DISSERTATION

EVALUATION OF WINTER RANGE HABITAT TREATMENTS ON OVERWINTER SURVIVAL, DENSITY, AND BODY CONDITION OF MULE DEER

Submitted by

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ABSTRACT

EVALUATION OF WINTER RANGE HABITAT TREATMENTS ON OVERWINTER SURVIVAL, DENSITY, AND BODY CONDITION OF MULE DEER

The management and research of mule deer (*Odocoileus hemionus*) in Colorado and throughout the Rocky Mountain West is an exciting arena for wildlife professionals as the prevailing view among biologists, managers, researchers, hunters, wildlife viewers and general wildlife enthusiasts is that they would like to see more deer on the landscape. This desire, and the subsequent support it generates for mule deer research, has paved the way for research projects to evolve: each project has generated new data, new knowledge and answers to questions, but each projected has also generated new questions. My research has been a part of this evolution; it benefited from and was built on existing information, it adds new knowledge and hopefully, it will help guide future research.

Past research has provided insight into Colorado’s mule deer management by providing strong evidence that deer herds are limited by browse availability and condition on winter range. Specifically, this research demonstrated that when winter nutritional condition of mule deer is elevated, population productivity increases. However, while this past research gave insight into which ecological process was likely limiting Colorado’s mule deer populations, it did not evaluate the effectiveness of habitat management as a strategy for increasing deer herds. Habitat management actions focused on improving mule deer browse availability and browse quality has often been employed in Colorado. For my research, habitat management practices included mechanical disturbance in the form of hydro-axe and roller-chopper treatments, but also reseeding with desirable browse species and chemical control of weeds. Mechanical disturbance was utilized with the objective of removing pinyon pine (*Pinyon edulis*)- Utah juniper (*Juniperus osteosperma*) forests that had encroached into open meadow complexes and replaced desirable browse species such as sagebrush (*Artemesia* spp.), cliffrose (*Purshia mexicana*), antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus* spp.), or rabbittbrush (*Ericameria* spp.).

In Chapter 1, I used 4 years of data and 8 study units to evaluate the effect of habitat management on the overwinter survival of mule deer fawns. Habitat management consisted of different levels of habitat management efforts: reference study units received no habitat management, traditional habitat treatment units received mechanical disturbance and advanced habitat treatment units were comprised of both mechanical disturbances as well as follow-up chemical control of weeds and reseeding with desirable browse species. Mule deer fawns that overwintered on areas that received both a traditional treatment as well as follow-up treatments experienced an improvement in survival ($\hat{S}$= 0.768, SE = 0.085) over deer on winter range without habitat treatments ($\hat{S}$ = 0.675, SE = 0.112). When partitioned into different levels of treatment intensity, mule deer inhabiting winter range that advanced treatments (i.e., both traditional treatments and follow-up treatments) experienced higher survival ($\hat{S}$ = 0.768, SE = 0.0849) than deer on areas that experienced only traditional treatments ($\hat{S}$ = 0.687, SE = 0.108), which in turn experienced higher survival than in areas that had received no treatments ($\hat{S}$ = 0.669, SE = 0.113).

In my second chapter, I relied on recent advancements in abundance estimation methodologies to determine if habitat management strategies increased mule deer density. In order to estimate mule deer density, I conducted annual helicopter mark-resight surveys across the 8 study units that were utilized in chapter 1. Resighting probabilities (range 0.070–0.567) were best modeled as an interactive function of study unit and year, although sampling method was also important. A consistent pattern of higher deer density on advanced treatment study units was not observed despite its being the primary hypothesis of the study. Total deer densities did vary by latitude with 20–84 deer/km^2 in southern study units and 4–12 deer/km^2 in northern study units. I conclude that if population density is to be used as a population response variable, it only be used in tandem with other, possibly more sensitive parameters, such as overwinter survival of mule deer fawns.

