Development of an Innovative Statewide Population Monitoring Program for Mule Deer

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DEVELOPMENT OF AN INNOVATIVE STATEWIDE POPULATION MONITORING PROGRAM FOR MULE DEER

by

Heather H. Bernales

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Wildlife Biology

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ABSTRACT

Development of an Innovative Statewide Population Monitoring Program for Mule Deer

by

Heather H. Bernales, Master of Science
Utah State University, 2010

Major Professors: Dr. Mary M. Conner and Dr. Michael L. Wolfe
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Monitoring population trend and estimating vital demographic parameters are essential for effective management of a mule deer (*Odocoileus hemionus*) population. Because of financial constraints, many wildlife agencies use computer models to obtain indirect indices of population size and trend as an alternative to annual field-based estimates of population size. These models are based primarily on herd composition counts and harvest rates from hunter-harvest surveys, and are rarely field validated. I developed an alternative method for monitoring population dynamics of wintering populations of mule deer. I designed a hybrid monitoring program that combined annual vital rate monitoring to track changes in population growth rate with a field-based approach for estimating population abundance. The program allocated resources optimally towards the most critical components of mule deer population dynamics, and
consisted of 4 field surveys: annual monitoring of age ratios, overwinter fawn survival, and annual doe survival, with field-based estimates of population size only once every 4 years. Surveys were conducted from 2006 to 2008 in Wildlife Management Unit (WMU) 2, Utah, and cost $29,298 per year, prorated over 4 years. Unfortunately, financial constraints prohibit the implementation of this monitoring program in every WMU in Utah. Instead, the program can be implemented in select WMUs throughout the state, with survival data collected in these core units, providing estimates for nearby satellite units. To establish core-satellite unit pairs, I developed a proxy method for determining correlation in survival rates between core and satellite units using model-simulated estimates. I demonstrated this core-satellite method using WMU 2 as a core and WMU 3, an adjacent unit, as a satellite. Finally, I compared a multiple data sources (MDS) model with a herd composition-based population model, POP-II. The MDS model better approximated observed data, and provided statistical rigor. Overall, the hybrid program was less costly and provided more precise estimates of population trend than could be achieved with a monitoring program focused on abundance alone, and was more defensible than herd composition monitoring. After establishing correlations in doe and fawn survival between core and satellite units, data collected in core units via the hybrid program could then be used to model the mule deer population dynamics of other units using MDS modeling procedures. This combined approach could be an effective statewide program for monitoring mule deer populations.
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CHAPTER 1

INTRODUCTION

Mule deer (*Odocoileus hemionus*) are valued as a symbol of the American West by hunters and non-hunters alike (Heffelfinger and Messmer 2003, Mule Deer Working Group 2004). Mule deer are the premier game animal in most states across the West, including Utah (Wallmo 1981, Heffelfinger and Messmer 2003, Utah Division of Wildlife Resources 2008). Due to the popularity of this species, declines in mule deer populations, such as those observed during the 1960s, 70s, and 90s, could have negative repercussions both socially and economically (Heffelfinger and Messmer 2003). Therefore, wildlife managers need well-designed monitoring strategies for mule deer to obtain accurate data about population size and trends. This information is important from 2 management perspectives: 1) assessing the effectiveness of population management via hunter-harvest manipulation (hunting regulations), and 2) evaluating the positive and negative impacts, respectively, of habitat improvement projects as well as potentially detrimental practices.

Wildlife management agencies employ a variety of survey techniques to determine population abundance and trends of big game populations. Rabe et al. (2002) summarized the big game survey methods used by wildlife agencies in 9 western states. Five states, Colorado, Idaho, Montana, New Mexico and Oregon, used aerial-based surveys exclusively to monitor mule deer populations. Wyoming, Arizona, Washington, and Utah used some combination of aerial and ground-based surveys. All states collected herd composition data, while most collected counts of deer seen, group size, and habitat
types. There was high variability in methods of visibility correction, sampling design, scale, and timing. States also varied in their use of information collected from surveys: most estimated population size indirectly from herd composition data, while some also estimated survival and fawn recruitment. Rabe et al. (2002) stressed the need for direct population size estimation, formal, random sampling design, and increased emphasis on estimation of adult female and fawn survival.

There are 4 main field-based methodologies that have been used to estimate population size for mule deer: 1) mark-resight, 2) distance sampling, 3) quadrat counts, and 4) quadrat counts adjusted for visibility bias. In a mark-resight study, population size is estimated from an initial sample of mule deer that are captured and marked, with recaptures obtained by observing the deer, not by re-capturing them. Aerial mark-resight has been tested on known populations of mule deer (Bartmann et al. 1987) and white-tailed deer (*O. virginianus*; Rice and Harder 1977). Aerial and ground-based mark-resighting procedures have also been successfully used on other ungulate species including moose (*Alces alces*; Bowden and Kufeld 1995) and mountain sheep (*Ovis canadensis*; Neal et al. 1993). However, the mark-resight procedure is more expensive, especially at a large-scale such as a Wildlife Management Unit (WMU), and more invasive than aerial transect and quadrat methods, due to the annual capture requirements for marking animals. In addition, the number of collared animals that are alive from the previous years’ collaring efforts needs to be determined (potentially with some supplemental radiocollars) at the start of each re-sighting effort. This method may be
cost competitive in areas where deer have habituated to humans and can easily be captured and re-sighted.

Theoretically, line transects, or more specifically, distance sampling could be adapted for use on mule deer via aerial transects (Eberhardt 1978, Buckland et al. 1993). Line transects require minimal effort to establish and have been successfully employed on a relatively small scale (<47 km²) to estimate mule deer population size using both driven transects (Koenen et al. 2002) and aerial transects (White et al. 1989). However, both these studies identified similar problems with the method: its sensitivity to violation of critical assumptions. By design, White et al. (1989) compared distance sampling to quadrat counts, and found distance estimates of population size to be slightly more economical and less biased than quadrat counts, for a given measure of precision. However, a “major problem with the use of distance sampling is the number of decisions that must be made to generate an estimate” (White et al. 1989). The “fussiness” of data collection protocols required to meet model assumptions are generally not practical for large-scale use.

Aerial quadrat counts represent the most commonly used method for directly estimating mule deer population size (Gill 1969, Kufeld et al. 1980, Bartmann 1983, Bartmann et al. 1986). The approach, typically employed at large scales, involves helicopter counts of animals on pre-determined quadrats based on a stratified random-sampling scheme (Thompson et al. 1998). In some instances the results are adjusted for visibility bias (Pollack and Kendall 1987, Samuel et al. 1987). However, costs prohibit state wildlife agencies from directly estimating mule deer population sizes for all
populations statewide on an annual basis. Typically, population size is only estimated via quadrat methods for a small subset of representative populations. Another problem with aerial quadrat counts is that the confidence interval of the population size estimate is typically large, which prevents the detection of increases or decreases in population size at the level of management interest. The number of quadrats required to increase precision to levels where 10-20% declines over 5-10 years could be detected is prohibitively expensive. Therefore, a scientifically defensible monitoring strategy consisting of direct estimation of population size via aerial quadrat counts alone is expensive and impractical.

Currently, the Utah Division of Wildlife Resources (UDWR) estimates mule deer age and sex composition from post-hunting-season surveys in each respective WMU and obtains annual harvest estimates from hunter-harvest surveys (Bernales et al. 2009). These parameters serve as inputs into a computer-based population model, POP-II (Fossil Creek Software, Fort Collins, CO), in order to extrapolate estimates of mule deer population size and determine population trends (Bernales et al. 2009). POP-II is a deterministic model that simulates a closed population using “bookkeeping” techniques to subtract animals in the form of mortality and add for natality (Bartholow 2003). Many other state wildlife agencies use POP-II and other similar post-hoc population models to obtain indirect indices of population size and trend as an alternative to annual field-based estimates of mule deer population size (Bowden et al. 1984, Rabe et al. 2002). This approach often does not accurately portray mule deer numbers or trends (Bowden et al. 1984, Rabe et al. 2002). Furthermore, a strictly model-based approach is undesirable
because there is no way to evaluate how well the model works without some validation via field-based estimates. However, many wildlife managers contend that population modeling and simulation are essential for successfully managing a deer population (Roseberry and Woolf 1991). As population models are increasingly used to manage wildlife populations, more rigorous and objective methods should be employed to provide input estimates (such as population size, survival rates, etc.) for these models so that they can withstand public scrutiny by an increasingly involved and diverse set of stakeholders (White and Lubow 2002).

As an alternative to a strictly model-based approach or quadrat counts alone, White and Bartmann (1998) recommended monitoring total population size (via quadrat counts), recruitment rate of juveniles into the adult population, and juvenile and adult survival rates. These are the 4 main elements required for a scientifically defensible model used to estimate population size. Bowden et al. (2000) described a methodology for allocating resources to the 4 main samples needed to monitor a harvested mule deer population by optimizing allocation of resources to minimize the variance of the estimated adult female population size or population growth rate for a given budget. This method was predicated on the assumption that only females are critical to the population dynamics and, consequently, only requires data on females.

Following White and Bartmann (1998), a Utah mule deer monitoring plan should be based on 2 crucial philosophical goals. First, management decisions should be driven by data, and second, good data on a few mule deer populations are better than poor data for all populations. The overall goal of this project was to develop a portable,
statistically-based population monitoring program for mule deer statewide that was readily adapted to different regions in Utah with different deer densities, habitats, and management objectives.

In Chapter 2, I designed a hybrid population monitoring program for mule deer that focused primarily on monitoring vital rates while still incorporating occasional population size estimates. The program consisted of annual monitoring of age ratios, overwinter fawn survival, and doe survival, as well as field-based estimates of population size once every 4 years. I compared costs and precision of the hybrid monitoring strategy to those of a more traditional monitoring approach that focuses primarily on estimating population abundance. The design provided a relatively sensitive monitoring scheme for a comparatively low annual cost.

In Chapter 3, I developed population models for mule deer herds in a core unit and a satellite unit using multiple data sources (MDS) integrated population modeling techniques, and compared these modeling techniques with the more traditional POP-II population model currently used by many wildlife management agencies throughout the Intermountain West. I developed a proxy method for determining correlations in fawn and doe survival rates between core and satellite units when field data were not available. This proxy method could be used to establish core-satellite unit pairs for implementing statewide monitoring initially, until enough survival data could be collected to estimate survival correlations directly. I demonstrated how survival data from a core unit could be combined with herd composition and harvest data from a nearby, satellite unit and used to efficiently model the population dynamics of that mule deer herd.
LITERATURE CITED


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deer/elk workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.


CHAPTER 2

OPTIMAL ALLOCATION OF RESOURCES TO A

HYBRID POPULATION MONITORING

PROGRAM FOR MULE DEER

ABSTRACT

Wildlife managers need a monitoring program for mule deer (*Odocoileus hemionus*) with the ability to detect whether a population is increasing, decreasing, or remaining numerically stable. I tested a hybrid program for monitoring a mule deer population that combined annual monitoring of vital rates to track changes in population growth rate with the more traditional approach of estimating population abundance. The strategy was designed for a precision rate of CV = 6.5%, which would allow detection of a ≥18% decline in population growth rate over a 5-year period, or a ≥13% decline in population growth rate over a 10-year period. Focusing on population growth rate rather than population size, the program consisted of 4 field surveys, namely annual monitoring of recruitment, overwinter fawn survival, and annual doe survival, and field-based estimates of population size only once every 4 years. Surveys were conducted from 2006 to 2008 in WMU 2, Utah, and cost $29,298 per year, prorated over 4 years. Overall population growth rate was 1.08 (SE = 0.07), which achieved the desired precision of CV = 6.5%. When resources were optimally allocated, it was possible to collect precise and repeatable data on multiple aspects of population dynamics. Although costs for monitoring fawn and doe survival were initially high, when amortized over several years, this monitoring program was less costly and provided more precise estimates of
population growth rate than could be achieved by monitoring population abundance alone.

**INTRODUCTION**

Abundance is the most commonly monitored attribute for tracking ungulate population dynamics, with the goal to maintain population levels close to pre-defined, sustainable numerical objectives (Thompson et al. 1998, Bowden et al. 2000, Williams et al. 2001). However, population size ($N$) alone reveals little about the long-term sustainability of a population (Lancia et al. 2005). Wildlife managers also need the ability to detect whether the population is increasing, decreasing, or remaining stable, so that appropriate management action can be implemented in order to meet future population size objectives (Thompson et al. 1998, Williams et al. 2001). This change in a population over time is defined as the finite rate of population increase ($\lambda$), or population growth rate (Gotelli 2001, Morris and Doak 2002).

