owners, such as the effects of continuing to use the land for farming and ranching with and without acceptance of the MSHCP by land owners. The SDA model was designed to increase participant understanding of how sage-grouse productivity is tied to the local landscape and help the District determine which land types and possible conservation efforts may be most important for sage-grouse recovery in central Washington.

3.2.2 Population viability analysis-PVA

A growing body of case studies demonstrates the practical application of PVA to threatened and endangered species management (Westley and Miller, 2003; Akçakaya et al., 2004). PVA is a type of computer simulation modeling that assesses long-term viability of small populations by synthesizing species-specific demographic parameters and life stage information into an analytical population model. Quantitative methods are used to assign probabilities of population persistence over a specified time period (Akçakaya, 2000; Ralls et al., 2002). PVA models are designed to account for environmental stochasticity, the annual variability of the natural environment and resulting fluctuations in carrying capacity and demographic rates, and also the effects of demographic stochasticity, or chance demographic events that cause small populations to be unstable (Lacy, 2000).

A quantification of probable future population status conducted with typical PVA software (e.g., Vortex, Ramas) is useful in assessing the relative effect of different land management options and in determining a target population size that produces a socially acceptable level of extinction risk. Risk determinations through PVA may also be instrumental in affecting listing decisions under the U.S. Endangered Species Act (Morris and Doak, 2002). Johnson and Braun (1999) used PVA for a Colorado sage-grouse population that identified survival of adults and juveniles as the most important demographic parameters. Their model allowed them to suggest directions for habitat management as well providing an analysis of the effects of hunting on overall mortality. Sachot et al. (2006) performed PVA analysis for the European Capercaille (*Tetrao urogallus*) that predicted considerable risk of decline and extinction over the next 50 years. They were able to recommend that management efforts focus on adult survival and habitat enhancement through silvicultural practice. However, while PVA is frequently used to project probabilities of population growth and persistence, PVA has not widely been incorporated into more comprehensive systems dynamics models for conservation planning for endangered species.

3.3 Methods.

3.3.1 System dynamics analysis – SDA

We built the system dynamics model with Vensim software,PLE Plus 32 v5.3 and DSS32 version 5.4b (Ventana Systems Incorporated 2003). A larger array of variables and inputs were included in the SDA than was readily possible in the PVA (Table 3.1). Although it may at first appear to include a daunting assortment of information, the number of inputs for a systems model is relative to the type and amount of data required to satisfy stakeholder concerns. The model is organized into several smaller data structures that can be explored and verified individually for additional study and added transparency in overall model function. For example, 11 land categories, each with a breeding and winter habitat suitability rating, were used to define how this migratory population of sage-grouse uses available land types in Douglas County. The model used a monthly time step to separate use of the two habitat types. Losses or gains in habitat affect population size through feedback loops involving the apparent carrying capacity (K = 650) of the various land types, which was determined from a 12-year series of annual population estimates (M. Schroeder, pers. com.). Habitat limitation operates in the model as a shortage of nesting space (Figure 3.3) that limits the size of the female breeding population, although the exact ecological mechanisms are unknown. Outputs from the systems dynamic model were customized as graphs and tables for all parameters of interest to the FCCD related to sage-grouse population size and to the amounts of land in different categories at various suitability ratings.

The two main components of the SDA model are sage-grouse life history (Figure 3.2), the central theme of the model, and habitat availability and condition in the human-dominated agricultural landscape (Figure 3.3). Mean demographic rates (Table 3.2) were entered as constants, therefore, SDA simulations are deterministic (do not illustrate environmental and demographic variation). One major density dependent positive feedback loop was used in the reproductive cycle (bold in Figure 3.2) to link available breeding habitat to the empirically-defined limits to sage-grouse population size. Negative feedbacks in the system resulting from mortality in different life stages caused the model population to find a stable equilibrium at K.

3.3.2 Population viability analysis - PVA

In a separate model, we performed a standard population viability analysis (PVA) for the Douglas County sage-grouse using Vortex population modeling software, version 9.5 (Lacy et al., 2005). Each model scenario was run 1000 times for 50 years, the proposed time line of the MSHCP. The model required 25 inputs (Table 3.1), which are the statistical estimates of the demographic rates for reproduction and mortality with standard deviations (Table 3.2) plus the assumed carrying capacity of the current habitat (K = 650). Habitat limitation is incorporated as ceiling density dependence that truncates any population greater than K back to

K at the next time step. Vortex models demographic stochasticity as a binomial distribution of life history processes for individuals in the population (e.g., sex, survival probability, and variation in reproductive success) and environmental variability by sampling from a normal distribution with a standard deviation which we set at 10% of K. Because density dependence is undefined for this species (next section) our definition of extinction in the PVA is no surviving birds.

3.3.3 Sensitivity analysis

A potential problem with small and declining populations is inverse density dependence or an Allee effect (Akçakaya et al., 1999), such as inbreeding depression, that can cause growth rates to decline with decreasing population size. However, specific information about how density dependence affects survival and reproduction is generally lacking for most species (Sachot et al., 2006) and is not yet defined for species of sage-grouse (K. Reese pers. com.; Gunnison Sage-grouse Rangewide Steering Committee, 2005). However, inbreeding depression is a critical element in the risk of extinction faced by small populations (Mills and Smouse, 1994; O'Grady et al., 2006) and its interaction with demographic and environmental conditions can create a positive feedback loop or an extinction vortex (Gilpin and Soulé, 1986). Brook et al. (2002) stated that ignoring inbreeding depression will substantially underestimate risk assessment. Inbreeding depression may have multiple effects on survival, productivity, susceptibility to disease and behavior (Keller and Waller, 2002) and would probably take the general form of reduced fitness (Reed and Frankham, 2003). The Douglas County population of sage-grouse shows reduced genetic variability and therefore may be subject to the effects of inbreeding depression in the future (Oyler-McCance et al., 2005). A decline in heterozygosity from a demographic bottleneck was correlated with reduced productivity in the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*) in Illinois (Bouzat et al., 1998; Westermeier et al., 1998). Toefler et al. (1990) suggested that populations of prairie chickens falling below 100 lekking males are likely to disappear and Connelly et al. (2004) recommended the cessation of hunting at the same population level for sage-grouse. At this time, inbreeding depression must be accounted for by indirect means, such as changes to demographics rates affected by inbreeding depression. Our models allowed us to explore this type of uncertainty at small population sizes.

We used manual perturbation (Mills and Lindberg, 2002) of demographic rates in both SDA and PVA sage-grouse population models to identify important life history stages and critical values for vital rates that indicated long-term population decline, high probability of extinction (PE) or negative growth rates. In the SDA model, the most sensitive inputs were identified by determining a threshold value for any demographic rate that resulted in extinction, i.e., zero birds at the end of a 50-year simulation. Each of the demographic parameters was made into a variable control slider on the user interface that could be varied individually or in tandem (i.e., Vensim synthetic simulation mode: any user adjustment of the variable control slider results in an immediate response in the graphical representation of the sage-grouse population). These critical demographic rates identified in the SDA were then entered into the PVA to independently analyze the associated risk of extinction produced by modeling a stochastic population dynamic.

Sensitivity analysis by manual perturbation assumes that all rates except the one being tested remain constant. It is more likely, however, that demographic parameters do not change independently because environmental variability may affect many vital rates simultaneously (Allendorf, 2002), and because of the threat to small populations that accrues from the loss of genetic diversity and inbreeding depression (Brook et. al., 2002). In the systems model, possible effects of inbreeding depression were explored by using the synthetic simulation mode to simultaneously change demographic rates that would likely become more negative with inbreeding depression. These four rates were chick mortality, female mortality, the number of eggs/hen and breeding success, which is the proportion of females producing young (Table 3.3). A test for the effects of inbreeding depression was conducted by changing these same rates downwards at the same time by 10% of their mean value. These four modified rates were also entered into the PVA model to estimate PE.