In my third chapter, I investigate the relationships between habitat, body condition, and life history characteristics. With the increased availability of portable ultrasound machines and the refinement of hormonal assays, assessment of ungulate body condition has become a more accessible monitoring strategy. I employed body condition scoring, estimation of % ingesta-free body fat (%IFBF) and assessment of thyroid hormones (FT4 and FT3) as metrics to determine if landscape-level habitat manipulation affected body condition of adult (≥1.5 years old) female mule deer. All body condition related metrics were measured on 2 study units — a reference unit and an advanced treatment study unit. A consistent trend of higher %IFBF was observed in the advanced treatment study unit ($\widehat{\%\mathrm{IFBF}} = 7.100$, SE = 0.455) than in the reference study unit ($\widehat{\%\mathrm{IFBF}} = 6.566$, SE = 0.455), although variation of estimates weakened my ability to draw strong conclusions. A similar pattern in thyroid hormone concentrations was observed with higher concentrations consistently being observed in the advanced treatment study unit, but large amounts variation within concentrations of estimates made it difficult to conclusively distinguishing between study units difficult. Population-level impacts stemming from my observed differences in body condition parameters were likely nominal, although the consistent pattern of higher body condition related estimates in my advanced treatment study unit prevented complete dismissal of my methods as viable population monitoring strategies.

For my final chapter, I assimilate the knowledge and information gained from my first 3 chapters with the existing knowledge base surrounding mule deer population dynamics and population limitation within Colorado. Such reviews have been conducted periodically (e.g., 1960s and late 1990s) and have been precipitated by mule deer population declines. A dramatic decline in mule deer populations was detected during the final years of my field research but the underlying cause of this decline is yet to be determined. Past reviews identified research and management experiments that would benefit mule deer and many of those topics have been addressed between the 1990s and present time, but the new knowledge and information has not been compiled in a review. Based on the best available information and evidence, the working hypothesis in Colorado is that mule deer herds are limited by winter range habitat. This hypothesis is primarily influenced by experimental research that demonstrated how elevating overwinter nutritional condition of mule deer increased population productivity. Research focused on other potential limiting factors did not elicit a similar response. In light of this evidence, my review identifies new gaps in knowledge, and potential, future research topics are identified. In particular, I suggest that mule deer density reduction experiments, as well as bear and mountain lion predation research be future research foci.

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I am exceptionally fortunate to have been surrounded by smart, creative and enthusiastic people at Colorado State University and at Colorado Parks and Wildlife. One of the expectations of turning my field research project into a graduate research program was that the final product would be improved. There is no question that this expectation was met. This was in no small part due to the efforts of my adviser, Dr. Paul Doherty. The energy and encouragement that Paul infused into my work would be difficult to match and I am thankful for the opportunity to have worked with him. Likewise, the opportunity to have had Dr. Gary White serve on my graduate committee was a privilege. Beginning in the 1980s and continuing through present day, Gary's influence on Colorado's mule deer research and management has been unparalleled. The contributions of the remainder of my graduate committee did not deviate from this pattern. Dr. Dhruba Naug and Dr. Edwin Chong each brought a unique perspective to my work, forcing me to think in new ways and to tackle challenging questions. As individuals and collectively as a committee, these 4 individuals challenged me as a scientist and improved the quality of my work. Their efforts are appreciated. In addition to my committee, I benefitted from many people that were associated with Colorado State University. In particular, I received many rounds of comments and constructive criticism from my lab mates and other graduate students in the Department of Fish, Wildlife, and Conservation Biology. I would like specifically acknowledge Phillip Street and Dr. Amy Davis for their support and friendship, it was appreciated. While my interactions with many individuals associated with the Fish, Wildlife, and Conservation Biology departments were not as frequent as with those mentioned above, the enthusiasm for wildlife research expressed by everyone associated with the department was contagious and fostered a productive environment.