The simplest method of determining population growth rate is to obtain estimates of population size at the beginning and end of a set time interval and then take the ratio of these 2 estimates, expressed mathematically as $\lambda = N_{t+1}/N_t$ (Morris and Doak 2002, Dinsmore and Johnson 2005). However, ungulate species are often spatially arranged in clusters or clumps, so $N$ estimates typically have high variance (Thompson et al. 1998), making it difficult to detect small or even moderate changes in $N$ with this method (Gibbs et al. 1998). Furthermore, estimating $N$ alone does not provide any information on the underlying processes that affect population change. An alternative approach is to determine $\lambda$ by monitoring the vital rates of a population, namely 1) the ratio of juveniles
to adult females (age ratio: \( R_J \)), 2) juvenile survival (\( S_J \)), and 3) adult female survival (\( S_F \)). Assuming a simple 2-age class Leslie matrix model (Leslie 1945),

\[
\lambda = 0.5R_JS_J + S_F,
\]

where the value 0.5 represents a 50:50 ratio of males to females at birth and only females are considered in this equation as only females give birth (White and Bartmann 1998, Morris and Doak 2002, Lancia et al. 2005). Population growth rate calculated as a function of age ratios and survival has a much smaller variance with a concomitant sensitivity to detecting a decline. Even if the ultimate goal of a monitoring strategy is to track population change over time through monitoring of vital rates, \( N \) must still be estimated occasionally in order to convert the rate to easily interpretable numbers of mule deer (Bowden et al. 2000). Moreover, estimates of \( N \) are still necessary to validate models of \( \lambda \) and recalibrate population models (Roseberry and Woolf 1991, Mayer et al. 2002, White and Lubow 2002).

The combination of \( N \)-estimation and vital rate monitoring can a powerful tool for wildlife managers for assessing the status of mule deer (\textit{Odocoileus hemionus}) herds and determining if population objectives are being met. I designed and evaluated a hybrid population monitoring program for mule deer that focused primarily on monitoring vital rates with periodic estimates of population size. The program consisted of annual monitoring of age ratios, overwinter fawn survival, and yearlong doe survival, as well as field-based estimates of population size once every 4 years. The design followed recommendations of Bowden et al. (2000) and optimally allocated resources to sampling effort in order to maximize precision while minimizing costs. I compared the cost and
precision of this hybrid monitoring program to those based solely on vital rates or population size.

**STUDY AREA**

I conducted this study in northern Utah in Wildlife Management Unit (WMU) 2 (Fig. 2-1). The WMU bordered both Idaho to the north and Wyoming to the east, and comprised of Cache County, the northern half of Rich County, and small portions of Box Elder and Weber Counties. WMU 2 consisted of roughly 1,301 km² of mule deer winter range, of which 41% was privately owned, 29% was owned by the Bureau of Land Management, 16% was owned by the U.S. Forest Service, and 14% was other public lands (Fig. 2-1), and 2,005 km² of mule deer summer range, of which 30% was privately owned, 55% was owned by the U.S. Forest Service, and 15% was other public lands (Utah Division of Wildlife Resources 2006; Fig. 2-2). Mule deer range in WMU 2 included 3 major, semi-isolated areas: the Wellsville and Clarkston Mountains lying along the county line between Box Elder and Cache Counties, Cache Valley and the Wasatch Range to the east, and the private and public range lands of northern Rich County (Summers et al. 2006).

The Wellsville and Clarkston Mountains range in elevation from a lower limit of 1,340 m to an upper limit of over 2,835 m. The Wellsville Mountains are primarily Wasatch-Cache National Forest Wilderness land, and the Clarkston Mountains are primarily part of the Caribou National Forest. Vegetation types on the Wellsville Mountains were mountain big sagebrush (*Artemisia tridentata vaseyana*) community with some Utah juniper (*Juniperus osteosperma*; Summers et al. 2006). Other browse
shrubs included: rubber rabbitbrush (*Chrysothamnus nauseosus albicaulis*), broom
snakeweeds (*Gutierrezia sarothrae*), and smooth sumac (*Rhus trilobata*; Summers et al.
2006).

The Wasatch Range east of Cache Valley was the largest portion of WMU 2. Mule deer summered at high elevations on the forest, and wintered along south-facing
canyon slopes and above Cache Valley restricted by the upper limits of cities and towns
(Summers et al. 2006). Vegetation types on winter range included grass/mountain big
sagebrush community, while vegetation types on summer range included mountain brush,
mixed conifer and aspen (*Populus tremuloides*) communities (Summers et al. 2006).

Elevation of the Rich County portion of WMU 2 ranges from 1,800 m at Bear
Lake to 2,775 m at Swan Peak. Vegetation types included Wyoming big sagebrush
(*Artemisia tridentata wyomingensis*), mountain mahogany (*Cercocarpus montanus*), and
scattered juniper woodland communities (Summers et al. 2006). Much of the lower
country was privately owned and used for grazing and agriculture (Summers et al. 2006).

Cache and Rich Counties had climates typical to the Intermountain West with dry,
warm summers and cold, snowy winters. Total annual precipitation (based on 30-yr
means) averaged 51.8 cm in Richmond, Cache County, and 33.8 cm in Laketown, Rich
County (Western Regional Climate Center 2010a, b). Minimum and maximum
temperatures (based on 30-yr means) in Richmond, Cache County, averaged from 0.9° C
to 16.2° C, and from -1.8° C to 13.0° C in Laketown, Rich County (Western Regional
Climate Center 2010a, b).
The Utah Division of Wildlife Resources (UDWR) mule deer management objective for WMU 2 was to maintain a target post-hunting season population size of 25,000, with a 3-year average post-hunt sex ratio of 15-20 bucks:100 does on the general hunt portion and 25-35 bucks:100 does on the Crawford Mountain limited entry area (Utah Division of Wildlife Resources 2006). The mule deer post-hunting season population size in 2005 was estimated at 14,000 (Bernales et al. 2009).

METHODS

Optimal Allocation for Determining Sample Sizes

A monitoring program should be sensitive enough to detect changes in population abundance over a given time period, and have adequate statistical power (Gerrodette 1987, Thompson et al. 1998). I determined the maximum coefficient of variations (CVs) of the population size and population growth rate estimates for my monitoring design to be sensitive enough to detect fixed percent declines (changes) in population size. CV is a measurement of relative precision and can be useful for comparing the precision of different types of estimates, e.g., comparing the precision of an estimate of $N$ to that of an estimate of $\lambda$. I used Program TRENDS (Southwest Fisheries Science Center, La Jolla, CA) to estimate the maximum CV allowable to detect fixed percent declines for 5-year and 10-year time frames. The CV was based on the following inputs: type I error = 0.10, type II error = 0.20 (power = 0.80), linear decline, variance proportional to the square root of the estimate, and a one-tailed test because I was only interested in declines as a starting point (Gerrodette 1993). I also calculated the costs associated with the above CVs and detectable percent declines for estimating $N$ and $\lambda$, using the procedures
outlined in Examples 1 and 3 from the optimal allocation methodology of Bowden et al. (2000). This methodology optimally allocates resources to the 4 main surveys needed to monitor a harvested mule deer population, by minimizing the variance of $N$ or $\lambda$, based on a given budget (Bowden et al. 2000). No survival data or field-based population size estimates existed for the WMU 2 mule deer population, so I used parameter and variance estimates from the Piceance deer population in Colorado and the last modeled estimate of population size for WMU 2 as initial data inputs (Bowden et al. 2000). Costs were based on 2006 estimates (Table 2-1). I examined the cost-precision-power tradeoffs that I could expect from a monitoring strategy that included both vital rate monitoring and estimation of $N$ in a single year, as well as those that could be expected from a $\lambda$-monitoring strategy consisting of monitoring only vital rates. This helped me determine what range of precision I could expect, given a specified budget. A $N$-monitoring program with CV = 11-13% would cost between $55,000 and $85,000, with a minimum detectable overall decline in population size of $\geq 28-32\%$ over a 5-year time frame, or $\geq 21-24\%$ over a 10-year time frame (Fig. 2-3a). For a monitoring program that did not include estimation of $N$, a CV = 5.6-6.9% would cost between $18,000 and $28,000, with a minimum detectable overall decline in population growth rate of $\geq 19-22\%$ over a 5-year time frame, or $\geq 14-16\%$ over a 10-year time frame (Fig. 2-3b).

My goal for a mule deer monitoring program was a hybrid between a $N$-monitoring strategy and a $\lambda$-monitoring strategy, specifically, estimation of $N$ every fourth year and annual monitoring of vital rates to track change in $\lambda$. Based on my budget and the cost-precision-power tradeoffs above, I selected a precision target for $\lambda$
of $CV = 6.5\%$, which would provide the ability to detect minimum declines in $\lambda$ of $\geq 18\%$ over a 5-year time frame, or $\geq 13\%$ over a 10-year time frame. I chose a precision target for estimating $N$ of $CV = 17\text{-}20\%$. Estimation of $N$ was costly, and this hybrid strategy allowed for a relatively high $CV$ on $N$ to reduce costs.

Following Example 3 from the optimal sampling strategy of Bowden et al. (2000), I calculated respective sample sizes for surveys of age ratio, overwinter fawn survival, and doe survival based on a precision target of $CV(\hat{N}) = 6.5\%$. Sample sizes were 11 quadrats, 54 doe collars, and 11 fawn collars, respectively. Following Example 1 from Bowden et al. (2000), I calculated sample sizes for estimating $N$ via helicopter quadrat counts, based on a mid-point precision target of $CV(\hat{N}) = 18.5\%$. Sample size was 70 quadrats. I predicted total first year start-up costs for this monitoring strategy to be $77,075, while costs in years 2, 3, and 4 were $19,225 per year (Table 2-2). When prorated over 4 years, total cost per year for this strategy was predicted to be $33,688. I assumed a 15\% annual doe mortality rate, so the prorated cost to monitor $\lambda$ annually included the costs of recollaring approximately 8 does each year, as well as 25 hours per year for fixed-wing telemetry flights at $225 per hour. I did not include the costs of personnel time, vehicle expenses, supplies, etc. Personnel costs can be highly variable and typically are already built into wildlife agency budgets.

**Field Procedures**

I conducted helicopter quadrat counts to obtain an estimate of population size, post-hunting season, for mule deer during the winter of 2006. I randomly selected 70 $2.59$-km$^2$ (1-mi$^2$) quadrats from a sampling frame grid overlaying mule deer winter range
maps for WMU 2, for a total sampling area of 1,126.65 km² (435 mi², Fig. 2-4). I excluded all quadrats that touched municipal areas or water. This was conservative to ensure I did not fly too close to urban areas or water bodies, to minimize disturbance to people and livestock. The sampling frame was a grid of square quadrats which didn’t match up well with curved and angular range boundaries, so quadrats along the edges of winter range varied in the amount of area included that was actually considered winter range. Therefore, I imposed a second sample-selection rule that only quadrats containing >50% mule deer winter range were included in the sampling frame. To avoid double-counting, none of the sampled quadrats were adjacent to one another—a modification of a simple random sample design. I flew quadrats following the protocol of Freddy et al. (2004). During quadrat counts, I recorded deer group size and activity level, as well as environmental sightability factors such as vegetation type, snow cover, light conditions, etc. I conducted a second helicopter count in 2008 to further refine protocols and provide additional data for comparison of different monitoring strategies. The monitoring program included a population size survey once every 4 years, so the survey conducted in 2008 was not considered in the final cost analysis given that this third year count would not be included in the monitoring program as originally designed.

I estimated age and sex ratios with a helicopter survey, post-hunting season, during the winter of 2006, following the methodology of Bowden et al. (2000). Survey replicates were randomly selected 2.59-km² (1-mi²) quadrats from areas with high probability of deer occupancy, e.g., within mule deer winter range (Fig. 2-4). I classified deer by age group (fawn or adult) and sex (male or female). The following 2 winters,
2007 and 2008, UDWR personnel conducted ground-based herd composition surveys within mule deer winter range, after the hunting season had ended, to estimate age and sex ratios.