Additional sensitivity analysis was conducted with statistical screening in Vensim DSS32 v5.4b. This analytical tool uses a simple correlation coefficient to screen for parameters having the greatest statistical influence on model output (Ford and Flynn, 2005). Six parameter estimates of interest and a range of values for each based on one standard deviation were entered into the screening function. Breeding habitat and winter habitat were included as a way to individually evaluate these parameters and also to analyze population sensitivity to K. Because changes in male mortality had only minor effects on model output, it was eliminated as a variable from this analysis.

In the PVA model, we ran a baseline population simulation using environmental and demographic stochasticity. Then we ran simulations that changed one demographic parameter at a time from the baseline value to a high and low value based on its 95% confidence interval (Table 3.2), except for the maximum age of female reproduction, which was raised from 9 to 13, and the percent of males available for breeding, lowered from our estimate of 47 to 10 because these values have been used with other grouse models (Brook et al., 2002; GUSG, 2005). These analyses produced a PE for each value and also showed the effect of the change on the stochastic growth rate. We also tested the stochastic model for sensitivity to K.

3.4 Results

Both the SDA and PVA models clearly showed the Douglas County sage-grouse population has demographics that produce positive growth rates. The SDA model seeded with 50 birds grew to K in 30 years, a deterministic growth rate (R_d) of 1.09, although this model is not designed to indicate growth rates and different beginning population sizes will produce different rates. The baseline PVA model has an R_d of 1.17, and a stochastic growth rate (R_s) of 1.16 (SD 1.51-0.90) with a PE of 0% in 50 years. This population does not exhibit sensitivity to K unless it falls to <50 in a stochastic model.

Determinations for threshold values of demographic rates that produced extinction in the deterministic SDA model also produced high PE values and negative R_d and R_s rates when entered into the PVA model (Table 3.4). The amount of change required to reach the extinction threshold was smallest for chick mortality followed by the productivity measures of breeding success, eggs/hen, and then by female mortality. The simultaneous change of the four surrogate values used to investigate possible effects of inbreeding depression at small population size produced extinction in 32 years in SDA from a population at K, and resulted in a PE of 97% and negative growth rates in PVA (R_d = 0.87, R_s = 0.87 SD 0.64-1.19).

Sensitivity analysis of stochastic variation in demographic rates conducted in PVA exhibited a range in risk of extinction (Table 3.2) and stochastic growth rates (Figure 3.4). The highest PE was related to the low test value for chick mortality indicating this was the most sensitive parameter, followed by eggs/hen. The range of the stochastic growth rate in the PVA, as a measure of model sensitivity to individual parameters, showed similar results to the SDA modeling. Chick mortality was the most sensitive parameter, followed by eggs/hen. Maximum age of females and breeding success were shown to be less significant drivers of the population dynamic. Males in this polygynous species did not affect productivity in these models. These results support the choice of a female-based life history for the systems model and are in accord with studies showing that only a few males are likely responsible for most of the breeding in the sage-grouse lek mating system (Connelly et al., 2004)

Statistical screening of input variables in the SDA model produced a series of correlation coefficients that indicate the importance of each input as a driver of the system (Table 3.5). Again, chick survival was the variable most responsible for performance of the sage-grouse population over time (R^2=0.82). Female mortality was the next most sensitive parameter. Eggs per hen and breeding success were not as important. This analysis found that breeding and winter habitat have relatively small but equal influence on the system, in keeping with expert opinion that both are equally limiting to sage-grouse in central Washington at this time (M. Schroeder, pers. com.).

Statistical screening in the SDA model displayed the trajectories of the various populations generated by the analysis. The graphical display of 50 simulations was divided into 28 populations that succeeded and 22 populations that failed. We analyzed these runs to determine whether there were common parameter associations among failed populations. Only one common factor was discovered among all declining populations, a reduction in chick survival, and in all cases its value was below its mean of 0.17, sometimes by only a small amount. Consequently, our analyses in both SDA and PVA models showed chick mortality was the most sensitive model parameter affecting population growth or decline of Greater sage-grouse in central Washington.

3.5 Discussion

Threatened and endangered species management will benefit from the synthesis of existing scientific knowledge into decision-making tools that can be used to improve conservation plans and support management actions on both public and private lands. Stakeholders have a variety of perspectives and concerns about land use and wildlife conservation which results in different kinds of information being brought into the discussion, all of which needs to be integrated and communicated effectively to produce a coherent picture of regional conservation issues. We suggest that integration of both scientific and local knowledge, and incorporation of local land use concerns are necessary to formulate and achieve successful conservation plans, because without landowner acceptance, recommended changes in land use may be far more difficult to implement. Land owners who make their living managing their systems on a daily and seasonal basis use historical information, personal experience, and an intense personal ecological knowledge developed by close ties to their land. This form of knowledge may not stand up to scientific peer review, yet this knowledge is valid and because people's livelihoods may be at stake, their needs must be properly considered in decision making processes.

To achieve the goal of integrating various forms of knowledge and including a variety of stakeholder groups and their concerns, we utilized two different kinds of mathematical models to explore the sage-grouse and land-use system in Douglas County, WA. Combining the two model types, SDA and PVA, provided a robust method for sharing and verifying data input and model performance and for improving group learning about sage-grouse in Douglas County (Beall and Zeoli, in press). The SDA model was built around sage-grouse biology because it is an umbrella species (Rich and Altman, 2004; Rowland et. al., 2006) for shrub-steppe habitats and the FCCD expressed concern over how land use in their district might affect the regional sage-grouse population. The SDA model format allowed us to explicitly and simultaneously incorporate many factors including habitat variables, potential land use changes and the economic implications of those changes into a comprehensive visual-based modeling system that could be understood by participants in the MSHCP process (Beall and Zeoli, in press). The visual structure of the SDA model and the ability to construct user-friendly interfaces specific to a local situation, provides land owners and land managers with the opportunity to interactively and visually explore both sage-grouse demographics and other parts of their land-use system in an accessible and holistic format. The SDA can be used to explore the effects of changes to specific land categories, individually or in tandem, on the size of the sage-grouse population. Both models can explore the effects of changes in demographic rates while the PVA can assess the risk and potential growth rates involved with any such change.

By contrast, the PVA model used demographic data in a projection model to provide a stochastically based risk analysis pertinent to small populations (Akçakaya, 2000; Reed et al., 2002). However, the PVA model format, operation and analysis require expert operation and are not particularly "user friendly". Although this is in no way a limitation on the applicability and usefulness of PVA, we think it is a potential limitation on its acceptance by some managers, many stakeholders and the general public, because they cannot as readily be part of the process of constructing or operating the model. Because both SDA and PVA models are capable of performing sensitivity analysis on input parameters, we chose that as a basis of model comparison. Complimentary results increased confidence in the outputs of both models and also demonstrated the capability of systems modeling to be compatible with many of the typical functions and uses of traditional PVA modeling for conservation biology.

Sensitivity analysis conducted in both models showed chick mortality/survival to be the key model input. Our tests showed that no matter what possible combinations of demographic rates might develop because of environmental or demographic stochasticity, chick survival was consistently the strongest driver of this sage-grouse system. Because chick survival is also the most uncertain estimate of all the demographic rates (M. Schroeder pers. com.), we recommended that monitoring and study resources be spent on obtaining the best possible estimate for this rate as well as exploring the environmental factors that influence it. As well, any downward trend in chick survival could be an early warning of a significant, longer-term population decline. The models also showed that small and simultaneous changes in demographic parameters, as could occur with inbreeding depression in small populations, can have large influences on population dynamics.

Biologists and managers seeking to improve habitat conditions for Greater sage-grouse can use these models to explore the impacts of management decisions in advance of implementation. The models can simulate a variety of theoretical futures and include the logistical and financial implications of the decisions that create such futures. The PVA/SDA combination can also be incorporated into an adaptive management program. The models can be updated and revisited with monitoring data, and as well provide a repository and analytical tool for these data. Building quantitative models takes time and resources and returns on the initial cost can be increased when the models are seen as a long-term investment that can be extended by updating data over time. Finally, the models produce quantitative and graphical outputs that are convincing tools to present to stakeholders and other agencies to explain the need and value of selected management activities.