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CHAPTER 1

Effect of Habitat Management on Overwinter Survival of Mule Deer Fawns in Colorado

Wildlife managers and ecologists are often compelled to identify the primary limiting factor to population growth in order to facilitate population management. Due to their iconic status and economic value, mule deer (*Odocoileus hemionus*) are not exempt from this need. Habitat management, in the form of mechanical or chemical manipulation of the vegetative landscape, has been utilized as a population management strategy to bolster mule deer populations. Yet evaluation of this strategy in the form of deer population response has been lacking. To address a knowledge gap and to evaluate the effectiveness of habitat management as a deer population management strategy, I conducted a 4-year study that measured the overwinter survival of mule deer fawns on study units that had experienced different levels of habitat management efforts. Mule deer that overwintered on areas that received both a traditional treatment as well as follow-up treatments experienced an improvement in survival ($\hat{S}$= 0.768, SE = 0.085) over deer on winter range without habitat treatments ($\hat{S}$ = 0.675, SE = 0.112). When partitioned into different levels of treatment intensity, mule deer inhabiting winter range that received both traditional treatments and follow-up treatments experienced higher survival ($\hat{S}$ = 0.768, SE = 0.085) than deer on units that experienced only traditional treatments ($\hat{S}$ = 0.687, SE = 0.108), which in turn experienced higher survival than deer in areas that had received no habitat treatments ($\hat{S}$ = 0.669, SE = 0.113). My study provides evidence supporting the long-held view that habitat management is a viable and economically feasible population management strategy for mule deer.

INTRODUCTION

A common trend among many terrestrial, mammalian systems is a tendency to cycle between population highs and lows (Jedrzejewska and Jedrzejewski 1998, Krebs et al. 2001, Clutton-Brock and Pemberton 2004). While the true cause of these cycles is likely due to many factors (e.g., habitat quality, weather, disease, predation, hunting, and competition), wildlife managers and ecologists are often compelled to identify the primary limiting factor to population growth. Without exception, mule deer populations have demonstrated a tendency to show large fluctuations with several dramatic declines being evident since the turn of the 19th century (Workman and Low 1976, Connolly 1981, Gill 2001, Unsworth et al. 1999, Peek et al. 2002). More specifically, a general increase in mule deer populations was observed as early as the 1920s, with subsequent peak numbers being observed from the 1940s through the early 1960s. A decline occurred during the late 1960s through the 1970s, followed by a smaller increase during the 1980s. The most recent decline started during the early 1990s (Unsworth et al. 1999, Bergman et al. 2011). The mule deer in Colorado reflected these trends, with sections of the state experiencing long-term population declines by as much as 50% between the 1960s and the present (Gill 2001). Primarily due to the value of mule deer as a big game species, wildlife managers' challenges are two-fold: understanding the underlying causes of mule deer population change and implementing management actions that can dampen the effects of these fluctuations, or alternatively, be utilized as a mitigation strategy to offset population declines.

Considerable amounts of energy and money have been invested in assessing the role of different factors on mule deer populations. During the past 15 years the role of predation and habitat quality as limiting factors have been experimentally tested in a number of ways (Bartmann et al. 1992, Bishop et al. 2009, Hurly et al. 2011). Initial work conducted in Colorado used experimental manipulation to test the hypothesis of compensatory mortality (Bartmann et al. 1992). Results from this work demonstrated that density played a primary role in population performance, with predators being a proximate source of mortality. More recently, collaborative research conducted by the Colorado Division of Parks and Wildlife and Idaho Fish and Game has further assessed the roles of predation and habitat on overwinter fawn survival. The overwinter survival of fawns has largely been identified as playing a key role in population dynamics (Gaillard et al. 1998, Unsworth et al. 1999, Gaillard et al. 2000, Lukacs et al. 2009). In Idaho, the effect of predator removal on overwinter fawn survival was experimentally tested by applying different levels of predator control to different study areas (Hurley et al. 2011). No effect on fawn survival was detected through these experiments and changes in population trends were not observed (Hurly et al. 2011). In Colorado, the role of forage quality and quantity on overwinter fawn survival was tested using a treatment and control cross-over design with *ad libitum* pelleted food supplements as a substitute for instantaneous high quality habitat (Bishop et al. 2009). Bishop et al. (2009) found that supplemental forage treatments improved overwinter fawn survival with corresponding fewer predation events. Thus, Bishop et al. (2009) concluded that overwinter nutrition was the primary limiting factor on that population. This research elucidated some of the underlying processes in mule deer population regulation, but did not test the effectiveness of desirable habitat management techniques. Due to the undesirable effects of feeding wildlife (e.g., artificially elevating density, increased potential for disease transmission, cost, and time), a more appropriate management strategy for achieving a high quality nutrition enhancement needed to be assessed.