I captured and radiocollared fawns and does during the winters of 2006, 2007, and 2008, to estimate overwinter fawn survival and annual doe survival for the 3 years of the study. Commercial helicopter capture companies performed the capture and collaring during this study. The capture protocol was approved by the Utah State University Institutional Animal Care and Use Committee (IACUC Protocol #1286) and UDWR.

Deer were captured from a helicopter with a net-gun, physically restrained, fitted with a radiocollar with motion-sensitive mortality sensor (Lotek Engineering, Inc., Newmarket, Ontario, Canada; Telonics, Inc., Mesa, AZ), and released on site. During the first year of the study, I assumed an equal survival probability for male and female fawns, and fawns captured and collared were of both sexes. The next 2 years I collared only female fawns based on research that suggested unequal fawn survival probability between sexes (Unsworth et al. 1999b). Every 1-2 months, I located collared deer from the air by fixed-wing aircraft. Fawn collars were designed to drop off between April–June, at which time fawns were considered to be recruited into the adult population. I retrieved fawn collars as they dropped off, so that I could reuse them the following winter. Does were monitored year-round. I also retrieved collars from deer that died during the year, and placed them on new animals the following winter. I did not determine cause of death. There were no doe hunts in WMU 2, so I did not need to account for hunting mortality.
Data Analysis

I used a known-fate model in Program MARK (White and Burnham 1999) to estimate overwinter (1 Dec–31 May) fawn survival and annual doe survival. Annual Doe survival was estimated for the period from 1 December to 30 November. I fit 4 a priori models for the mule deer data: 1) constant survival, 2) survival varying by age class, 3) survival varying by year, and 4) survival varying as an interactive effect of age class and year. I based model selection on Akaike’s Information Criterion adjusted for small-sample size (AICc; Burnham and Anderson 2002).

I calculated age and sex ratios as fawns per 100 does and bucks per 100 does, respectively, from information collected during herd composition surveys. In 2006, I calculated age and sex ratios and associated variances using the 2.59-km² quadrats as the primary sampling units (Bowden et al. 1984). In 2007 and 2008, UDWR personnel conducted ground-based herd composition surveys on traditional winter range areas of varying sizes across the WMU. Although the areas surveyed were not randomly selected from a sampling frame, I still considered each individual area surveyed as a sample replicate so that variances for age and sex ratios could be calculated. An alternative approach would be to have considered each individual deer as primary sampling unit, but I did not use this approach because it tends to underestimate variance due to lack of independence between the number of fawns and the number of does (Bowden et al. 1984).
**Evaluation of Population Monitoring Strategies**

To evaluate the overall performance of the hybrid monitoring strategy, I calculated annual and overall estimates of $\lambda$ and compared CVs to the program objective of $CV = 6.5\%$. I also compared realized costs to predicted costs. To compare costs for a fixed precision level, I compared 3 monitoring strategies based on predicted sample sizes that would yield a $CV = 10\%$. I used estimates obtained from the 4 field surveys and calculated sample sizes and costs associated with monitoring programs focused on $N$-only, $\lambda$-only, and the hybrid program that monitored both $N$ and $\lambda$. For a $N$-only strategy, I bootstrapped from my 2006 quadrat count data to obtain sample sizes and costs. Specifically, I drew different sample sizes using random sampling with replacement (1,000 replicates each), and then determined the sample size that corresponded to a $CV(N) = 10\%$. Then, I calculated costs based on this sample size, assuming that costs increased linearly with increasing sample size (Fig. 2-5). I used the same procedures described previously to calculate sample sizes and costs for the $\lambda$-only and hybrid strategies, but this time I used field data from WMU 2 as inputs and constrained $CV(\lambda) = 10\%$. I prorated costs for conducting helicopter quadrat counts for the hybrid strategy over 4 years.

**RESULTS**

**Field Survey Estimates**

In 2006, I counted a total of 1,605 mule deer in 170 groups. Quadrats took an average of 11 minutes to survey completely. During the flight, I excluded 4 of the 70 selected quadrats because they did not contain an adequate portion of mule deer winter...
range. For the 2008 helicopter survey, these quadrats were removed and replaced with 4 new randomly chosen quadrats. In 2008, I counted a total of 2,684 mule deer in 265 groups. Quadrats took an average of 10 minutes to survey completely. The estimated population size was 10,481 (SE = 1,821) in 2006 and 16,526 (SE = 3,225) in 2008. The CV associated with both years’ estimates fell within the predicted CV = 17-20% for N-only surveys (Table 2-3).

During the winter of 2006, I classified a total of 420 deer from a helicopter (n = 7 quadrats). In 2007, UDWR biologists classified a total of 630 deer (n = 8 quadrats), and in 2008 they classified 681 deer (n = 10 quadrats). Age ratios remained relatively constant during the 3 years of the study (Fig. 2-6). In 2006 and 2007, sex ratio estimates fell within the UDWR target range of 15-20 bucks per 100 does, but dropped below this target in 2008 (Fig. 2-6).

I radiocollared a total of 11 fawns and 54 does during the winter of 2006. I recollared 11 fawns and 4 does in 2007, and 11 fawns and 15 does in 2008. In 2006, 1 doe died within 2 weeks of being radiocollared and was censored from the study as a capture mortality. In 2007, 1 doe collared the previous year disappeared and was censored from the study that year. In 2008, 1 newly-collared doe and 1 doe collared in 2007 disappeared and were censored for that year. In addition, 2 of the 2007 doe mortalities were discovered just before the 2008 capture took place and no collars were available to replace them, so the final doe sample size for 2008 was 50.

The AICc-selected best model indicated year-specific and age class-specific survival (Table 2-4). Estimates of overwinter fawn survival varied greatly during the 3
years of this study, from 100% survival in 2006 to only 27% survival the following year (Fig. 2-7). Annual doe survival estimates followed a similar trend, although to a less extreme extent (Fig. 2-7).

Population growth rate estimated from vital rates (doe and fawn survival, age ratio) was 1.30 (SE = 0.06) in 2006, 0.81 (SE = 0.08) in 2007, and 1.12 (SE = 0.07) in 2008 (Table 2-3). Over the entire time frame of this study, $\hat{\lambda}$ averaged 1.08 (SE = 0.07), and precision met the desired objective CV($\hat{\lambda}$) = 6.5%.

**Evaluation of Population Monitoring Strategies**

Actual cost of the mule deer population monitoring program during the first year was $67,489, which was about $10,000 lower than the predicted cost (Table 2-5). Overall, the realized cost of this monitoring program was $29,298 per year when costs were amortized over 4 years. Helicopter herd composition surveys cost more than double what was originally predicted because I did not account for flight time between quadrats and to and from fueling areas in my original estimates (Tables 2-2 and 2-5). Personnel from UDWR conducted ground-based herd composition surveys instead of helicopter surveys in 2007 and 2008, so costs for herd composition surveys were only included for 2006. When summed over 4 years, actual cost of collaring of does and fawns was less than originally predicted (Tables 2-2 and 2-5). Capture costs in 2006 were $200 less than initially predicted, and $125 less in 2008. Actual life of the fawn radiocollars was 2 years instead of the anticipated 5 years, so I refurbished the fawn collars in the third year for an additional expense of $1,722. Also, a few radiocollars that were irretrievable or went missing were replaced for an added expense.
Winter conditions in 2006 were less severe compared to long-term averages (Western Regional Climate Center 2010a, b; Fig. 2-8a, b), as reflected by the high survival rates of fawns and does during this time. 2007 winter conditions were more severe (Western Regional Climate Center 2010a, b; Fig. 2-8a, b), with decreased fawn and doe survival rates in 2007, although age ratios remained relatively unchanged. Reallocating resources using data from 2006 only, the sample size required to monitor vital rates in a mild winter could be decreased to \( n = 50 \). This sample size would still achieve a precision of \( \text{CV}(\hat{\lambda}) = 6.5\% \), for an estimated cost of $16,950 per year (Table 2-6). In a severe winter with low survival rates, sample size would need to be increased to maintain precision \( (n = 105) \), for an estimated cost of $30,550 (Table 2-6).

Comparing the effort and costs required for different monitoring programs with a goal of achieving a minimum \( \text{CV} = 10\% \), monitoring \( N \)-only would require a sample size of 200 quadrats and would cost $46,583 (Table 2-7). In contrast, focusing solely on \( \lambda \) with herd composition and doe and fawn survival surveys, the sample sizes necessary for achieving \( \text{CV} = 10\% \) were 2 quadrats, 19 does collared, and 5 fawns collared, respectively, for an annual cost of $11,225 (Table 2-7). The hybrid method, optimized for obtaining annual estimates of \( \lambda \) and estimates of \( N \) every 4 years required the same sample sizes for herd composition and doe and fawn survival as the \( \lambda \)-only strategy,

\[ \hat{S} = 0.909 \] (1 mortality out of 11, SE = 0.087) for these calculations.
while the sample size for estimating $N$ of 92 quadrats. The total monitoring cost of this hybrid strategy was $15,825 (Table 2-7).

**DISCUSSION**

The hybrid monitoring program cost only $4,600 more per year (prorated over 4 yr) than a $\lambda$-only monitoring program, and provided estimates of abundance, population growth rate, overwinter fawn survival, annual doe survival, age ratio, and sex ratio. Costs of collaring and monitoring survival comprised the bulk of the costs in the first year, while the costs of the helicopter quadrat counts were relatively inexpensive by comparison. However, the allocation of resources for estimating $N$ was not designed so that the estimate could stand alone, but to obtain an estimate for validating population models and to translate vital rates into interpretable numbers of deer. The CV associated with $\hat{N}$ was 17.4%. With a CV of this size, the minimum decline in mule deer population size that I could detect over a 5-year time frame would be 41%, or 31% over a 10-year time frame (Program TRENDS, Gerrodette 1993). This is unacceptable from a management standpoint, if the goal is to monitor changes in population size so that responsive management actions can be implemented. In contrast, the precision of my overall estimate of $\hat{\lambda}$ was CV = 6.5%. With a CV of this size, the minimum decline in mule deer population size that I could detect over a 5-year time frame would be 18%, or 13% over a 10-year time frame (Program TRENDS, Gerrodette 1993). A $N$-only monitoring strategy with sufficient precision to approach that of a hybrid program would require a sample size of 420 quadrats (97% of my entire sample frame) at a cost of over $92,000 (Fig. 2-5).
A common problem with helicopter quadrat counts is that they routinely underestimate $N$ because of missed animals, termed visibility bias, which results in inaccurate estimates (Samuel et al. 1987). In a monitoring program focused on field-based estimates of $N$ alone, this bias could lead to erroneous conclusions about the population trajectory. Lacking visibility bias corrections to field-based population size estimates, one made the illogical assumption of constant detection probability across habitat type, environmental conditions, observer, species behavior, etc. (Anderson 2001). Absent a visibility bias correction for mule deer, Bartmann et al. (1986) noted that a 50% upward adjustment to the quadrat population estimate would provide a better estimate of true population size. A 50% upward adjustment would bring my 2006 field-based estimate of 10,481 closer to the UDWR-modeled estimate of 14,500 (Bernales et al. 2009). However, in 2008 the field-based estimate of population size, assuming no visibility bias, was 16,526. The UDWR-modeled estimate was lower than this, estimated at 13,700, and fell within the 95% confidence interval of the field-based estimate (Bernales et al. 2009). Applying the 50% upward adjustment for visibility bias as recommended by Bartmann et al. (1986) would put the field-based estimate well above the modeled estimate.

I attempted to correct estimates of $\hat{N}$ for visibility bias by incorporating a sightability model into aerial surveys, as recommended by Steinhorst and Samuel (1989). During helicopter quadrat counts, I collected information on sightability factors such as snow cover, vegetation, deer activity, group size, etc., with the intent to apply the mule deer sightability model developed by the Idaho Department of Fish and Game (Unsworth
Conflicts between the recommended study design for measuring sightability and this study design made incorporation of the sightability model impractical. Since mule deer tended to cluster in groups on winter range and my quadrats were small, the counts in many quadrats were 0. The sightability model was unable to correct counts of 0, and I could not determine whether quadrats with counts of 0 were “true” 0s (i.e., no deer were present on the quadrat), or 0 because deer were present but not seen. The appropriate quadrat size to minimize this problem would have been one that required about 1 hour helicopter search-time (Unsworth et al. 1999a), approximately 4-5 times larger than those used in my aerial surveys.