We found that systems dynamics and PVA models, each with different internal structures and capabilities, can augment and support each other by providing different ways of looking at the same problem. SDA and PVA models are readily available tools that can serve the needs of local conservation groups seeking to improve their management of threatened and endangered species by providing them with a more complete and visual understanding of how their local or regional land-use system affects wildlife conservation. Using these two types of models in parallel engages a wider audience of both experts and stakeholders who need to know that their knowledge, perspectives and concerns are being addressed appropriately. Our testing showed that the synthetic capabilities of a systems modeling method, SDA, are comparable to those of an established biological modeling method, PVA, for population analysis in endangered species management. After results of PVA and SDA have been compared and shown to be similar the comprehensive SDA model may be used as a management support tool with greater confidence. Because of its visual structure and variable slider controls to perform "what-if" investigations, the system dynamics model more readily allows users to interact with and explore the model. Furthermore, stakeholders will likely have more confidence in a modeling process and management decisions using that process when their local land use and social/economic system has been defined and visually represented with their needs and concerns acknowledged and respected. Our experience indicated that system dynamics modeling has great potential for use in the collaborative and comprehensive conservation planning needed for Greater sage-grouse across its entire range.

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Table 3.1. Comparison of SDA and PVA approaches for modeling Greater sage-grouse.

	System Dynamics Analysis (SDA)	**Population Viability Analysis (PVA)**
Model value	System-wide synthesis of scientific data, land use and socially significant information Model can be accessed and run by stakeholders	Stochastic projections produce a risk analysis for assessment of management options or target population size and growth rates
Software	Vensim Vensim PLE Plus 32 v5.3, and DSS32 v5.4b (Ventana Systems 2003)	Vortex 9.5 (Lacy et al. 2005)
Type of Inputs	Demographic, habitat, economic, other as needed	Demographic
Number of Inputs	273	25
Randomness	No, deterministic (equilibrium)	Yes, stochastic
Time step	Month	Year
Simulation time	50 years	50 years
User view of model structure	In visual stock and flow diagrams (Figure 3.2)	Not available
How K is handled	Experimentally change habitat to investigate potential K	Experimentally change K to investigate potentials from habitat change
Sensitivity analysis	1) Manual perturbation of demographic rates to explore threshold values indicating population decline. 2) Statistical screening.	Manual perturbation of demographic rates to explore effects on risk of extinction and growth rate

Table 3.2. Parameter estimates for simulation models and risk analysis of the Douglas County, WA, Greater sage-grouse.

	Baseline[a]		**Test Value**		**Risk of Extinction (%)**	
Parameter	Mean	SD	Low	High	Low	High
Breeding success	0.59	0.06[b]	0.47	0.71	0	0
Eggs/hen	8.74[c]	2	4.74	10.74	26	0
Maximum female age	9	na	5	13	0	0
Chick mortality	0.83	0.07[d]	0.69	0.97	0	100
Adult female mortality	0.25	0.07	0.11	0.39	0	0
Adult male mortality	0.43	0.07	0.29	0.57	0	0
% Males breeding	47	na	10	100	0	0
Carrying capacity (K)	650	65	100	1000	0	0

[a] Data from Schroeder 1997, and Stinson et al. 2004, unless otherwise noted.

[b] 10% of the mean as for a similar species, Gunnison sage-grouse (GUSG 2005).

[c] 9.1 eggs/hen * 0.96 hatch rate (Schroeder 1997).

[d] as for Gunnison sage-grouse (GUSG 2005).

Table 3.3. Changes in demographic rates used as surrogates for inbreeding depression.

	Mean	**Value at 10% Negative change**
Chick mortality	0.83	0.91
Adult female mortality	0.25	0.28
Eggs/hen	9.1	8.2
Breeding success	0.59	0.53

Table 3.4. Correlation coefficients from statistical screening of SDA model inputs.

Parameter	**Correlation Coefficient**
Chick survival	0.835
Female mortality	-0.327
Eggs/nest	0.009
% Successful females	0.063
Breeding habitat	-0.182
Winter habitat	0.228

Table 3.5 Threshold values for demographic rates determined by sensitivity analysis in SDA with results when subsequently entered into PVA.

	Mean	**SDA threshold for extinction at 50 years**	**% Change**	**PE from PVA (%)**	**Stochastic growth rate from PVA Mean(SD)**	**Deterministic growth rate from PVA**
Chick mortality	0.83	0.92	11	36	-0.12 (0.34)	0.93
Breeding success	0.59	0.30	48	48	-0.08 (0.25)	0.95
Eggs/nest	9.1	4.6	50	55	-0.08 (0.24)	0.95
Adult Female mortality	0.75	0.49	104	76	-0.09 (0.31)	0.96

Figure 3.1 Conceptual diagram with system dynamics modeling as a central processing tool for integration of diverse forms of knowledge, interests and analyses to connect endangered species, people and management in a shared and positive response.

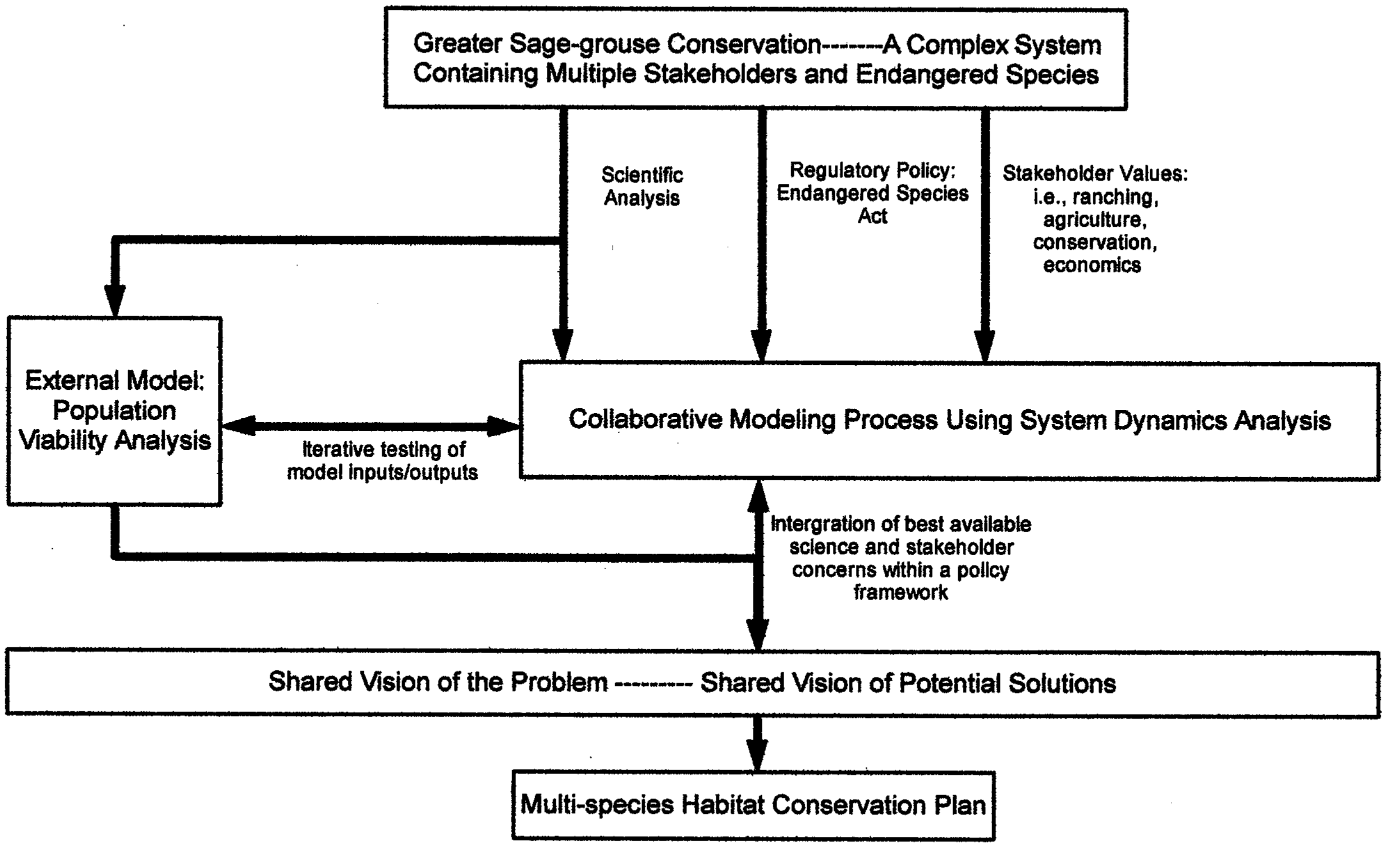


Figure 3.2 Stock and flow diagram of female Greater sage-grouse life history.