Of specific interest to my study, during the last 40 years state and federal natural resource management agencies have conducted large scale habitat treatments with the purpose of improving habitat quality for wildlife. Many of these treatments were designed to improve the quality of winter range for mule deer by increasing browse abundance or quality. Research focused on mule deer utilization of treated areas has been conducted (Kie 1984, Long et al. 2008). However, research connecting mule deer population performance to actual habitat quality has been indirect. As such, habitat evaluation programs that measure the productivity and availability of browse species, as well as assess cover quality, cannot be directly translated into deer population performance. The nature of the relationship between habitat management and mule deer population performance needs to be established.

To address this knowledge gap, I measured the overwinter survival of 6-month old mule deer fawns across a suite of study units. My objective was to determine if increased overwinter survival could be detected on mule deer winter range that had received habitat manipulation actions that were intended to improve the quality of mule deer winter range. I specifically measured survival on 3 types of study units: traditional treatment units, advanced treatment units, and reference units. The underlying hypothesis for this research was that mule deer population performance, expressed in the form of overwinter survival rates of 6-month old fawns, would be highest in areas that had received follow-up habitat treatments and lowest in reference areas.

STUDY AREA

I conducted this research on the southeastern portion of the Uncompahgre Plateau and in neighboring drainages of the San Juan mountain range in SW Colorado (Fig. 1.1). A total of 8 study units, composed of mule deer winter range, were identified for inclusion in this study (Table 1.1). Study units fell between 38° 15’ N and 38° 49’ N latitudes and between 107° 41’ W to 108° 28’ W longitudes with elevation 1,670–2,380 m. In general, the Uncompahgre Plateau follows a southeast to northwest direction, feeding the Uncompahgre and Gunnison watersheds to the east and north and the San Miguel and Dolores watersheds to the west and south (Pojar and Bowden 2004). Winter (Dec.–Feb.) high temperatures ranged between 3.7° C and 7.1° C and low temperatures ranged between -9.1° C and -5.7° C (Western Regional Climate Center [WRCC] 2011). Mule deer winter range across the study area and all study units was primarily composed of pinyon pine (*Pinyon edulis*) - Utah juniper (*Juniperus osteosperma*) forests. Most of these forests were late-seral stage, typified primarily by open understory and occasional sagebrush (*Artemesia spp.*), cliffrose (*Purshia mexicana*), antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus spp.*), or rabbittbrush (*Ericameria spp.*) plants. Mule deer winter range grasses included western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), Indian ricegrass (*Achnatherum hymenoides*) and bluegrass (*Poa spp.*).

The study units for this research fell within Data Analysis Units (DAUs) 19 and 40. While each DAU in Colorado had an individual management plan, the management objectives for D-19 and D-40 were very similar to one another. In particular, both DAUs were managed for overall population sizes that balanced the need to minimize conflict (i.e., agricultural damage and vehicle collisions) and prevent overuse of habitat, but also to provide ample hunting opportunity. Desired post-hunt sex ratios were 25–35 adult males per 100 adult females for these DAUs. All study units were centered on public lands (U.S. Bureau of Land Management and State Wildlife Areas), although most study units had private land at their lower elevations. Elk (*Cervus elaphus*) were present at all study units, although spatial overlap with deer was nominal as elk tended to use higher elevations.