An additional problem with the high frequency of quadrats with counts of 0 was that it resulted in estimates of $\hat{N}$ with high variance and correspondingly broad confidence intervals that rendered virtually meaningless estimates. For this study, I used a simple random sampling design for my helicopter quadrat counts. To determine if the use of 2 simple strata, such as high and low deer density, would have helped to reduce the variance, I created a post-hoc stratification of my sampling frame and recalculated $\hat{N}$ and its associated variance. Many of the quadrats with 0 deer fell within the high density stratum, which negated any improvement in the precision of $\hat{N}$ from stratification.

Another possible approach to reduce variance of $\hat{N}$ is adaptive cluster sampling. One issue with this method is the difficulty in determining sample size. Also, for moderately abundant species, such as mule deer, there is the possibility of counting a substantial number of quadrats (i.e., due to many counts >0 in adjacent quadrats), which could be costly and inefficient.
Delineation of an appropriate sampling frame is another spatial sampling limitation of field-based estimation of $N$. My sampling frame was not entirely representative of the total mule deer winter range in WMU 2 because of the restrictions I imposed. These restrictions excluded some important high density areas of winter range, particularly in the foothills above Cache Valley where groups of mule deer reside along the edge of new housing developments. The consequence of excluding areas of winter range from the sampling frame is that it could lead to a low-biased population estimate.

Furthermore, by excluding quadrats from the sampling frame that contained <50% winter range, and including quadrats that contained portions of non-winter range, approximately 39% (703 km²) of mule deer winter range was excluded from the final sampling frame, and approximately 10% (106 km²) of the final sampling frame included areas not considered to be winter range. This could introduce both positive and negative bias into the estimate of $N$.

The winter range map initially used to design the sampling frame was not field validated, so I did not know how accurately this map represented “true” mule deer winter range. Further survey work will assist to field-validate and improve maps of winter range, as was begun during the 2006 survey when 4 quadrats were removed from the sampling frame because they were determined unlikely winter range for mule deer. In the future, it may be necessary to delineate a new sampling frame that is more representative of mule deer winter range, by incorporating topographic features that serve as natural boundaries, such as ridges and drainages, as the boundaries for sampling units instead of using square quadrats. Also, drawing sampling boundaries by hand would
allow one to align the sampling frame with the upper limits of municipal areas and include more critical winter range missed by the quadrat sampling grid.

Over the span of this study, WMU 2 experienced extremes of winter severity, providing insight into upper and lower limits for fawn and doe survival, and in turn, their effect on $\hat{\lambda}$. Mean overwinter fawn survival and mean annual doe survival from studies conducted in Colorado, Idaho, and Montana were 0.444 (SE = 0.033) and 0.853 (SE = 0.011), respectively (Unsworth et al. 1999b). In 2006, survival rates of fawns and does in WMU 2 were both higher than these averages, while in 2007, survival rates were lower.

The winter of 2006 was milder than a typical WMU 2 winter, with snowfall primarily limited to upper elevations, and patchy, light snow cover on much of the mule deer winter range (Fig. 2-8a, b). The winter of 2007 was more severe, especially in Cache County, with heavy snowstorms and prolonged periods of freezing temperatures that led to deep snowpack for several months (Fig. 2-8a, b). Winter range is the primary limiting factor for mule deer populations in WMU 2 (Utah Division of Wildlife Resources 2006), and deer were forced to concentrate even further onto already limited critical winter ranges. As a result, emergency winter feeding was initiated by UDWR in several areas of Cache County from January to March. Winter conditions in 2008 were more typical, with cold temperatures, average snowfall, and intermittent thaws. The comparison between a mild winter and a severe winter indicated it would take more monitoring effort and resources during years of low survival and for a decreasing population (e.g., during droughts or severe winters) to achieve desired precision, than would be needed for monitoring an increasing population during mild winters (when $\hat{\lambda} > 1.0$). However,
being unable to predict the severity of an approaching winter, it may be necessary to increase sample sizes and effort to monitoring vital rates above that calculated by optimal allocation, in case survival or age ratios are lower than expected in any given year.

$CV(\hat{\lambda})$ from 2006 and 2008 were lower than the objective $CV(\hat{\lambda})$ of 6.5%, but higher in 2007. Age ratios remained relatively constant over the duration of this study, so the observed loss of precision in 2007 was due to the combined effect of the decreased value of $\hat{\lambda}$ resulting from decreased survival rates and the increased variance of the survival estimates. In order to maintain $CV$ at the desired level, sample sizes should be increased in the case of 1) a declining population ($\hat{\lambda} < 1.0$; Morris and Doak 2002), or 2) a year with survival estimates approaching 0.5, which maximizes the variance of the estimate (White and Garrott 1990). Managers may also wish to increase the sample size above the optimally allocated level for estimating fawn survival for several reasons. First, small sample variation can lead to unrealistic or unworkable estimates, as I experienced with the fawn overwinter survival estimate of 1.0 in 2006 ($n = 11$). Second, it may be necessary to provide short-term or single year results to stakeholders and invested public, because survival rate estimates with large confidence intervals due to low sample size could bring into question the credibility or value of the monitoring program. Also, as survival estimates approach 0 or 1, the corresponding variance shrinks, leading to the optimal allocation of even fewer samples for estimating fawn survival and further exacerbating the small sample size problems mentioned above. The optimal allocation of resources for estimating fawn survival rate was designed to minimize the overall variance of $N$ or $\hat{\lambda}$, and was not necessarily meant to provide
precise estimates of fawn survival each year. Fawn survival is highly variable year to year, while doe survival varies only slightly, but population models are much more sensitive to doe survival than fawn survival, requiring more precise estimates of doe survival than fawn survival each year (White and Bartmann 1998). Still, to satisfy stakeholders and maintain credibility, more fawns could be monitored annually.

UDWR is mandated by legislative code to work towards population size objectives and to provide population size estimates for mule deer, but there exists no requirement for field-based estimates of population size specifically. A monitoring program that focused on \( \lambda \) could provide sufficient data to fulfill this mandate when coupled with population modeling, while providing additional information about critical processes of mule deer population dynamics. A strictly model-based approach is unacceptable from 2 standpoints: first, there is no way to evaluate how well the model works without some validation via field-based estimates. Second, stakeholders and members of the public may not understand, and therefore, not trust complex population modeling techniques. As a result, they may insist for field-based estimates of \( N \) (Freddy et al. 2004). Wildlife agencies are increasingly challenged in litigation by special interest groups on the scientific validity of their data and methods used to make management decisions (Murphy and Noon 1991, Freddy et al. 2004). Adopting this adaptive hybrid strategy, which was optimized for precise estimates of \( \lambda \) but still incorporated field-based \( N \) estimates once every 4 years, would be less costly than conducting field-based population counts every year and would provide enough information to validate population models and satisfy stakeholders.
MANAGEMENT IMPLICATIONS

Reliable information about mule deer populations is necessary for proper management, but it doesn’t have to be prohibitively expensive. This study demonstrated that, when resources are optimally allocated, it is possible to collect precise, repeatable, and reliable data on multiple aspects of population dynamics, at a lower cost than what would be typically spent if annual field-based population estimates are used alone. Shifting resources to the collection of survival data allows for more precise monitoring of population growth rate, while providing useful information for population models that project population size. Field-based population size estimates can be conducted infrequently to validate population models, but do not need to be the main focus of a population monitoring program.

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Table 2-1. Cost, precision (CV), and minimum detectable decline inputs used for optimally allocating resources towards strategies for monitoring a mule deer population.

<table>
<thead>
<tr>
<th>Inputs</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Cost per population quadrat$^a$</td>
<td>$200</td>
</tr>
<tr>
<td>Cost per age and sex ratio quadrat$^a$</td>
<td>$200</td>
</tr>
<tr>
<td>Cost per adult female capture</td>
<td>$600</td>
</tr>
<tr>
<td>Cost per adult female radiocollar</td>
<td>$250</td>
</tr>
<tr>
<td>Life of adult female radiocollar (yr)</td>
<td>4</td>
</tr>
<tr>
<td>Cost per fawn capture</td>
<td>$600</td>
</tr>
<tr>
<td>Cost per fawn radiocollar</td>
<td>$250</td>
</tr>
<tr>
<td>Years of use of fawn radiocollar</td>
<td>5</td>
</tr>
<tr>
<td>Cost/hour flying time for survival</td>
<td>$225</td>
</tr>
<tr>
<td>CV( (N) )</td>
<td>17-20%</td>
</tr>
<tr>
<td>CV( (\lambda) )</td>
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</tr>
<tr>
<td>5-yr min detectable decline in (N)</td>
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</tr>
<tr>
<td>10-yr min detectable decline in (N)</td>
<td>34%</td>
</tr>
<tr>
<td>5-yr min detectable decline in (\lambda)</td>
<td>18%</td>
</tr>
<tr>
<td>10-yr min detectable decline in (\lambda)</td>
<td>13%</td>
</tr>
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</table>

$^a$ Based on $800/hour for helicopter time and counting 4 quadrats per hour.
Table 2-2. Predicted sample sizes and costs for estimating mule deer population size once every 4 years and monitoring vital rates every year.

<table>
<thead>
<tr>
<th>Activity Description</th>
<th>Yr 1</th>
<th>Yr 2, 3, and 4(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n)</td>
<td>Costs</td>
</tr>
<tr>
<td>Quadrats for population size surveys (helicopter)</td>
<td>70</td>
<td>$14,000</td>
</tr>
<tr>
<td>Quadrats for age ratio surveys (helicopter)</td>
<td>11</td>
<td>$2,200</td>
</tr>
<tr>
<td>Does radiocollared</td>
<td>54</td>
<td>$45,900</td>
</tr>
<tr>
<td>Fawns radiocollared</td>
<td>11</td>
<td>$9,350</td>
</tr>
<tr>
<td>Telemetry flights (fixed-wing aircraft)</td>
<td>25 hrs</td>
<td>$5,625</td>
</tr>
<tr>
<td>Total cost</td>
<td></td>
<td>$77,075</td>
</tr>
<tr>
<td>Total cost prorated over 4 yr</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Per year.

\(^b\) Assumed mean annual doe mortality of 15\% (~8 does).
Table 2-3. Estimates of mule deer population size (\( \hat{N} \)) and population growth rate (\( \hat{\lambda} \)) in WMU 2, Utah, USA, from 2006 to 2008.

<table>
<thead>
<tr>
<th>Population parameter</th>
<th>Yr(^a)</th>
<th>n</th>
<th>Estimate</th>
<th>SE</th>
<th>CV</th>
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</thead>
<tbody>
<tr>
<td>Population size (( \hat{N} ))</td>
<td>2006</td>
<td>66</td>
<td>10,481</td>
<td>1,821</td>
<td>17.4%</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>70</td>
<td>16,526</td>
<td>3,225</td>
<td>19.5%</td>
</tr>
<tr>
<td>Population growth rate (( \hat{\lambda} ))</td>
<td>2006</td>
<td>71</td>
<td>1.30</td>
<td>0.06</td>
<td>4.6%</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>72</td>
<td>0.81</td>
<td>0.08</td>
<td>10.3%</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>71</td>
<td>1.12</td>
<td>0.07</td>
<td>6.0%</td>
</tr>
</tbody>
</table>

\(^a\) Year corresponds to bioyear (1 Jun–31 May) and not calendar year (1 Jan–31 Dec).
Table 2-4. Known-fate model selection results, number of parameters ($K$), small-sample-adjusted Akaike’s Information Criteria (AIC$_c$), differences in AIC$_c$ values ($\Delta$AIC$_c$), model weights, and model deviance for mule deer survival in WMU 2, Utah, USA, from 2006 to 2008. Age classes were fawns and adults.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>AIC$_c$</th>
<th>$\Delta$AIC$_c$</th>
<th>AIC$_c$ weight</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>{S(yr*age)}</td>
<td>6</td>
<td>156.365</td>
<td>0.000</td>
<td>0.992</td>
<td>0.000</td>
</tr>
<tr>
<td>{S(yr)}</td>
<td>3</td>
<td>166.076</td>
<td>9.711</td>
<td>0.008</td>
<td>16.043</td>
</tr>
<tr>
<td>{S(age)}</td>
<td>2</td>
<td>178.806</td>
<td>22.441</td>
<td>0.000</td>
<td>30.838</td>
</tr>
<tr>
<td>{S(.)}</td>
<td>1</td>
<td>186.074</td>
<td>29.710</td>
<td>0.000</td>
<td>40.150</td>
</tr>
</tbody>
</table>
Table 2-5. Realized sample sizes and costs for estimating mule deer population size once every 4 years and monitoring vital rates every year in WMU 2, Utah, USA, from 2006 to 2009.