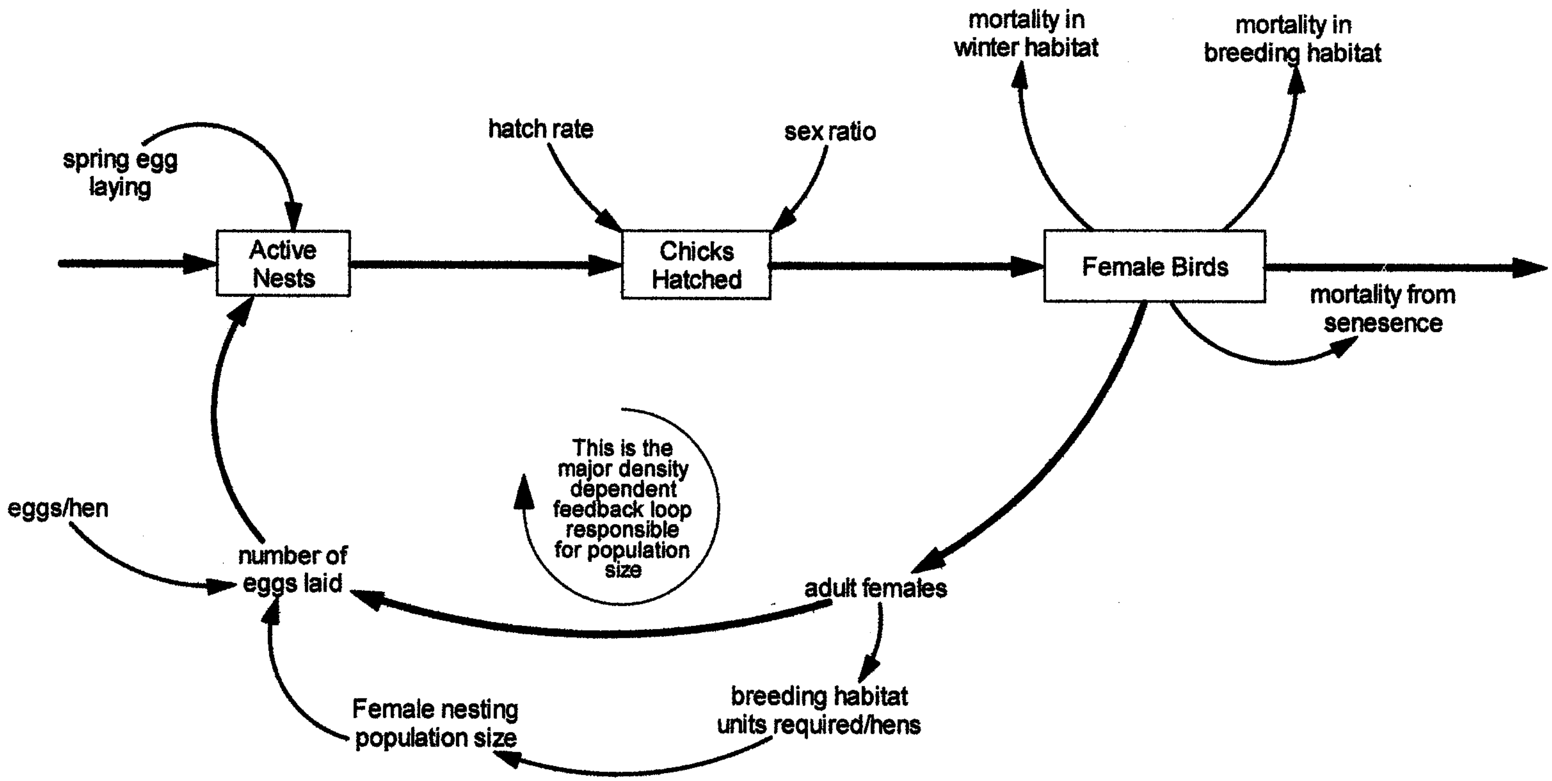


Figure 3.3 Habitat limitation in the systems model of Greater-sage-grouse operates through a space limitation for breeding females.

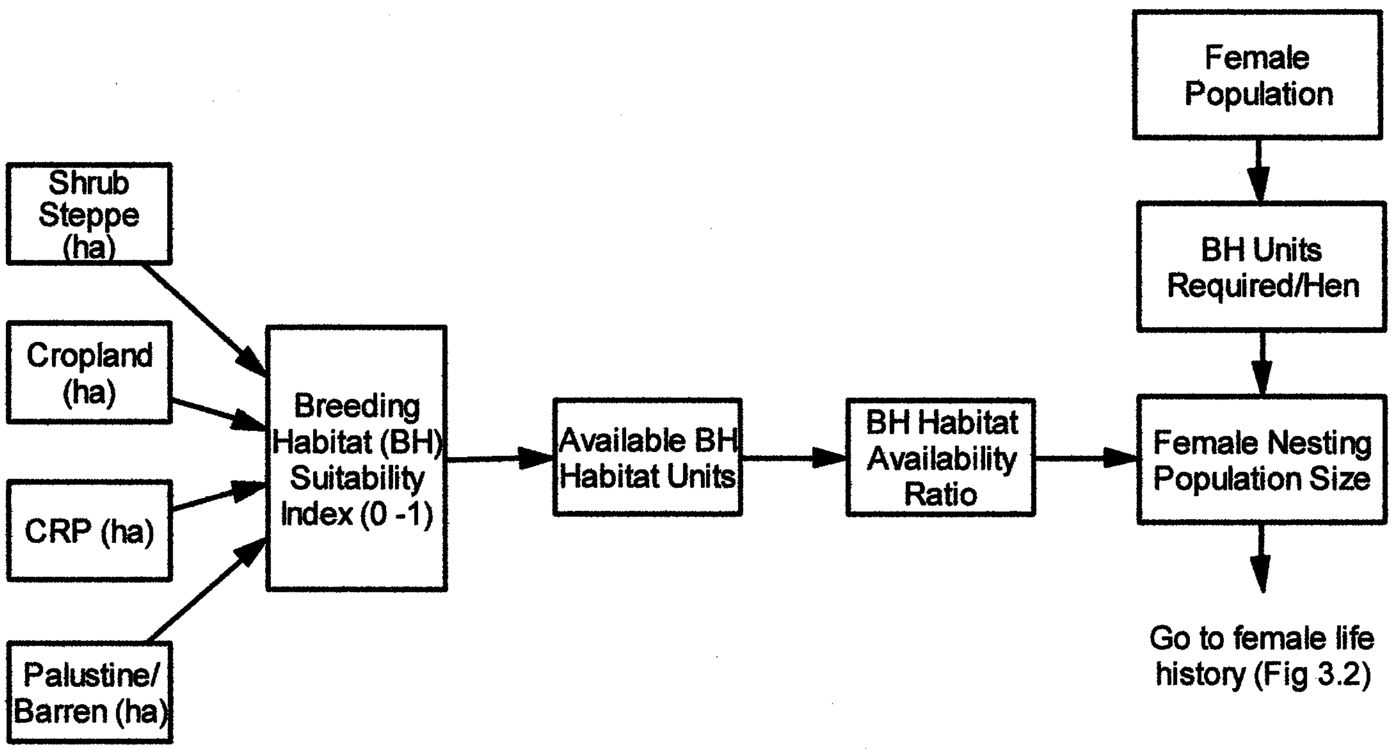
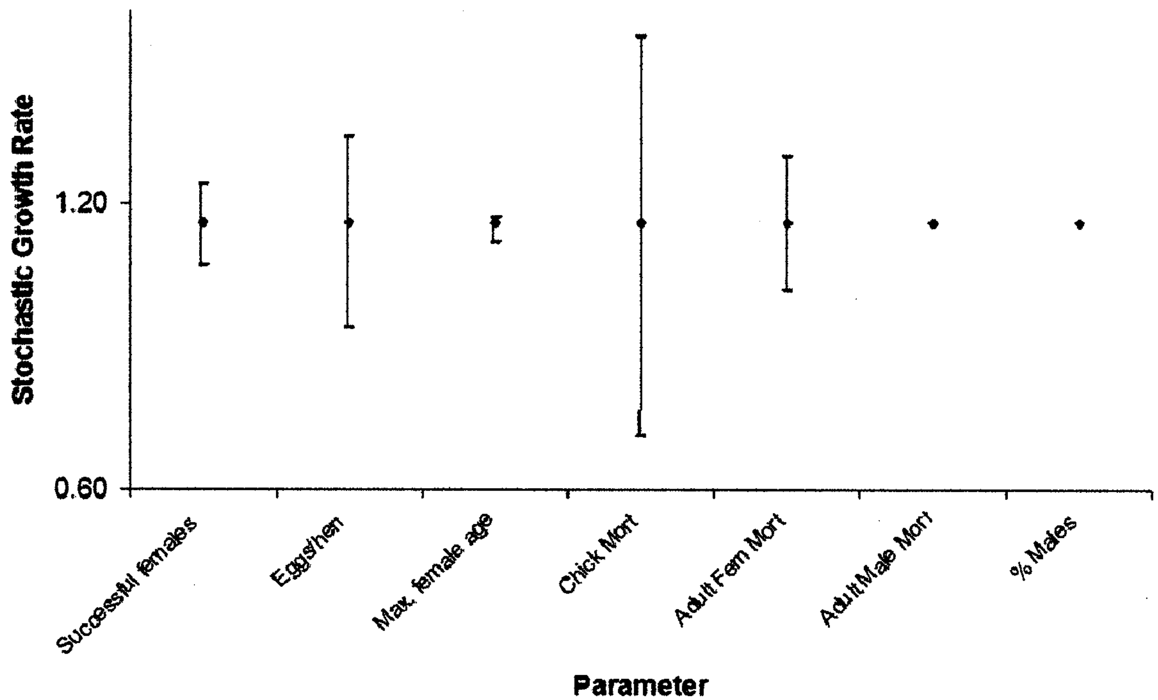