METHODS

Study units were classified into 3 different groups: traditional treatment units, advanced treatment units and reference units. For a portion of winter range to be labeled as either an advanced or traditional treatment unit, it needed to have received some form of mechanical disturbance within the previous 10 years. Mechanical disturbances included hydro-ax or roller-chop treatments. A hydro-ax was a boom-mounted mulcher on a reticulated tractor (Watkins et al. 2007). Hydro-axes were capable of selectively removing individual trees and resulted in smaller but more precise treatments. A roller-chopper consisted of a large drum, affixed with perpendicular blades, that was pulled behind a bulldozer (Watkins et al. 2007). The blade of the bulldozer was used to uproot trees and other vegetation and the drum was pulled over the newly downed vegetation, breaking it into smaller pieces. Roller-chop treatments typically resulted in larger and more open treatment areas that were delivered at a lower cost per unit of area treated. Both types of mechanical treatment resulted in forest canopy openings that were typified by high edge/area ratios and were covered with a mulched ground cover that was beneficial for holding moisture and created a bed for vegetative reseeding. Reseeding efforts that occurred concurrently with the mechanical disturbance treatments typically had seed mixes comprised of grass and forbs species (e.g., western wheatgrass, Indian ricegrass, penstemon (*Penstemon spp.*), small burnet (*Sanguisorba minor*), ladak alfalfa (*Medicago sativa*)). Advanced treatment units were also typified by traditional landscape treatment methodologies, but also experienced a follow-up treatment effort. Follow-up treatments were typically smaller scale reseeding and weed control efforts that occurred 2–4 years after a traditional mechanical disturbance. The follow-up reseeding efforts used seed mixes composed of desirable browse species for mule deer (bitterbrush, cliffrose, sagebrush, serviceberry (*Amelanchier alnifolia*), and four-wing saltbush

(*Atriplex canescens*)). Follow-up weed eradication, via herbicide application, targeted cheatgrass (*Bromus tectorum*) and jointed goatgrass (*Aegilops cylindrica*). In order to expedite follow-up habitat treatment work and to target treatments specifically for deer, each advanced treatment unit was centered on a State Wildlife Area. State Wildlife Areas were managed by the Colorado Division of Parks and Wildlife, and thus, management authority was controlled by the agency responsible for the research. Reference units were typified by portions of mule deer winter range that had not received mechanical disturbance at any time during the past 50–60 years.

Study Unit Selection

Eight study units were selected based on their habitat treatment history. Due to the aggressive habitat and landscape management history throughout the study area, reference unit availability and location proved to be a limiting factor in study site selection. To address concerns over variation in weather patterns, the selection process for study sites was stratified by latitude. In particular, 1 reference unit and advanced treatment unit pairing was located in both the northern (study units A and B; Table 1.1) and southern halves (study units G and H; Table 1.1) of the study area. Additionally, reference units and advanced treatment units were spatially paired such that they were not greater than 10 km apart, yet they needed an adequate buffer to prevent the movement of animals between study units. I focused on these paired reference and advanced treatment study units each year of my study. In addition, I included a different traditional treatment study unit each year of my 4-year study. These 4 units (study units C–F; Table 1.1) were identified prior to the start of the study and the year that each was utilized was randomly selected. Incorporation of traditional treatment study units was motivated by the desire to offset the consequences stemming from my inability to randomly select reference and advanced treatment study units. The addition of traditional treatment units increased the amount of the greater study area that was incorporated into the study and strengthened the level of inference to which results could be applied. As such, my hypothesis was tested on 8 study units (2 reference units, 2 advanced treatment units and 4 traditional treatment units) over a 4-year period.

Field Methods

Due to the remote location of several study units, helicopter net-gunning (Barrett et al. 1982, van Reenen 1982, Potvin and Breton 1988) was the primary method of capturing deer. In study units that were easily accessible from roads, baited drop nets (Ramsey 1968, Schmidt et al. 1978, White and Bartmann 1994) were also used for capture. All captured deer were fitted with temporary VHF radio-collars that were designed to drop off animals after 6 months (LOTEK Wireless, INC., Newmarket, ON, Canada). All radio-collars were equipped with mortality sensors, which would increase the pulse rate of transmitted signals after remaining motionless for 4 hours. At the time of capture, all deer were also weighed and sex was recorded. Captures occurred between 1 December–1 January. To accommodate mortalities associated with capture and to remove potential bias from survival estimates due to the capture process, deer did not enter the survival analysis for the first week following capture.