<table>
<thead>
<tr>
<th></th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2009&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Costs</td>
<td>n</td>
<td>Costs</td>
<td>n</td>
</tr>
<tr>
<td>Quadrats for population size surveys (helicopter)</td>
<td>70</td>
<td>$15,372</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Quadrats for age ratio surveys (helicopter)</td>
<td>7</td>
<td>$4,788</td>
<td>8</td>
<td>$0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td>Does radiocollared</td>
<td>54</td>
<td>$35,206</td>
<td>4</td>
<td>$2,400</td>
<td>15</td>
</tr>
<tr>
<td>Fawns radiocollared</td>
<td>11</td>
<td>$7,623</td>
<td>11</td>
<td>$7,446&lt;sup&gt;d&lt;/sup&gt;</td>
<td>11</td>
</tr>
<tr>
<td>Telemetry flights (fixed-wing aircraft)</td>
<td>20 hr</td>
<td>$4,500</td>
<td>20 hr</td>
<td>$4,500</td>
<td>20 hr</td>
</tr>
<tr>
<td>Total cost</td>
<td></td>
<td>$67,489</td>
<td></td>
<td>$14,326</td>
<td></td>
</tr>
<tr>
<td>Total cost prorated over 4 yr</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Estimated based on the average of 2007 and 2008.

<sup>b</sup> Ground-based surveys were conducted by UDWR biologists. Personnel costs were not included in cost estimates.

<sup>c</sup> Includes 1 new replacement collar.

<sup>d</sup> Includes 3 new replacement collars and refurbishment of surgical tubing on 8 collars.

<sup>e</sup> Includes refurbishment of surgical tubing on 11 collars and battery replacement on 8 collars.
Table 2-6. Optimal allocation of sampling effort for monitoring vital rates of a mule deer population in WMU 2, Utah, USA, during mild winters with high fawn and doe survival rates, and during severe winters with low fawn and doe survival rates, 2006 and 2007, respectively. Optimization was performed with the assumption $\lambda = 1.0$, SD = 0.065 (CV = 0.065).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Cost</td>
</tr>
<tr>
<td>Quadrats for age ratio surveys (helicopter)</td>
<td>12</td>
<td>$2,400</td>
</tr>
<tr>
<td>Does radiocollared</td>
<td>30</td>
<td>$5,250</td>
</tr>
<tr>
<td>Fawns radiocollared</td>
<td>8</td>
<td>$4,800</td>
</tr>
<tr>
<td>Telemetry flight (fixed-wing aircraft)</td>
<td>20 hrs</td>
<td>$4,500</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>$16,950</td>
</tr>
</tbody>
</table>
Table 2-7. Costs per year for different mule deer population monitoring programs designed to achieve estimates with a CV = 10%.

<table>
<thead>
<tr>
<th>Survey</th>
<th>Quadrat counts only (N)</th>
<th>Vital rates only (λ)</th>
<th>Hybrid (optimally allocated λ + N)(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadrats for population size surveys (helicopter)</td>
<td>200 $46,583</td>
<td>NA</td>
<td>92 $4,600(^b)</td>
</tr>
<tr>
<td>Quadrats for age ratio surveys (helicopter)</td>
<td>NA</td>
<td>2 $400</td>
<td>2 $400</td>
</tr>
<tr>
<td>Does radiocollared(^b)</td>
<td>NA</td>
<td>19 $3,325</td>
<td>19 $3,325</td>
</tr>
<tr>
<td>Fawns radiocollared(^b)</td>
<td>NA</td>
<td>5 $3,000</td>
<td>5 $3,000</td>
</tr>
<tr>
<td>Telemetry flight (fixed wing aircraft)</td>
<td>NA</td>
<td>20 hrs</td>
<td>20 hrs $4,500</td>
</tr>
<tr>
<td>Total cost per yr</td>
<td>$46,583</td>
<td>$11,225</td>
<td>$15,825</td>
</tr>
</tbody>
</table>

\(a\) Optimized for CV(N) = 18.5% and a CV(λ) = 10%.

\(b\) Prorated over 4 years.
Figure 2-1. Mule deer winter range in WMU 2, Utah, USA.
Figure 2-2. Mule deer summer range in WMU 2, Utah, USA.
Figure 2-3. Costs and precision of (a) population size estimates \( CV(N) \) and (b) population growth rate estimates \( CV(\lambda) \), and associated minimum detectable declines over 5-year and 10-year time frames, for a mule deer monitoring program that monitors both population size and vital rates, and vital rates-only, in a single year, respectively.
Figure 2-4. Sampling frame and sample units for helicopter quadrat counts and herd composition surveys for mule deer in WMU 2, Utah, USA.
Figure 2-5. Estimated costs and precision [CV(N)] associated with varying sample sizes for estimating mule deer population size with helicopter quadrat counts.
Figure 2-6. Estimates of age ratio (fawns per 100 does) and sex ratio (bucks per 100 does) for mule deer in WMU 2, Utah, USA, from 2006 to 2008. Error bars represent 95% confidence intervals.
Figure 2-7. Overwinter fawn and annual doe survival rate estimates for mule deer in WMU 2, Utah, USA, from 2006 to 2008. Error bars represent 95% confidence intervals.
Figure 2-8. (a) Average monthly temperatures (°C) and (b) total monthly snowfall (cm) during the winters of 2006 and 2007 compared to long-term averages, WMU 2, Utah, USA. Totals shown are averages of Richmond and Laketown weather station data in Cache and Rich Counties, respectively. Error bars represent SD.
CHAPTER 3
MODELING THE POPULATION DYNAMICS OF
MULE DEER FROM BOTH DATA-RICH AND
DATA-POOR MANAGEMENT UNITS

ABSTRACT

The use of mathematical models to derive mule deer (*Odocoileus hemionus*) population size and project population trends has become standard practice for many wildlife management agencies throughout the Intermountain West. I evaluated the efficacy of using integrated population modeling with multiple data sources (MDS) for mule deer populations in Utah, and compared these modeling techniques to POP-II, a herd composition-based population modeling program currently used by many state wildlife agencies. I developed a proxy method for determining correlations in survival rates between core and satellite units when field data were not available. Then, I demonstrated how survival data from a core unit, Wildlife Management Unit (WMU) 2, could be combined with data from a satellite unit, WMU 3, and used to efficiently model the mule deer population dynamics of the latter unit. I constructed MDS and POP-II population models for 2003–2008 that incorporated field-based estimates of WMU 2 doe and fawn survival rates from 2006–2008. The MDS models for both WMUs performed well for the years for which I had field data (2006–2008), but these models were limited in their usefulness when data were missing (2003–2005). POP-II modeled estimates approximated the observed data with reasonable fit, although not as well as the MDS-modeled estimates. MDS-modeled estimates for population size and doe and fawn
survival in WMU 2 fell within the 95% CI of my observed field estimates in each year (2006–2008). The population size estimates predicted by the POP-II models were slightly higher than those predicted by the MDS models for 2003 to 2007, but converged to similar estimates for 2007 and 2008. Fawn survival rates from WMU 2 and WMU 3 were positively correlated, as were doe survival rates. This proxy method for determining survival correlations could be used to establish core-satellite unit pairs for implementing statewide monitoring initially, until enough survival data could be collected to estimate survival correlations directly.

**INTRODUCTION**

Monitoring population trend and estimating vital demographic parameters are essential for effective management of a wildlife population (Erickson et al. 2003). Abundance is the most commonly monitored attribute in a population monitoring program, with the goal to be able to detect important changes in an animal population over time (Thompson et al. 1998, Williams et al. 2001). Wildlife managers may also monitor fundamental demographic parameters such as survival and recruitment because they provide insight into the mechanisms driving population dynamics and because of their relevance to changes in abundance (Lancia et al. 2005).

However, because of financial constraints, most wildlife management agencies do not collect field-based estimates of survival or abundance for mule deer (*Odocoileus hemionus*) populations. Herd composition is often the only mule deer data collected directly in the field by most state wildlife agencies in the West (Rabe et al. 2002), and the use of mathematical models to derive projections of mule deer population size has
become standard practice for many agencies (Rabe et al. 2002, White and Lubow 2002, Carpenter et al. 2003). These models utilize hunter-harvest and herd composition data by reconstructing population scenarios to make vital rate values fit the observed age and sex ratios (Rabe et al. 2002, Skalski et al. 2005). The computer program POP-II (Fossil Creek Software, Fort Collins, CO) was developed as a tool to assist wildlife managers to simulate the dynamics of wildlife populations, and is the most common model used by state wildlife agencies for estimating mule deer abundance (Bartholow 2003, Carpenter et al. 2003, Mason et al. 2006). Model predictions are fit to observed data without the use of formal, statistical methods, and the use of imprecise data in these models and failure to meet critical assumptions have been recognized as limitations (McCullough 1994, White and Lubow 2002, Mason et al. 2006, Millspaugh et al. 2009).

In contrast to a POP-II or herd composition-based approach, the benefit of collecting several types of data is the ability to increase the precision of abundance estimates and demographic parameters by combining multiple data types in joint likelihoods. The method of using multiple data sources is called integrated population modeling, and has been developed using maximum likelihood, least squares, and Bayesian approaches (Besbeas et al. 2002, White and Lubow 2002, Gauthier et al. 2007, Schaub et al. 2007). However, White and Lubow (2002) suggested that some of these integrated modeling techniques were overly complex for wildlife management agencies to adopt and presented a more easily applied likelihood-based approach for harvest management. They presented a statistically rigorous but relatively simple model-fitting procedure for estimating parameters of population models from multiple types of
observed data, specifically annual doe survival, overwinter fawn survival, age and sex ratios, and population counts (White and Lubow 2002). These procedures used weighted least-squares and model selection based on Akaike’s Information Criterion (AIC; Burnham and Anderson 2002). This approach, which I refer to as a multiple data sources (MDS) model, incorporates field-derived annual survival estimates directly into the population model, in contrast to the POP-II modeling procedure that estimates annual survival indirectly by subjectively adjusting model parameters until predictions visually appear to approximate field data (White and Lubow 2002).

White and Bartmann (1998) determined that mule deer population models were more sensitive to values of survival than recruitment, and, accordingly, recommended shifting resources from herd composition surveys to direct monitoring of doe and fawn survival. Since costs and effort required to monitor survival were relatively high compared to herd composition surveys, they recommended monitoring survival intensively in “core” monitoring areas and occasionally in other “satellite” areas.

The Utah Division of Wildlife Resources (UDWR) currently derives abundance estimates for mule deer in Utah using POP-II population models parameterized with field-collected herd composition data and harvest data collected from UDWR hunter-harvest surveys (Bernales et al. 2009). Historically, UDWR has not conducted field-based survival surveys or counts for mule deer and relied on its population models to derive abundance estimates each year. Recognizing the need for accurate survival data to incorporate into its population models, UDWR recently implemented annual monitoring of doe and fawn survival in core Wildlife Management Units (WMUs) within the major
ecoregions in Utah (see Appendix), while still continuing annual hunter-harvest and herd composition surveys in both core and satellite mule deer management units. With these multiple types of data, population abundance could potentially be modeled for every WMU using the MDS modeling approach of White and Lubow (2002).

I evaluated the efficacy of using the MDS population modeling approach for simulating the population dynamics of the WMU 2 mule deer herd in Utah, and compared these modeling techniques to the more data-limited POP-II model. I developed a proxy method for determining correlations in fawn and doe survival rates between core and satellite units, WMU 2 and WMU 3, respectively, using model-simulated survival rates from POP-II models. I then examined whether field-based survival data from WMU 2 could be combined with other demographic data from WMU 3, a nearby unit that is similar in climate and habitat, to efficiently model the population dynamics of the WMU 3 mule deer herd, and compared MDS model predictions to those of a POP-II model. The overarching goal of this study was to, first, evaluate the MDS approach and compare it to POP-II, and second, develop a method for examining correlations in survival between management units for which field estimates of survival are unavailable.