Figure 3.4 Range of stochastic growth rate as a function of the 95% confidence interval for demographic parameters for a simulated population of Douglas County Greater sage-grouse. The baseline model growth rate is the central data point.



CHAPTER 4

LESSONS LEARNED

4 Lessons learned

4.1 Introduction

Arriving at this chapter of the dissertation marks the fulfillment of a long personal journey. Along the way, science as a discipline and the educational system have both demanded much of me. I have learned many things and to think in new ways, to challenge ideas and question with a growing intelligence. Many times it seemed as if my personal thoughts were not of much account or had to be subjugated to an immediate need to meet course requirements. Nevertheless, it has been an individual journey into new territory, and now that I have come through, it is time for me to speak from my own mind, to activate the "philosophy" part of the degree called a Ph.D. I write out of what I have learned over the last 12 years, the references which are not possible to compile and that involve countless individuals and groups as well as dialogue with teachers, friends, colleagues and strangers. I will write in my own style and speak in the first person with little use of formal external references.

As I look out upon the natural and human worlds, and seek opportunities to apply myself to the work of conservation biology, I cannot help but be intensely personal in my love and respect for life, for nature, and for the intense beauty of this one small planet. Neither can I separate science and life, knowledge and action. Science for me is a method of acquiring and testing knowledge, and a good one, yet one amongst the many that must be integrated in order to make conservation work. Conservation biology is science in a practical and applied form, and indeed the thrust of my work has been to figure out what is going on with rabbits and with sage-grouse, and how to do something about it by using the accepted techniques of scientific investigation. A concern I have developed is the need to communicate such scientific findings to people outside academia and to promote the wider application of academic expertise to practical conservation problems. Science can appear as an unapproachable society because of jargon or complicated methodologies and specializations that tend to have singular, and therefore exclusive, focus. Uncertainty, easily understood by scientists, is a double-edged sword in the larger world and can be a stumbling block to the acceptance and application of important knowledge. Those of us involved in science need to talk about how it works and how it gets translated into society and actively assist that translation process. We need bridges from reductionism and research to workable decisions on the ground and we need more people who can walk across them to influence decisions at both the personal and aggregate levels of culture. In the end, science is a human endeavor. It is people who perform scientific investigation and people who apply it in the service of conservation.

As individuals and as a society, we make decisions about conservation issues every day. In fact we have always done so and cannot stop doing so. It has been said that you cannot do just one thing (Hardin's law). It has also been said that not to decide is to decide (Harvey Cox). There is no way out. We are making daily decisions and choices that change the future condition of our planet and its life support system. Choices may appear small, personal or local, but the effects are potentially and perhaps actually global (the butterfly effect). Nature is a complex interacting system which we do not well understand (or our research needs would be few indeed) but which we move in some direction every day. What we have to think about is how we can make better, more informed decisions about the effects of our actions in the face of uncertainty.

Decisions are made from the information at hand whether historical, current, true or contrived. We take what we know or think we know, formulate it into mental models and put it into the context of the future, of what we expect to ensue from a decision. Thus our decisions are based on a perceived cause and effect relationship: If I (we) do this, such and such will likely happen. Decisions do not have to be earth shaking or extend beyond the next few moments, but they are made with mental models that put our needs or expectations together with our knowledge. What do I want in my coffee this morning? How should we prioritize the protection and restoration of the remaining shrub-steppe in central Washington? Different questions, indeed, but our decisions are made with the same method, a model of action and reaction, of choice and outcome.

Our mental models tell us what we think we should be doing, and in truth, the very highly valued thing we call "expert opinion" is a mental model grounded in intimacy with a system. We trust and hope that more accurate knowledge and deeper understanding begets better decisions, yet our knowledge, and this is especially true of science and of natural systems, is incomplete and always will be. One does not have to investigate ecological and natural systems, or any complex system for that matter, for long before realizing that cause and effect does not always produce direct or immediate results. There are time delays and non-linear relationships not easily understood or charted in the human brain. Natural systems are complex and involve myriad interrelationships many of which we are unable to detect or understand with conventional statistical analysis. Looking at it another way, we could know all there is to know about an ecosystem today, but when we got up in the morning it would be different and new things would await discovery because natural systems are always in flux and have emergent properties. Because of these things, there is much uncertainty, and science involves itself in uncertainty analysis, presenting results as levels of probability.

I have heard from many scientists both in their own words and in their writings that we do not know enough to make the best decisions. Scientific articles often end with the statement that more study is needed. There are times when I feel that it takes the guise of a disclaimer. Although scientific knowledge will never be complete, in a practical, political and economic sense, we do not, and indeed cannot, wait for the ultimate state of knowledge to emerge. A statement once came from a prominent scientist, whom I respect and who shall remain nameless, that he was afraid people would actually put some of their conservation plans (for sage-grouse) into practice, meaning that enough information was not yet available and that scientists should be the ones to oversee those plans when and only when they themselves had enough knowledge to formulate them. But such a state of unconditional knowledge and of waiting for the precise moment when all our studies cohere into a perfect plan is a pipe dream. People who work and use the land make management decisions every day; they must in order to survive. At the same time there is intense political pressure to formulate conservation plans for sage-grouse as well as other species and ecosystems of concern. Time is of the essence if we are to save threatened and endangered species and create sustainable societies that value the natural world as the basis of our physical and spiritual well-being. The livelihoods of people who own and work the land, and the condition of the land itself, is affected by many pressures that are not based in science and that cannot wait for science to achieve a state of perfect knowledge. Even with good evidence and knowledge at hand, it is still axiomatic that human beings make decisions from biases and preconceived ideas because they want certain outcomes that are not necessarily for the common good. There is no requirement that the current or "best" state of knowledge be put to use, or that the common good be the paramount concern, at least not in the unbridled economic drive for personal and corporate wealth of the 20^{th} and 21^{st} centuries.