All radio-collared deer were routinely monitored between the time of capture and 15 June of each year. Routine monitoring included ground monitoring 2–4 times per week. However, not all radio-collared deer could be reliably detected via ground monitoring. Thus, weekly monitoring flights were also conducted to ensure that the live or dead status of each deer was determined at least once per week. When detected, mortalities were investigated as quickly as possible to improve estimates of the date of death and to determine cause of death.

Analytical Methods

Based on the results of past research, I wished to have statistical power to detect a 20% difference in survival between reference units and advanced treatment study units. Sample size and power calculations were based on $\alpha = 0.050$, $ß = 0.300$ and long term overwinter fawn survival estimates of 0.444 (SD = 0.217; Unsworth et al. 1999). The desired sample size for each study unit, each year, was determined to be 25 deer.

I conducted survival analyses using the known-fate model in program MARK (White and Burnham 1999) and model selection and variable weighting strategies followed the methods of Burnham and Anderson (2002). I built models that allowed survival to vary by study unit, treatment intensity, week and year were built. Models that accounted for treatment intensity partitioned all study units into 3 categories (reference units, traditional treatment units and advanced treatment units; Table 1.1). In addition to this management-level variation, models that partitioned data by sex and mass were also built. Following the suggestion of Doherty et al. (2012), all possible combinations of additive models were built. However, some model variables were confounded (i.e., treatment intensity and study units), reducing the all possible models comparison to a set of 80 models.

For *a posteriori* exploratory purposes, several additional models were built. First, a highly-parameterized, multiplicative interaction model that allowed survival to vary within a single year and between different years was built. Likewise, based on initial model results, a subset of models was built in order to assess the role of treatment history. As opposed to the original model structures, the exploratory treatment history models partitioned all study units into 2 categories: treated units (i.e., traditional treatment and advanced treatment units were pooled), and untreated units. Thus, these models did not differentiate between traditional treatment and advanced treatment units. None of the exploratory modes were included in the cumulative model weights or final model comparisons.

RESULTS

Across the study area, hydro-axe treatments reduced mean percent tree cover by 12.752% (SD = 18.076) and increased the mean percent cover by grass and browse by 2.767% (SD = 7.309; A. Clements, personal communication). Likewise, roller-chop treatments reduced mean percent tree composition by 6.492% (SD = 17.341) and increased mean percent cover by grasses and browse by 0.553% (SD = 12.695; A. Clements, personal communication).

I captured a total of 498 6-month old mule deer fawns as part of this study. Due to radio-collar malfunction and mortalities that occurred within 1 week of capture, 22 of these deer were censored from the survival analyses. One animal was censored due to a mid-winter movement from one study unit to a neighboring unit. Post censorship, average sample size for each study unit, each year, was ~24 animals. The smallest sample for a study unit during a single year was 18 (n = 1) animals and the maximum was 25 (n = 10). Of the 476 animals entering the survival analysis, 224 were males and 252 were females. Mean mass at the time of capture was 37.6 kg (SD = 4.12 kg) for males and 34.5 kg (SD = 3.92 kg) for females.