**STUDY AREA**

I conducted this study in northern Utah in WMU 2 and WMU 3 (Fig. 3-1). WMU 2 bordered both Idaho to the north and Wyoming to the east, and was made up of Cache County, the northern half of Rich County, and small portions of Box Elder and Weber Counties. WMU 2 consisted of roughly 1,301 km² of mule deer winter range, of which 41% was privately owned, 29% was owned by the Bureau of Land Management, 16%
was owned by the U.S. Forest Service, and 14% was other public lands (Utah Division of Wildlife Resources 2006a; Fig. 3-1). Mule deer range in WMU 2 included three major, semi-isolated areas: the Wellsville and Clarkston Mountains lying along the county line between Box Elder and Cache Counties, Cache Valley and the Wasatch Range to the east, and the private and public range lands of northern Rich County (Summers et al. 2006).

Cache and Rich Counties had climates typical to the Intermountain West with dry, warm summers and cold, snowy winters. Total annual precipitation (based on 30-yr means) averaged 51.8 cm in Richmond, Cache County, and 33.8 cm in Laketown, Rich County (Western Regional Climate Center 2010a, b). Minimum and maximum temperatures (based on 30-yr means) in Richmond, Cache County, averaged from 0.9° C to 16.2° C, and from -1.8° C to 13.0° C in Laketown, Rich County (Western Regional Climate Center 2010a, b).

Vegetation types on mule deer winter range in Cache County were mountain big sagebrush (*Artemisia tridentata vaseyana*) community with some Utah juniper (*Juniperus osteosperma*), while vegetation types in Rich County included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain mahogany (*Cercocarpus montanus*) and scattered juniper woodland communities (Summers et al. 2006). Summer range vegetation types in both Cache and Rich Counties included mountain brush, mixed conifer, and aspen (*Populus tremuloides*) communities (Summers et al. 2006).

WMU 3 was located to the south of WMU 2 and was made up of the southern portion of Cache County, Weber County, and small portions of Morgan and Box Elder
Counties. Mule deer range in this area was similar to that of the Wellsville Mountains and Wasatch Range portions of WMU 2. Mule deer winter range consisted of 566 km², which was 10% federally owned, 10% state owned, and 80% privately owned (Utah Division of Wildlife Resources 2006b; Fig. 3-1). Total annual precipitation (based on 30-yr mean) averaged 82.2 cm at Pine View Dam, and minimum and maximum temperatures (based on 30-yr means) averaged from -1.6° C to 14.0° C (Western Regional Climate Center 2010c). Vegetation types typically found on mule deer winter range in WMU 3 were mountain big sagebrush-grass community with other key browse species such as antelope bitterbrush (*Purshia tridentata*) and low sagebrush (*Artemisia arbuscula*; Summers et al. 2006).

**METHODS**

**Field Estimates**

Previous work provided estimates of overwinter fawn and annual doe (>1.5 yr) survival, herd composition, and abundance in WMU 2, 2006–2008 (Table 3-1; see Chapter 2 for details). Overwinter fawn survival was estimated for the period from 1 December to 1 May (when radiocollars dropped off) and annual doe survival was estimated for the period from 1 December to 30 November. Age and sex ratio surveys for WMU 2 were conducted via helicopter in 2006; all other age and sex ratios for WMU 2 and WMU 3 from 2003 to 2008 were collected from ground-based post-season herd composition counts (Tables 3-1 and 3-2). I obtained buck (>1.5 yr) harvest estimates for both WMUs from the annual UDWR harvest survey, which was a telephone survey of a random sample of approximately 25% of licensed general season buck deer hunters.
(Bernales et al. 2009; Tables 3-1 and 3-2). No antlerless hunts were authorized in WMU 2 or WMU 3 from 2003 to 2008; any antlerless harvest during this time was for depredation mitigation and came from small, localized areas.

**POP-II Population Model**

*Modeling procedures.*—I constructed POP-II models for WMU 2 and WMU 3 for the period 2003–2008. The POP-II model is a deterministic model that essentially follows a 2-sex Leslie matrix approach (J. Bartholow, Fossil Creek Software, personal communication). The model uses “bookkeeping” techniques that add and subtract animals, similar in structure to the MDS model, but equations are not provided nor are they accessible for modification (Euler and Morris 1984). The POP-II model tracks population dynamics from one birth pulse to the next, 1 June to 31 May (Bartholow 2003), while the MDS model tracks from post-hunting season to the following post-hunting season, 1 December to 30 November (White and Lubow 2002). Since UDWR manages towards post-hunting season population objectives (e.g., population size, sex ratio, age ratio), I adjusted my POP-II “year” to correspond to the period 1 December–30 November. This way, the final projected population size for each year in the model was post-hunting season population size, which I could then compare to field estimates.

To set up the POP-II models initially, I defined the total number of age classes, sex ratio at birth, wounding loss rates, initial population proportions, minimum natural mortality rates (i.e., 1 – survival rate), annual age ratios, and annual hunter harvest. I used 15 years as the oldest age class (H. Bernales, UDWR, unpublished data). Sex ratio at birth was assumed to be 50:50. I used a wounding loss rate of 0.065 for bucks (>1.5
yr; H. Bernales, unpublished data). I used UDWR-modeled post-season population size estimates and age and sex ratios from 2003 to calculate starting proportions for each sex and age class. I based minimum annual natural mortality rates for fawns (termed subadults in POP-II) and adults (both does and bucks) on upper 95% confidence limits of mean overwinter fawn and annual doe survival, respectively, from Unsworth et al. (1999). Minimum annual natural mortality rate for fawns was 0.13, and 0.08 for adults of both sexes. Annual field-data incorporated into the model were age ratios and hunter-harvest data (Tables 3-1 and 3-2).

Once the initial inputs for the POP-II models were set, I then made individual adjustments to annual mortality rates by changing the curvilinear mortality severity index (MSI) for each year. The MSI is an adjustment factor used to increase the initial minimum natural mortality rates (i.e., decrease survival rates) for each year until predicted sex ratios match the observed values. Curvilinear MSI (as opposed to linear MSI) represents the hypothesis that stressful events influence mortality rates of subadults more strongly than they do the mortality rates of adults (Bartholow 2003). The curvilinear MSI is a multiplier on a scale from 0 to 99, with a value of 0 representing the best (i.e., lowest) possible mortality rate, which is no adjustment to minimum annual natural mortality, and 99 representing the worst possible mortality (Bartholow 2003). To apply the curvilinear MSI for adults, the annual mortality rate is divided by \((100 - \text{MSI}) / 100\); for subadults, the annual mortality rate is divided by this same factor squared (Bartholow 2003; Fig. 3-2).
*Model fitting and performance.*—POP-II computes a goodness of fit (GOF) statistic to measure how well observed values fit predicted values. This statistic is a standardized root mean squared error (RMSE) derivative ranging from 0 to 1, with 1 representing perfect fit (Bartholow 2003). I made adjustments to MSIs for each time step until predicted sex ratios closely matched observed sex ratios, essentially fitting “estimates” of annual survival for each age class. The MSI adjustment procedure is a “tinkering” process, so I used the GOF statistic to determine when I had reached the best fit of my model, i.e., when additional adjustments made no further improvement to the GOF statistic.

To evaluate the ability of the POP-II model to accurately simulate the population dynamics of the WMU 2 mule deer population, I compared the predicted values of fawn and doe survival from POP-II to field-based estimates using the GOF statistic. Since GOF was not computed for population size, I assessed whether POP-II predicted population sizes fell within the 95% confidence intervals of the field estimates. I only had field estimates of survival and population size for 2006 to 2008 so comparisons of predicted values to observed values were only made for these 3 years. I was not able to test the performance of the WMU 3 POP-II model because observed values of survival and population size were lacking for this population.

I used correlations in survival between WMUs 2 and 3, core and satellite units, respectively, to evaluate whether survival rates were comparable. I used simulated values of fawn and doe survival from POP-II models for the period from 2003 to 2008, and
performed a Pearson correlation analysis using PROC CORR from SAS 9.1 software (SAS Institute, Cary, NC) to determine correlation in survival between the 2 WMUs.

**MDS Population Model**

*Modeling procedures.*—I used the MDS population model and model fitting procedures of White and Lubow (2002) to estimate mule deer population abundance in WMUs 2 and 3 for the period 2003–2008 (an example spreadsheet of the procedure can be found at http://warnercnr.colostate.edu/~gwhite/). The model had the following structure:

Total population size \( N_T \), which was made up of the buck \( N_B \), doe \( N_D \) and fawn \( N_F \) segments of the population at time \( t \), was:

\[
N_T(t) = N_B(t) + N_D(t) + N_F(t).
\]

Each segment was calculated as:

\[
N_B(t+1) = r_S F(t)N_F(t) + S_B(t)N_B(t) - H_B(t+1),
\]

\[
N_D(t+1) = r_S F(t)N_F(t) + S_D(t)N_D(t) - H_D(t+1), \text{ and}
\]

\[
N_F(t+1) = R_F(t+1)N_F(t+1).
\]

\( S_B(t), S_D(t), \) and \( S_F(t) \) represented buck, doe, and fawn survival at time \( t \), respectively, with buck and doe harvests at time \( t+1 \) represented by \( H_B(t+1) \), and \( H_D(t+1) \), respectively. \( R_F(t) \) was the post-season age ratio, and \( r \) represented the fawn sex ratio, assumed to be 50:50 for this study.

Field-data included in the models were overwinter fawn survival, annual doe survival, age and sex ratios, hunter-harvest data, and field-based population estimates.
(Tables 3-1 and 3-2). I used WMU 2 survival data for both WMU 2 and WMU 3 population models. Although the overwinter fawn survival estimate in 2006 was $\hat{S} = 1.00$, I used an overwinter fawn survival estimate of $\hat{S} = 0.909$ (1 mortality out of 11, SE = 0.087) for 2006 because the estimate of $\hat{S} = 1.00$ was biologically unrealistic and had no sampling variance to contribute to the model fitting procedure. I had estimates of survival rates and population size from WMU 2 for only 2006–2008, but 3 years of data were insufficient to accurately simulate the population dynamics of the mule deer population. Since I did have observed values of age ratio, sex ratio, and buck harvest, I chose to include 3 additional years (2003–2005) in my MDS models, which provided enough data to better evaluate the MDS model without overwhelming the model with missing data. For years with missing data, I used mean values for doe and fawn survival, which were not adjusted during model-fitting and did not contribute to parameter penalties (White and Lubow 2002). No population size estimates were collected for WMU 3, so model fitting was performed using only age and sex ratios from 2003–2008, and WMU 2 survival estimates from 2006–2008.

Model fitting and performance.—For both WMUs 2 and 3, I fit 8 a priori models to field data following the ordinary least squares procedures of White and Lubow (2002). Models represented combinations of simplifying assumptions, varying by year versus constant fawn and doe survival respectively, and year-specific, constant, or linear-trend age ratios (Table 3-3). An additional 2 parameters, initial numbers of bucks and does, were required for each model (White and Lubow 2002). I performed model selection based on Akaike’s Information Criterion adjusted for small sample size ($AIC_c$; Burnham
and Anderson 2002). For WMU 2, I compared model predictions of my best model (i.e., lowest AICc) to field estimates of survival and population size. For both WMUs 2 and 3, I compared predicted values of my best models to predicted values from POP-II models.

RESULTS

POP-II Model

POP-II modeled estimates of doe survival rates for WMU 2 showed less temporal variation than observed estimates, but still exhibited high GOF (0.894; Fig. 3-3). Modeled values of WMU 2 fawn survival from 2007 and 2008 fell within the 95% CI of the observed estimates, while the 2006 value fell below the 95% CI (GOF = 0.769; Fig. 3-3).

I was able to adjust the curvilinear MSIs to make the POP-II modeled sex ratios match field estimates almost exactly, for both WMU 2 and WMU 3 (GOF = 0.998 and 0.999, respectively). The POP-II model does not predict age ratio estimates, i.e., the predicted age ratio estimates from the POP-II model are the same as the observed field estimates for each year. For 2008, the predicted population size from the POP-II model fell within the 95% CI of the field estimate, but the 2006 population size from the POP-II model was higher than the field estimate and fell outside its 95% CI (Fig. 3-4a). The WMU 2 and WMU 3 fawn and doe survival rates that were simulated using the POP-II model were positively correlated ($r = 0.686$ and 0.578, respectively; Fig. 3-5).
MDS Model

Of the 8 MDS models for WMU 2, the AICc top-ranked model had 77% of the Akaike weight and predicted year-specific fawn and adult survival and constant age ratio (Table 3-4). The 2 top-ranked models for WMU 3 had almost equal AICc values, differing only by 0.2 (Table 3-5). The best model, with 52% of the Akaike weight, predicted year-specific doe and fawn survival and constant age ratio, and was the same top model as that selected for WMU 2 (Table 3-5). The second best model for WMU 3, with 46% of the Akaike weight, predicted year-specific fawn survival, constant doe survival and constant age ratio. In order to directly compare model predictions of vital rates between WMU 2 and WMU 3, I used the top model for WMU 3 (which was the same as the top model for WMU 2) and did not model-average.