We are not, however, helpless. Our motivation to achieve a high state of civilization has brought into existence educational tools to increase and pass on knowledge and tools for the integration of that knowledge with social and political needs. One of these tools is model building. We can build computer models that are more extensive than our mental models simply because constructed models can synthesize and interpret many more things at the same time than our minds can hold and process. Microcomputers give us the opportunity to integrate and simulate knowledge, to study the performance of systems and to look into the future and weigh the potential consequences of our actions. Computers, however, are not a panacea, they are tools, and just having a tool does not mean one will do better work. But the possibilities are thereby expanded, and good tools put to good use are a hallmark of humanity.

Creating a simulation model is one of the explicit methods we have to link the past and the future and to explore causal relationships and logical consequences. Simulation modeling offers the functionality of projecting system performance into the future allowing investigation and insight into trends and system status. It is not magic. Modeling is a way to experiment with a system and with our understanding of it. Modeling is a form of prognostication but not a form of absolute prediction for the simple reason that our current state of knowledge is partial, data may be missing, and many assumptions form the basis of simulation modeling. A model is in truth a series of assumptions and generalizations about reality, the same as our mental models.

Assumptions do not negate the value of model building any more than they negate the value of our daily living; indeed they underlie every aspect of our lives and are a necessary step in any thinking or activity. For instance, you assume the floor is going to hold you up when you get out of bed in the morning, but you don't think about it first and asses the probability of a failure. You assume based on your best knowledge that what happened yesterday will continue to be the case today. Simple as it sounds, this is a very important assumption in many models, i.e., how a system functions today is how it will function tomorrow, that current parameter estimates are valid into the future.

One of the beauties of building a model is that it requires that we ask questions about the system under investigation, which often results in learning and increased awareness. By forcing us to think about a system, a model becomes both a learning and a teaching tool for the builder and for the client. Gaps in our knowledge must be accepted, recognized and sometimes filled in with our best guesses, filled in with expert opinion or substituted with data from other similar systems. However, good scientific estimates come with some range of variation, and these ranges of variation become the focus of uncertainty analysis that provides us with knowledge about what drives the system of concern or where it is most sensitive to change. Analysis of assumptions and uncertain data can provide direction for new research and in turn new research can be used to update models and promote better decisions in an adaptive framework.

A model provides a method by way of the simulation environment to find out what could happen if assumptions hold or do not hold, or if predictable or unpredictable changes occur in the future. These are broadly called "what if" scenarios. They are a way of conducting experiments and answering questions about a system that are not possible or too risky in the real system. For example, let us assume that natural processes will cause habitat quality for sage-grouse to improve by 0.5% each year for 25 years. We can test this in the model to determine how it might affect population size. We can then ask the question of whether it is enough to meet conservation goals or if managers need to increase the assumed rate of change? Or we could ask what if sage-grouse fecundity decreases by 10% due to the effects of inbreeding depression in a small population? What happens if both fecundity and juvenile survival decrease by 10%? In other words, what if current rates do not carry unchanged into the future? The simulation model can project effects on the bird population and help define the subsequent risk of decline or extinction the population faces under the stated circumstances. A very practical application of uncertainty and assumptions is to monitor the parameters that we assume will continue unchanged into the future but to which the model is sensitive. Change and the direction of change will alert managers to possible consequences and can thus lead to timely intervention.

Even deeper than assumptions about specific model parameters are underlying assumptions about our unconscious view of life, our world view. For instance, I am looking out the window of a jet airplane right now and the world looks like it is made up of squares almost all the same size. That is a mental model, put into practice, of how land should be divided up for ownerships and control. It is the root of land use planning in the western United States. A huge assumption underlies this type of survey and ownership, viz., it is our option to divide natural landscapes into any pattern we desire, especially if it is easy to manage on paper, and that other effects, if there even are any, are of lesser importance. This is a cultural assumption based on the western belief that humans are the measure of all things, the natural world is here for our unrestricted use, and that it must bow to our needs and desires. It is rare for such a deep cultural assumption to be stated. Nevertheless, many land agencies in our society have come to realize how difficult it is to manage a natural world that is strewn out beneath these squares in its own patterns, patterns we may not see unless we choose or are trained to see them. Another assumption in our land division and use is the priority of personal-corporate ownership coupled with the assumption that this is inherently a correct way, and probably the best way, for humanity to live happily on the earth. I think that most of us go through life not realizing that we have deeply rooted assumptions much less being able to state what they are. Nor does our educational system help us much with grasping them and their implications. We assume that our way of doing is the right way and the best way.

When we modeled the land use and sage-grouse system in Douglas County, WA (Beall and Zeoli 2005), we incorporated several uncertain parameters. We took advantage of expert opinion and made assumptions about some parameters (which are documented in a system dynamics model) but we neither stated nor investigated the assumption that the life style and land divisions in the county are worth preserving; in fact, we modeled because the Foster Creek Conservation District is hoping to preserve a lifestyle based on their rural landscape and how it has been used historically by European settlers. Perhaps you could say that such broad assumptions are not ours to question, and for the purpose of our work with the FCCD, you would be correct since we accepted an invitation to work with them on conservation planning relative to their sage-grouse population. Nevertheless, an awareness of the baseline conditions of our thinking is most helpful in understanding the purpose and use of a model describing some portion or our world. And it is safe to assume that for the foreseeable future, conservation must work within the current ownership framework, which logically means that involving real people who own property or have interests in conservation of land, lifestyle or biodiversity, is fundamental to planning success. Thus we model a system, but we must include diverse people and their concerns as well as multiple forms of knowledge, not limited to science, in order to have any hope of a supportable and functional decision making process.

4.2 How the foregoing models addressed practical issues in the conservation of threatened and endangered species

4.2.1 Pygmy rabbit PVA (Chapter 2)

The recovery of the Columbia Basin pygmy rabbit depends upon harvesting rabbits from a captive breeding program that was initiated as an emergency rescue operation in 2001. After six years of captive breeding, there were finally some "surplus" rabbits in the spring of 2007, and it was deemed appropriate to begin reintroduction. There were two real problems with the first reintroduction effort, although they were not readily apparent to everyone involved at the time. First, there were only 20 surplus animals available not considered essential to maintenance of the captive population. Such small populations are subject to demographic stochasticity, random events in birth, death, and productivity that cause them to be unstable, even if their projected growth rate is positive. The threshold for the effect is generally considered to be about 30 animals (Boyce 1992; Morris & Doak 2002). Unless the new population had a very good breeding season post-release and increased in size quickly, demographic stochastics would be a problem. The second problem was the ability of the captive population to produce enough surplus rabbits to support a sustained reintroduction effort. To establish and supplement several new wild populations of pygmy rabbits until they can become self-sustaining will require a continuous harvest each year over several years. When the first reintroduction proved unsuccessful, coupled with the fact that there were no surplus rabbits to continue releases in 2008, it became necessary to research the ability of the captive breeding population to support a sustained recovery effort for the Columbia Basin pygmy rabbit.

Modeling the captive population dynamic and mimicking harvest for release provided some new information for future planning. The data set from the captive breeding program is excellent thanks to extensive record keeping. Complete data for the years 2003-2007 were analyzed for vital rates, i.e., maternity, longevity, and mortality, and the rates were used to construct demographic models. Although only a short time series was available, it was necessary to analyze and project the growth of the captive population to determine at what level of harvest the current population could support reintroduction goals. The resulting population viability analysis and risk assessment indicated that the captive population, although it had a positive stochastic growth rate, exhibits high variability in that rate such that the number of surplus rabbits cannot be anticipated from year to year, and can be zero in any year. This accords with the reality of the last two years. In addition, continued annual harvest of as few as 30 animals per year for six years puts the captive population at high risk of extinction.

Even though long-term data are more desirable, it takes time to collect these data sets. Although we could hope for more, waiting would keep the recovery in a more uncertain predicament than using what data was available. At least now there is some quantified reason for the low surplus of rabbits produced to date. Model results also suggest specific directions for new research and where it may be most effective to intervene in the captive breeding system to improve demographic performance. I cannot think of a more practical application of simulation modeling.