Of the 80 models I constructed, the top 10 fell within ΔAIC_c of 7.0 and accounted for >99.5% of the AIC_c model weight (Table 1.2). The remaining models had ΔAIC_c values >11.0 and accounted for <0.5% model weight. Within the top 10 models, certain aspects of the model structure were consistent. In particular, additive year (AIC_c cumulative weight = 0.998) and week (AIC_c cumulative weight = 0.997) effects were always present (Tables 1.2 and 1.3). While yearly variation in survival estimates was expected, annual patterns in the variation of weekly survival were not. Likewise, individual mass (AIC_c cumulative weight = 0.999) consistently appeared in all of the top 10 models (Tables 1.2 and 1.3). Of note, in only 2 of the top 10 models did individual study units (AIC_c cumulative weight = 0.042) appear in the model structure (Tables 1.2 and 1.3). The AIC_c best of these 2 models had a ΔAIC_c value of 5.16 and only accounted for 2.8% of the total model weight (Table 1.2). Alternatively, and of primary interest to this study, models that accounted for habitat treatments (AIC_c cumulative weight for advanced treatments = 0.795, AIC_c cumulative weight for traditional treatments = 0.272) comprised the top 4 AIC_c best models (Tables 1.2 and 1.3). The single model best supported by my data was comprised of an intercept term, year, week, mass, and advanced treatment structures. Thus, this model did not distinguish between individual study units, but it partially accounted for treatment intensity (i.e., it distinguished advanced treatment units from all other units). Closely related to this top model, both in structure and model performance ($\Delta\text{AIC}_c = 1.34$), was the slightly more complex model that was built from the same structure except that it also included fawn sex. Also within ΔAIC_c of 2.0 was the AIC_c third best model which included traditional treatment effects and advanced treatment effects ($\Delta\text{AIC}_c = 1.91$). As opposed to the AIC_c best model, this model accounted for treatment intensity on all levels (i.e., reference units, traditional treatment units and advanced treatment units were all distinguished from one another). These top 3 models, based on AIC_c values, accounted for 37.6%, 19.3% and 14.5% of the total model weight, respectively. Survival estimates were also consistent between these models in that the effect of habitat treatments on survival was positive. For the AIC_c top model, the effect of advanced habitat treatments ($\hat{\beta} = 0.409$, SE=0.183) was strong. For the model in which full treatment history was included (the AIC_c third best model), advanced habitat treatment effects ($\hat{\beta} = 0.432$, SE=0.196) were much stronger than traditional treatment effects ($\hat{\beta} = 0.070$, SE=0.222). A consistent pattern was observed within models that were structured similarly in that models that accounted for all levels of treatment intensity, and thus having 2 additional parameters, received less support than models that only accounted for advanced treatments (see models 1 and 3, as well as models 2 and 4 models, Table 1.2). However, the $\hat{\beta}$ estimates for traditional treatments and advanced treatments were consistently positive throughout the results.

The AIC_c best model that did not account for habitat treatment history or intensity was marginally competitive ($\Delta AIC_c = 3.18$), but it accounted for considerably less model weight (7.7% of total model weight). Fawn sex consistently entered into several of the top AIC_c models, but models that neglected sex consistently received more support than otherwise identical models (Table 1.2). The remaining covariates of interest accounted for less than 50% of the cumulative AIC_c weight (Table 1.3), indicating that they were only present in the least supported models and did not meaningfully contribute to the overwinter survival of fawns.

In regards to annual variation in survival rates, a downward trend in survival rates, regardless of study unit type, was observed during the course of the study (Fig. 1.2). However, survival rates were high during all 4 years of the study. Estimated survival rates, based on my AIC_c best model, for advanced treatment units declined from 0.866 (SE = 0.032) to 0.678 (SE = 0.051) during the 4-year study period. Similarly, based on my AIC_c third best model, estimated survival rates for traditional treatment study units declined from 0.813 (SE = 0.046) to 0.574 (SE = 0.069) and survival rates in the reference units declined from 0.801 (SE = 0.043) to 0.552 (SE = 0.056). This downward trend did not correlate with winter severity. Average temperatures and snowpack were below average during the 2005, 2006 and 2008 winters, but above average during the 2007 winter. Based on the estimates from my AIC_c best model, there was a positive effect of mass on survival probability ($\hat{\beta} = 0.096$, SE = 0.021, Fig. 1.3).

Exploratory model results helped elucidate the appropriate level of complexity and structure that could be supported by my data. While not included in the *a priori* model set, the fully interactive model in which weekly survival rates were allowed to vary both within and between years would not have been competitive ($\Delta AIC_c = 47.38$). For the exploratory models in which survival was modeled based on treatment history (i.e., data from traditional treatment units and advanced treatment units were pooled), an intermediate treatment effect was observed, but the resulting standard error was improved due to the lack of partitioning within the data ($\hat{\beta} = 0.299$, SE=0.171). However, when placed in the context of the *a priori* model set, the performance of this model appears to be primarily driven by the strong advanced treatment effect.