The best MDS models for both WMUs had year-specific doe and fawn survival parameters, and WMU 2 doe and fawn survival rates were well within the 95% CIs of the observed estimates (Fig. 3-3). Age ratios in WMU 2 were relatively constant across the 5 years of this analysis, and this was reflected by a constant age ratio parameter of the best-fitted MDS model (Fig. 3-6a). The best-fitted MDS model for WMU 3 also had a constant age ratio parameter, although WMU 3 field estimates showed more variation than did the field estimates from WMU 2 (Fig. 3-6b). For WMU 2, predicted sex ratio estimates were within the 95% CIs of the observed sex ratios in all years but 2006 (Fig. 3-6a). All predicted sex ratio estimates were within the 95% CIs of the observed sex ratios for WMU 3 (Fig. 3-6b).
For WMU 2, the predicted population sizes from the MDS model fell within the 95% CIs of the actual field estimates (Fig. 3-4a). For both WMU 2 and WMU 3, the population estimates predicted by the POP-II models were initially higher than those predicted by the MDS model, but over time converged to similar estimates in the years 2007 and 2008 (Fig. 3-4a, b).

DISCUSSION

Population Size

Projections of WMU 2 and WMU 3 mule deer population sizes from the POP-II models were similar to those of the MDS models for 2007 and 2008, but POP-II estimates for 2003 to 2006 were slightly higher than estimates from the MDS models. The difference in values for the first 4 years was due mainly to the way in which the 2 models estimated initial starting population sizes. POP-II models began with a fixed initial population size (I used UDWR-modeled estimates; Bernales et al. 2009), while MDS models estimated initial population sizes (buck and doe population sizes were estimated separately) during the model-fitting procedure. Field estimates of population size for the first year of the MDS model would improve subsequent population size estimates. Without field estimates of fawn survival, doe survival, or population size to fit model predictions to, the MDS models were fairly limited in their ability to predict population size from 2003 to 2005, and valid comparisons between the MDS models and the POP-II models could only be drawn for the years 2006–2008.

Both the POP-II and MDS models predicted population sizes that were higher than the observed field estimate for 2006. Winter conditions were less severe than
normal, and snow was patchy or bare across most of the winter range when I conducted helicopter quadrat surveys in 2006. Consequently, deer had access to higher elevations and an expanded winter range not covered by my sampling frame, so population size may have been underestimated. Conducting helicopter counts in sub-optimal conditions may lead to biased population estimates and could potentially waste limited resources, so estimating population size from models such as POP-II and MDS may be preferred in these situations.

**Doe and Fawn Survival Rates**

For years in which field data were available (2006–2008), the predicted values of fawn and doe survival from the POP-II model reasonably approximated the observed data for WMU 2. However, predicted values from the MDS best-fitted model more closely represented the data than did values from the POP-II model. Although the top MDS model for WMU 3 included temporal variation in doe survival, the second best model, which had substantial weight (46%), had constant doe survival. The observed temporal variation in doe survival was primarily due to weather conditions that occurred in 2007. Winter was severe in northern Utah, particularly in WMU 3 (Western Regional Climate Center 2010b, c; Fig. 3-7a, b), and the mule deer herd in WMU suffered large losses to mortality during this time (D. DeBloois, UDWR, personal communication). Consequently, I concluded that the second best model for WMU 3 predicted an artificially high population estimate for 2008, due to a constant survival parameter of 0.887 for the harsh winter of 2007. This in turn could lead to seriously biased population trajectories due to the very high sensitivity of population models to adult female survival.
(White and Bartmann 1998). Therefore, I chose the top MDS model that included
temporal variation in doe survival, and did not model average.

In 2006, all of the 11 radiocollared fawns survived the winter. A survival
estimate of 1.0 was biologically unrealistic, and ineffectual for the population models due
to its lack of sampling variation, so the fawn survival value was arbitrarily adjusted
downward to 0.909 (10 survivors out of 11; SE = 0.087). Even with this downward
adjustment to the observed fawn survival estimate, the MDS and POP-II models
predicted still lower estimates of fawn survival in 2006. This illustrates how, with a
biased fawn survival estimate due to small sample size, the other parameters within the
population model can constrain the estimated survival parameter to fall within a realistic
range, a benefit of integrated population modeling techniques.

Unsworth et al. (1999) examined mule deer survival over a broad geographic area
in the Intermountain West, and estimated mean annual doe survival to be relatively
constant at 0.853 (SE = 0.011), and overwinter fawn survival to be highly variable year to
year, with a mean of 0.444 (SE = 0.033). Lukacs et al. (2009) reported a slightly lower
combined doe survival rate of 0.838 for mule deer in Colorado from 1998 to 2008, but
their combined fawn survival rate estimate of 0.721 was considerably higher than that
observed in this study or by Unsworth et al. (1999). My MDS top-model mean annual
doe survival in WMU 2 was 0.860, which was similar to the findings of other studies
(Unsworth et al. 1999, Lukacs et al. 2009). Overwinter fawn survival in my study
showed similarly high year to year variation but the overall mean from my best-fitted
MDS model ($\hat{S} = 0.554$) was higher than that of Unsworth et al. (1999) and lower than that of Lukacs et al. (2009).

Correlation in survival between core and satellite units.—POP-II model-simulated fawn and doe survival rates were positively correlated between WMU 2 and WMU 3, justifying the use of WMU 2 as a core unit that would represent WMU 3. However, White and Bartmann (1998) cautioned that correlations in survival rates between core and satellite units needed to be established directly with field data, and recommended monitoring a randomly selected subset of satellite units annually to develop these correlations. Bishop et al. (2005) monitored fawn survival among adjacent populations in Idaho, and concluded that survival rates from one unit did not adequately represent survival in other units. In contrast, Lukacs et al. (2009) found stronger than expected positive correlations in fawn survival between adjacent units in Colorado, and suggested that values of fawn survival from one unit could be used to inform population models for another unit. They explained that, even if values of fawn survival were not equal across units, an increase in survival in one unit suggested that an increase was probable in a correlated unit. My method of evaluating correlations in model-simulated survival could serve to establish core-satellite pairs initially. Correlation could then be field-verified once several years of data had been collected in both units, following the more rigorous statistical procedures described by Lukacs et al. (2009).

Age and Sex Ratios

Observed age ratios for WMU 2 fluctuated little from 2003 to 2008, and the MDS best-fitted model predicted constant age ratios for this period. The top model for WMU 3
also predicted constant age ratios, and although field estimates seemed to indicate that the year-specific model might be more appropriate, the large standard errors associated with the estimates probably influenced the more parsimonious constant age ratio estimate to fit the best. To calculate standard errors for age and sex ratio estimates in WMU 3, I considered each individual deer as the primary sampling unit, which tends to underestimate variance due to lack of independence between fawn and doe numbers (Bowden et al. 1984). Even so, standard errors were still large due to relatively small sample sizes for herd composition surveys in WMU 3. Since raw herd composition survey data was available for WMU 2 from 2006 to 2008, I was able to calculate standard errors using individual quadrats as the primary sampling units, which was a more appropriate method (Bowden et al. 1984). However, sample sizes for herd composition surveys during this time were low, resulting in large standard errors. Large standard errors may prevent the selection of models that predict year to year fluctuation in model parameters, because lack-of-fit penalties are given less weight when variance is large, which in turn gives more influence to parameter penalties (White and Lubow 2002). Performance of the MDS model selection could be improved if sample size, and thus precision, were increased for age ratio estimates.

Fawn recruitment has been considered to be chronically low in many mule deer populations in the West (Mule Deer Working Group 2004), and low fawn recruitment has been suggested as a driving factor behind declining mule deer populations in the 1960s and 70s (Schneegas and Bumstead 1977, Heffelfinger and Messmer 2003). White and Lubow (2002) found a decreasing trend in age ratios in Piceance Basin, Colorado,
between 1981 and 1997. Lukacs et al. (2009), also in Colorado, indicated that, based on their observed survival rates for does and fawns, the average inflection point in age ratio between an increasing or decreasing population size (i.e., age ratio value when $\lambda = 1.0$), was 47 fawns:100 does. The average age ratio observed during their study was >47 fawns:100 does, suggesting that the decline in mule deer populations seen in Colorado has likely ended.

I did not observe a decreasing trend in age ratio in WMU 2 or WMU 3 when I modeled the mule deer populations using the methods of White and Lubow (2002). The average inflection point based on doe and fawn survival rates from MDS modeled estimates was 50 fawns:100 does for WMU 2 and 59 fawns:100 does for WMU 3. Since 1993, age ratios in WMU 2 and WMU 3 only dropped below the inflection points once (in 2002; Bernales et al. 2009), indicating that during the last 15 years, the mule deer populations in these units had the potential to increase (barring female harvest) and did not necessarily fit into the declining mule deer population pattern purported to exist elsewhere in the Intermountain West (Unsworth et al. 1999, Heffelfinger and Messmer 2003).

**Model Comparison**

For WMU 2, POP-II provided similar estimates of population size to those of the best MDS model, although I used a temporally short data set with only 3 years of field estimates for survival and population size. However, the MDS best-fitted model approximated the data more closely overall, and the MDS procedures were much more straight-forward and less subjective. The MDS model fitting procedures that were used
to determine the maximum likelihood estimates took only seconds using the optimizer function in an Excel spreadsheet (Microsoft Office Professional Edition 2003; Microsoft, Redmond, WA). With the inclusion of multiple types of observed data, the POP-II modeling process is much more complicated. The user must make subjective decisions about the reliability of their data (Bartholow 2003), and make trade-offs between fitting predictions to observed values of one type of data over another, e.g., adjusting the MSI so that predicted values of doe survival more closely approximate observed values, at the expense of the goodness of fit for predicted sex ratios. When only sex ratio estimates were used for fitting predicted values, the POP-II model was relatively simple, though slightly more time-consuming than the MDS process.

MDS model fitting and model selection procedures improve with additional data (in this case, more years), in the sense that there would be more influence from model fit and less influence from parameter penalties. The MDS model can accommodate some sparse or missing data, although caution was advised because more subjective assumptions must be met (White and Lubow 2002). The MDS model is primarily data-driven, and without field estimates of doe survival, fawn survival, and population size, at least occasionally, the MDS model becomes more deterministic, similar to the POP-II model. White and Lubow (2002) cautioned that MDS model fitting using only age and sex ratios could drive projections of population size to infinity, because with a larger and larger population, harvest delivers less impact and allows for more flexibility to fit observed age and sex ratios. In this case, POP-II models may be preferred because the user has more control over fitting individual sex ratio values.
MANAGEMENT IMPLICATIONS

Population models improve with the incorporation of multiple types of data. However, financial constraints prohibit the collection of mule deer survival data in every WMU in Utah. In the absence of survival or population size estimates, POP-II models projected adequate estimates of vital rates and population size. Survival monitoring in core units could provide survival data for nearby satellite units, but correlations between core and satellite units need to be established. Using my proxy method, POP-II modeled survival estimates could be used to establish these correlations, which could then be verified once enough data has been collected. When field data were available to incorporate into the models, MDS models approximated observed data better than POP-II models and MDS modeling procedures were simpler to execute.

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Western Regional Climate Center. 2010b. Laketown, Utah.


Western Regional Climate Center. 2010c. Pine View Dam, Utah.


Table 3-1. Field-based estimate inputs to POP-II and MDS mule deer population models, WMU 2, Utah, USA, from 2003 to 2008. Missing data are shown as blank entries.