Scientific and uncertainty analysis have been put to use in the conservation and recovery of an endangered species by synthesizing available information, projecting the most likely outcomes and suggesting the next steps.

An important part of endangered species recovery is the building of PVA models. Model use is not restricted to and should not stop with the first set of analytical results. Full and most effective application of this model can be achieved if it is updated with new data on a regular basis and if it is revisited when new questions as they arise in an iterative process of learning. The PVA is a new tool in the pygmy rabbit recovery process and can be most effectively used if, over time, it becomes incorporated into research and planning, which will also extend the resources allocated to the production of the model.

4.2.2 Greater sage-grouse (Chapter 3)

Systems dynamics modeling was created to integrate the multitude of processes that are at work in complex systems and is able to incorporate a wide range of information types from "hard" science to "soft" intuition (Ford 1999). It is often used as a tool in participatory modeling to incorporate multiple stakeholder interests and a variety of pertinent information (see Chapter 3 for references). Systems models have been increasingly applied to many environmental problems and issues, yet have seldom been used in endangered species management. Since the sage-grouse is a species at risk, and PVA modeling is specifically designed for analysis of small population dynamics, we wanted to incorporate this accepted form of endangered species modeling into the larger more comprehensive framework of a systems model. This would allow us to make multiple stakeholder concerns besides sage-grouse explicit model elements. A systems model is able to directly incorporate land use and social values that affect land use as well as the quality of sage-grouse habitat on specific land types, whereas in PVA this type of information is incorporated indirectly by influences on demographic rates or the carrying capacity of habitat. Our concept was that if both modeling systems showed the biological system to have similar growth patterns as well as sensitivity to the same parameters, we would be confident that systems modeling could be an applied tool for integrating the many concerns surrounding endangered species management. Specific risk assessments could be done in the PVA as a scientifically defensible support for particular management actions that might affect population size or growth rate, while at the same time specific management actions could be explored in the land use and habitat options provided in the systems model. The visual model structure and graphical user interfaces of a systems model, which can be customized for every project, make it more readily accessible to users who can not only identify the components of their system, but can also run the model themselves. This promotes transparency and trust and provides a key tool for communication of system knowledge and exploration of possible futures.

The Sage-grouse and Human Systems Model (Beall and Zeoli 2005) is a combination of two model types. My part was largely a PVA for the sage-grouse of Douglas County, WA, and the life history portion of the systems model. The overall goal was to create a system dynamics model that tied sage-grouse biology to land type, habitat quality and land use in the county and linked it to some of the economic drivers of land use. The model building process was participatory in nature and involved members of the District, who in essence told us how their system worked. We modeled their system for them without prior knowledge.

It is too soon to conduct a retrospective of this particular modeling project. However, it was well-received. The communications we had with the District while building the model encouraged them to develop a more extensive and scientifically based Habitat Suitability Index. We were also able to model the effects of a loss of land in the Conservation Reserve Program, a particular concern of the District, and show that it could be offset by a certain percentage of private land signed onto a proposed Multi-species Habitat Conservation Plan, which is expressly designed to address endangered species in the county. Our hope is that the county will desire to update the model over time to incorporate the new information they are collecting and to extend the value of the initial model by using it to ask questions about their management options.

4.3 Closing Remarks

I have invested a great deal of time and energy in these modeling projects because I am convinced they are essential to synthesizing relevant data and knowledge into practical tools for species conservation. The models in this paper are not isolated academic exercises. They are work applied to real conservation problems, and as such form the basis for my future work in conservation biology. They represent both specific (PVA) and broad (SDA) methods for modeling that can be applied in threatened and endangered species management. These models are at the interface of theory and application, conservation biology and society, science and policy. Although the models do not belong to me personally, they are invested with my desire for positive action that is based on quantified, defensible and process-oriented thinking. To those who have supported these efforts, many, many thanks. Let these tools be one of the ways we can collaborate in honoring and maintaining life on this earth.

4.4 References

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APPENDIX

Appendix A. Record of pygmy rabbit mortalities at Sagebrush Flat, 2007.

Name	Stud Book	Field ID	Mortality Date	Notes
Females				
Kelby	468	F5	27-Mar-07	Unknown: Found dead near her artificial burrow, no apparent cause, no scavenging. Necropsy indicated possible raptor hit which she escaped.
Pansy	218	F7	15-Mar-07	Raptor: Pile of plucked fur with stomach and some entrails, 8m from artificial burrow 13C
Clementine[1]	216	F8	17-Mar-07	Unknown (suspect coyote): Empty collar on game trail (in a small draw) with no evidence in 10m circle. A few small hairs with blood were on collar. Collar tubing cut in two places.
Petunia	499	F6	30-Mar-07	Raptor: Collar clean, intact, in area relatively clear of sage. Very small bit of fur 2m away. Stomach, intestines, gall bladder in neat pile 3m away.
Bespin	591	F3	3-April-07	Unknown (suspect coyote): Empty collar found 1.4km from last position at artificial burrow. Possible blood stains on ground. One bite mark on collar. Known coyote activity and fresh sign in the area.
Sadie	217	F1	21-April-07	Unknown (suspect raptor): Empty collar found ~170m N of a dirt burrow she had been using for about a week that was ~200m N or her artificial burrow (6B).
Sally	319	F2	12-May-07	Raptor: Body parts found broken up and scattered, pile of plucked fur, kill still fresh. A large unidentified raptor came up from the site as technician approached. ~100m SW of her artificial burrow (1B).
Impala	599	F4	13-Aug-07	Suspect raptor: collar found 550 m south of last known location artificial burrow 10B on 8-Aug_07.
Males				
Cedar[1]	406	M3	21-Mar-07	Starvation: Found dead in old burrow hole. Necropsy indicates emaciation and probable

				starvation.
Munchkin	547	M4	24-Mar-07	Unknown (suspect raptor): Empty collar found near ridge top in barren area. 2 small tufts of fur 3m away.
Solo	568	M5	26-Mar-07	Unknown (suspect raptor): Empty collar found near ridge top in thick sage, as if dropped there, no other marks or evidence. Transmitter had small bite mark, collar tubing cut in three places, leader bitten in two.
ElCamino[2]	601	M7	17-Mar-07	Missing, presumed dead. Landowner does not grant permission to enter. Radio signal can be heard from SBF Road, still there as of 27 Mar 07.
Salem[2]	565	M8	17-Mar-07	Unknown (suspect coyote): Empty collar on game trail (in a small draw) with no evidence in 10m circle. A few small hairs with blood on collar..
Sir Hiss[1]	313	M9	15-Mar-07	Unknown (suspect raptor or coyote): Empty collar, 5 tufts of fur 1" diameter within 1m of collar, no other evidence in 10m circle..
Percy	500	M10	25-Mar-07	Starvation: Found dead in old dig hole, no apparent cause, no scavenging. Necropsy indicates emaciation and probable starvation.
Tug[2]	501	M11	16-Mar-07	Unknown (suspect raptor): Transmitter found in wheat stubble, no damage,
Kerr[2]	347	M12	16-Mar-07	Raptor: Empty collar found in dirt road adjacent to CRP with good sage cover small pile of fur, 2 short segments of intestine, 4 piles of raptor guano.
Utapau[2]	592	M6	27-Oct-07	Unknown (suspect raptor).

[1]On-site dispersal
[2]Off-site dispersal

Appendix B. Maternity calculations for pygmy rabbits as required for RAMAS and Vortex population modeling software.

We used two different software programs for population viability analysis of the Columbia Basin pygmy rabbit. Using two different modeling systems allowed us to take advantage of a wider range of outputs and to check for differing results that would indicate problems with data, input parameters, or model structure. Baseline models were tested for equality in deterministic growth rate (λ) and therefore underlying deterministic processes before proceeding with stochastic analyses. It was found that very small differences, even in the hundredth decimal place, in input parameters for maternity in Vortex, resulted in changes in λ that produced large differences in ending population size, as much as 150 animals in 10 years. In order to consider the models comparable, they need to the same deterministic growth rate (Brook et. al. 2000; Wielgus, pers. com.)