<table>
<thead>
<tr>
<th>Yr</th>
<th>Fawns: 100 does</th>
<th>SE</th>
<th>Bucks: 100 does</th>
<th>SE</th>
<th>Fawn survival</th>
<th>SE</th>
<th>Adult survival</th>
<th>SE</th>
<th>Population size</th>
<th>SE</th>
<th>Buck harvest</th>
<th>SE</th>
<th>Doe harvest</th>
<th>SE</th>
</tr>
</thead>
<tbody>
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<td>2003</td>
<td>77.3</td>
<td>3.76</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>1,556</td>
<td>36</td>
<td>32</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>88.4</td>
<td>4.71</td>
<td>19.6</td>
<td>1.77</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1,419</td>
<td>34</td>
<td>46</td>
<td>7</td>
<td></td>
<td></td>
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<tr>
<td>2005</td>
<td>81.7</td>
<td>4.68</td>
<td>11.8</td>
<td>1.40</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>30</td>
<td>32</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>8.24</td>
<td>15.8</td>
<td>3.66</td>
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<td>0.09</td>
<td>0.94</td>
<td>0.03</td>
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<td>1,821</td>
<td>1,410</td>
<td>34</td>
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<td>6</td>
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<td>7.84</td>
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<td>0.13</td>
<td>0.70</td>
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<td>1,607</td>
<td>34</td>
<td>97</td>
<td>8</td>
<td></td>
<td></td>
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<td>2008</td>
<td>74.7</td>
<td>9.60</td>
<td>10.9</td>
<td>2.20</td>
<td>0.55</td>
<td>0.15</td>
<td>0.92</td>
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<td>16,526</td>
<td>3,225</td>
<td>1,196</td>
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<td>100</td>
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<td>Mean</td>
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<td>6.47</td>
<td>15.2</td>
<td>2.15</td>
<td>0.58</td>
<td>0.12</td>
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<td>2,523</td>
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<td>7</td>
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<tr>
<td>SD</td>
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<td>0.11</td>
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<td></td>
<td></td>
<td></td>
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<td>199</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>CV (%)</td>
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<td>2.0</td>
<td>45.3</td>
<td>12.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>22.4</td>
<td>14.5</td>
<td>44.9</td>
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Table 3-2. Field-based estimate inputs to POP-II and MDS mule deer population models, WMU 3, Utah, USA, from 2003 to 2008. Missing data are shown as blank entries.

<table>
<thead>
<tr>
<th>Yr</th>
<th>Fawns:100 does</th>
<th>Bucks:100 does</th>
<th>Fawn survival</th>
<th>Adult survival</th>
<th>Buck harvest</th>
<th>Doe harvest</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
<td>Estimate</td>
<td>SE</td>
<td>Estimate</td>
<td>SE</td>
</tr>
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<td>2003</td>
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<td>17.0</td>
<td>3.23</td>
<td>529</td>
<td>20</td>
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<td>2004</td>
<td>75.0</td>
<td>5.42</td>
<td>16.0</td>
<td>2.04</td>
<td>662</td>
<td>22</td>
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<tr>
<td>2005</td>
<td>88.0</td>
<td>7.98</td>
<td>15.0</td>
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<tr>
<td>2006</td>
<td>94.9</td>
<td>8.49</td>
<td>14.0</td>
<td>2.49</td>
<td>624</td>
<td>22</td>
</tr>
<tr>
<td>2007</td>
<td>94.2</td>
<td>9.82</td>
<td>20.1</td>
<td>3.57</td>
<td>603</td>
<td>21</td>
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<td>2008</td>
<td>70.0</td>
<td>7.19</td>
<td>9.6</td>
<td>2.13</td>
<td>463</td>
<td>19</td>
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<tr>
<td>Mean</td>
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<td>SD</td>
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<td>0.11</td>
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<td>CV (%)</td>
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<td>45.3</td>
<td>12.9</td>
<td>16.3</td>
<td>62.1</td>
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Table 3-3. A priori MDS models fit to field data from WMU 2 and WMU 3, Utah, USA.

The number of estimated parameters fit for each component are shown in parentheses.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fawn survival</th>
<th>Doe survival</th>
<th>Age ratio</th>
<th>Initial population</th>
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<tbody>
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<td>1</td>
<td>Constant (1)</td>
<td>Constant (1)</td>
<td>Constant (1)</td>
<td>Buck &amp; doe (2)</td>
</tr>
<tr>
<td>2</td>
<td>Constant (1)</td>
<td>Constant (1)</td>
<td>Yr-specific (6)</td>
<td>Buck &amp; doe (2)</td>
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<td>3</td>
<td>Yr-specific (3)</td>
<td>Constant (1)</td>
<td>Constant (1)</td>
<td>Buck &amp; doe (2)</td>
</tr>
<tr>
<td>4</td>
<td>Yr-specific (3)</td>
<td>Constant (1)</td>
<td>Linear trend (2)</td>
<td>Buck &amp; doe (2)</td>
</tr>
<tr>
<td>5</td>
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<td>Yr-specific (3)</td>
<td>Linear trend (2)</td>
<td>Buck &amp; doe (2)</td>
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<tr>
<td>6</td>
<td>Yr-specific (3)</td>
<td>Constant (1)</td>
<td>Yr-specific (6)</td>
<td>Buck &amp; doe (2)</td>
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<tr>
<td>7</td>
<td>Yr-specific (3)</td>
<td>Yr-specific (3)</td>
<td>Yr-specific (6)</td>
<td>Buck &amp; doe (2)</td>
</tr>
<tr>
<td>8</td>
<td>Yr-specific (3)</td>
<td>Yr-specific (3)</td>
<td>Constant (1)</td>
<td>Buck &amp; doe (2)</td>
</tr>
</tbody>
</table>
Table 3-4. Model selection results (sorted in decreasing order of model likelihood), number of parameters \((K)\), small-sample-adjusted Akaike’s Information Criteria \((AIC_c)\), differences in \(AIC_c\) values \((\Delta AIC_c)\), model weights, and model likelihoods for MDS population models fit to data collected from a mule deer herd in WMU 2, Utah, USA, from 2003 to 2008.

<table>
<thead>
<tr>
<th>Model</th>
<th>(K)</th>
<th>(AIC_c)</th>
<th>(\Delta AIC_c)</th>
<th>(AIC_c) weight</th>
<th>Model likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>9</td>
<td>70.452</td>
<td>0.000</td>
<td>0.767</td>
<td>1.000</td>
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<tr>
<td>3</td>
<td>7</td>
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<tr>
<td>2</td>
<td>10</td>
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<td>0.000</td>
</tr>
<tr>
<td>7</td>
<td>14</td>
<td>145.488</td>
<td>75.036</td>
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<td>0.000</td>
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Table 3-5. Model selection results (sorted in decreasing order of model likelihood), number of parameters ($K$), small-sample-adjusted Akaike’s Information Criteria ($AIC_c$), differences in $AIC_c$ values ($\Delta AIC_c$), model weights, and model likelihoods for MDS population models fit to data collected from a mule deer herd in WMU 3, Utah, USA, from 2003 to 2008.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$AIC_c$ weight</th>
<th>Model likelihood</th>
</tr>
</thead>
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<tr>
<td>8</td>
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<td>0.516</td>
<td>1.000</td>
</tr>
<tr>
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<td>0.898</td>
</tr>
<tr>
<td>4</td>
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<td>0.034</td>
</tr>
<tr>
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<td>10</td>
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<td>0.005</td>
</tr>
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Figure 3-1. Mule deer winter range in WMU 2 and WMU 3, Utah, USA.
Figure 3-2. Adjustments to mortality rate by the curvilinear mortality severity index (MSI) of a POP-II model, based on a minimum subadult mortality rate of 0.13 and a minimum adult mortality rate of 0.08.
Figure 3-3. Multiple data sources (MDS) modeled, POP-II modeled, and observed estimates of fawn and doe survival rates for the mule deer population in WMU 2, Utah, USA, from 2006 to 2008. Error bars represent 95% confidence intervals.
Figure 3-4. Multiple data sources (MDS) modeled, POP-II modeled, and observed estimates of population size for the mule deer populations in (a) WMU 2 and (b) WMU 3, Utah, USA, from 2003 to 2008. Error bars represent 95% confidence intervals.
Figure 3-5. POP-II simulated values of fawn and doe survival rates for WMU 2 and WMU 3 mule deer populations, Utah, USA, from 2003 to 2008.
Figure 3-6. Observed age (fawns:100 does) and sex (bucks:100 does) ratios compared to predicted estimates from best (AICc) fitted multiple data sources (MDS) model for the mule deer populations in (a) WMU 2 and (b) WMU 3, Utah, USA, from 2003 to 2008. Error bars represent 95% confidence intervals.
Figure 3-7. Winter of 2007 (a) average monthly temperatures (°C) and (b) total monthly snowfall (cm) in WMU 2 and WMU 3, Utah, USA. Climate data shown for WMU 2 are averages of Richmond and Laketown weather station data in Cache and Rich Counties, respectively. Climate data shown for WMU 3 are from the Pine View Dam weather station in Weber County.
Reliable information about mule deer (*Odocoileus hemionus*) populations is necessary for proper management, but it doesn’t have to be prohibitively expensive. In Chapter 2, I demonstrated that, when resources were optimally allocated, it was possible to collect precise, repeatable, and reliable data on multiple aspects of population dynamics, at a lower cost than what would be typically spent on annual field-based population estimates. More precise estimates of population trend were obtained by shifting resources to the collection of survival data. Field-based population size estimates could be conducted infrequently to validate population models, but did not need to be the main focus of a population monitoring program.

Financial constraints prohibit the collection of mule deer survival data in every Wildlife Management Unit (WMU) in Utah. Survival monitoring in core units could provide survival data for nearby satellite units, but correlations between core and satellite units need to be established. Using the proxy method from Chapter 3, survival estimates from POP-II models could be used to establish these correlations, which could then be verified directly once enough data has been collected. Survival data collected in core units could be incorporated into satellite unit population models, and I showed how projections of population size and vital rates were improved with the incorporation of multiple types of data into population models.
APPENDIX
DETERMINING MAJOR ECOREGIONS WITHIN UTAH FOR CORE MONITORING OF MULE DEER SURVIVAL

For a comprehensive statewide monitoring program for mule deer in Utah, annual monitoring of doe and fawn survival will be conducted in core Wildlife Management Units (WMUs) within the major ecoregions in Utah, as well as annual herd composition surveys in all mule deer WMUs. To determine major ecoregions within Utah, I used the North American Mule Deer Conservation Plan (Mule Deer Working Group 2004). This document identified major ecoregions across mule deer range in the west, following the broad vegetative complexes called Provinces as described by Wallmo (1981). I compared these ecoregion classifications to those described by Bailey et al. (1994), who identified 14 ecosystem sections within Utah, and Omernik (1987), who identified 7 level III ecoregions in Utah.

Wallmo (1981) identified 3 ecoregions in Utah – Intermountain West, Southern Desert, and Colorado Plateau Shrubland and Forest. Further delineating these 3 major ecosystem types, Omernik (1987) described 7 level III ecosystems, and Bailey et al. (1994) identified 6 ecosystem provinces in Utah. The major distinction between Bailey et al. (1994) and Omernik (1987) classifications for Utah and that of Wallmo (1981) was their distinction of the Wasatch and Uinta Mountains, the mountain ranges that separated the greater ecoregions of the Colorado Plateau to the east and Great Basin to the west. The Wasatch and Uinta Mountains should be included as an important Utah ecoregion in mule deer ecoregional-based decision making because there are major climatic
differences between this mountainous region and the Great Basin to the west, and also because the majority of mule deer range in Utah lies along this mountain corridor. Other Utah ecoregions described by Omernik (1987) included small, isolated patches of the Wyoming Basin, Northern Basin and Range, and the Southern Rockies, which could be reasonably lumped into the broader Wallmo (1981) ecoregions of the Great Basin/Intermountain West (first 2) and Colorado Plateau Shrublands and Forests (Southern Rockies). Bailey et al. (1994) splits out the southern half of the Wasatch and Uinta Mountains ecoregion into a distinct High Plateau and Mountains ecoregion, which is reasonable for delineating ecoregions for mule deer because large differences have been observed between northern and southern Utah mule deer populations.

I outlined 5 major ecoregions within Utah, the Great Basin, Wasatch and Uinta Mountains, High Plateau and Mountains, Colorado Plateau, and Southern Desert (Fig. A-1). Core units for mule deer monitoring in Utah should represent these 5 major ecoregions. In 2009, UDWR selected 7 units to initiate mule deer survival monitoring (K. Hersey, UDWR, personal communication). The 7 units adequately represented the northern and southern halves of the state and the 5 major ecoregions in Utah (Fig. A-1).

LITERATURE CITED


Figure A-1. Mule deer winter and summer ranges within the 5 ecoregions of Utah, and the 7 core units selected for core monitoring of mule deer survival in Utah.