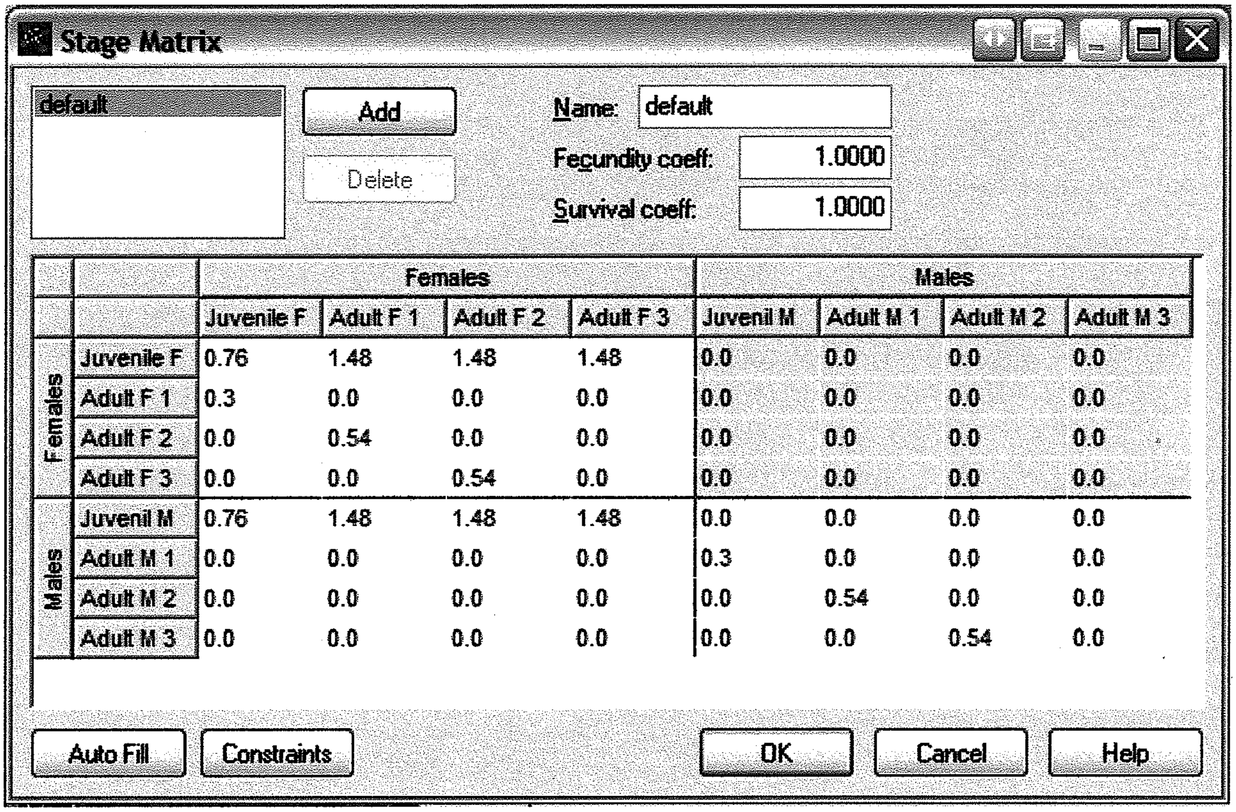
We determined that the differences were in how the models use maternity. Vortex bases maternity calculations on the number of females that actually produce young (% of successful females), litter size, and maximum possible number of young. Each reproductive parameter is entered into Vortex as an individual input. In RAMAS, maternity is the instantaneous rate which is the total number of young/total number of females breeding. It is not necessary to know the number of successful females or litter size because the rate has already incorporated them. Instantaneous maternity is then used to calculate a fecundity value which is a composite value of maternity estimates multiplied by an age specific survival rate.

There were four years of data on maternity for the Intercross rabbit population, 2004-2007 (Appendix E). The mean and standard deviation (SD) of those values are the model inputs, SD representing environmental stochasticity, i.e., year to year variability in the environment that affects reproductive success. We used the arithmetic mean for all parameters in RAMAS. We found that we had to use the grand mean for the % of successful females in Vortex, not the arithmetic mean, in order to produce the same λ in both model systems. SD for the grand mean rate was calculated from the arithmetic mean. Refer to Appendix E for all demographics.

References.

Brook, B.W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, and R. Frankham. Predictive accuracy of population viability analysis in conservation biology. Nature. **404**, 385-387.

Appendix C. Stage matrix for the baseline pygmy rabbit population viability analysis in RAMAS used to test for deterministic growth rate (λ).



		Females				Males			
		Juvenile F	Adult F 1	Adult F 2	Adult F 3	Juvenil M	Adult M 1	Adult M 2	Adult M 3
Females	Juvenile F	0.76	1.48	1.48	1.48	0.0	0.0	0.0	0.0
	Adult F 1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Adult F 2	0.0	0.54	0.0	0.0	0.0	0.0	0.0	0.0
	Adult F 3	0.0	0.0	0.54	0.0	0.0	0.0	0.0	0.0
Males	Juvenil M	0.76	1.48	1.48	1.48	0.0	0.0	0.0	0.0
	Adult M 1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
	Adult M 2	0.0	0.0	0.0	0.0	0.0	0.54	0.0	0.0
	Adult M 3	0.0	0.0	0.0	0.0	0.0	0.0	0.54	0.0

Appendix D. Inputs for the baseline pygmy rabbit population viability analysis in Vortex used to test for deterministic growth rate (λ).

VORTEX 9.72 -- simulation of population dynamics

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1 population(s) simulated for 10 years, 1000 iterations

Extinction is defined as fewer than 30 individuals

No inbreeding depression

EV in mortality will be concordant among age-sex classes

First age of reproduction for females: 1 for males: 1

Maximum breeding age (senescence): 3

Sex ratio at birth (percent males): 50

Polygynous mating; % adult males in breeding pool = 100

% adult females breeding = 83

Of those females producing progeny, ...

Mean number of progeny per breeding female per year = 6.6

% mortality of females between ages 0 and 1 = 70

% mortality of adult females (1<=age<=3) = 46

% mortality of males between ages 0 and 1 = 70

% mortality of adult males (1<=age<=3) = 46

Initial size of Population 1: 70

Carrying capacity = 500

Appendix E. Demographic rates for the intercross population of the Columbia Basin pygmy rabbit, 2003-2007.

	Survival[1]					Maternity									
	Adult	Infant 4 day	Juvenile 24 day	Sub-adult 337 day	Juvenile Period 365 days	# Females Breeding	Total # Kits	# Females with ≥ 1 litter	Maternity RAMAS[2]	Juvenile Fecundity RAMAS[3]	Adult Fecundity RAMAS[4]	Percent Successful Females	Kits/ Successful Female	Max # Kits/ Female	Kits/ Litter
2003[5]		0.53	0.92	0.86	0.42										
2004	0.60	0.96	0.71	0.47	0.32	5	21	4	4.2	0.66[6]	1.27[6]	80	5.25	8	3.50
2005	0.54	0.82	0.87	0.55	0.40	15	96	14	6.4	1.27	1.72	93	6.86	23	3.31
2006	0.60	0.52	0.74	0.65	0.25	35	185	27	5.29	0.66	1.58	78	6.85	20	2.98
2007	0.42	0.40	0.63	0.55	0.14	29	187	25	6.45	0.45	1.36	86	7.48	22	3.02
Mean	0.54	0.64	0.78	0.62	0.30				5.58	0.76	1.48	84	6.61		3.20
SD	0.08				0.11				1.07	0.35	0.21	7	0.95		0.25

[1] Juvenile survival was calculated by the Mayfield method. It was divided into 3 periods (infant, juvenile, sub-adult) that distributed mortality evenly over each period for an unbiased estimate. The rates of the 3 periods were multiplied for an annual rate.
[2] Maternity RAMAS = Total # Kits/# Females Breeding.
[3] Juvenile Fecundity RAMAS = Juvenile survival * Maternity RAMAS.
[4] Adult Fecundity RAMAS = Adult survival * Maternity RAMAS.
[5] The first intercross (Columbia Basin x Idaho) rabbits were born in 2003, therefore only survival is available for that year.
[6] Small discrepancies in these rates are the result of rounding to 2 decimal points after calculations were made.