DISCUSSION

Based on data collected during this study, there is evidence that habitat treatments, delivered at the landscape level can improve mule deer fawn survival. However, my model results demonstrate that follow-up treatment efforts in the form of reseeding with preferred mule deer browse species and chemical control of weeds are essential to fully realize the benefits of mechanical disturbance. More specifically, while mechanical disturbance filled the crucial role of opening up the forest canopy and reducing vegetative competition with mature trees, there likely was not a rich enough native browse seed base to benefit mule deer. While these results were quite strong, I note that my study did not assess mule deer survival immediately following mechanical disturbance. While the possibility exists that traditional treatment units experienced an increase in fawn survival immediately following the delivery of the habitat treatments, with a subsequent decline in survival rates as the treatment effect wore off, my study would not have detected such a result. If this phenomenon occurred, it highlights the potential longevity of the effects of habitat management, given that the average time since delivery of habitat treatments in the traditional treatment study units was 10 years. Alternatively, traditional treatment study units in my study may have never experienced the peak survival rates that were observed in the advanced treatment units. Regardless of which scenario reflects truth, the importance of following-up on mechanical treatments is apparent. In particular, the average survival rate for advanced treatment study units was 0.767 (SE = 0.085) during the 4 year study, whereas it was 0.675 (SE = 0.112) for traditional treatment and reference units. This difference reflects a 1.14× magnitude increase in advanced treatment units. When traditional treatment and reference units are separated, this difference in survival reflects a 1.12× magnitude increase over traditional treatment units and a 1.15× magnitude increase over reference units. Similarly, and despite not being supported as the AIC_c best model, survival estimates from traditional treatment units reflect a 1.03× magnitude increase in survival beyond that observed in reference units. Thus, while the effectiveness of traditional habitat treatment practices is uncertain, having follow-up treatments as part of the overall planned treatment process is a viable management strategy for mule deer populations.

While the increase in survival between types of study units was not surprising, the lack of a true manipulative experimental design does not rule out that other variables were correlated with the treatment definitions. Of note, the advanced treatment study units were all located on State Wildlife Areas. However, these areas were acquired primarily as mitigation offsets for development projects that occurred on nearby mule deer winter range. Thus, while they constitute mule deer winter range, they were not believed to be intrinsically better in quality than surrounding federally owned lands. Similarly, while my results indicate a strong correlation between advanced treatment efforts and mule deer fawn survival, there could have been an alternative, unmeasured, variable associated with the areas that caused this result.

Based on the $\hat{\beta}$ estimates from my AIC$_c$ top model, advanced habitat treatment efforts provide a substantial boost beyond the increased overwinter survival of mule deer fawns that was observed in traditional treatment and reference areas. Fortunately, in most cases the delivery of advanced treatment efforts (i.e., follow-up reseeding or chemical control of undesirable species) can be incorporated into an original habitat management plan. In many cases, especially on federally managed lands, the planning and implementation process for delivering mechanical habitat treatments includes acquiring National Environmental Policy Act (NEPA) and archaeological clearances as well as writing a formal Environmental Impact Statement (EIS). Due to the fact that the primary disturbance occurs during the traditional treatment stage, extending the treatment to include advanced treatment activities (e.g., follow-up use of herbicide or reseeding) would require minimal additional cost or time, as compared to the costs associated with the initial treatment. However, the benefits of traditional habitat treatment efforts should not be trivialized. Traditional habitat treatment methods were an essential step in the advanced habitat treatment process. In some areas, particularly those with rich native browse seed banks and high annual moisture, the necessity of follow-up treatments may be diminished.

The declining trend in annual survival rates observed during this study was not expected, although it has not been cause for alarm. In comparison to long-term overwinter survival rates of mule deer fawns in Colorado (Unsworth et al. 1999, Lukacs et al. 2009), the survival rates observed as part of my study were high. Only during the last year of this study was a survival rate observed to be below those reported by Lukacs et al. (2009). If a more severe winter had occurred during this study, the observed differences in survival between advanced treatment, traditional treatment and reference units probably would have been further exacerbated. Despite the fact that week was repeatedly observed in my top models, no discernable trend was observed across weeks. No obvious biological processes that explain the phenomenon were observed during the study and this result is likely an artifact of the sample size and data collection method used. As was expected, based on existing literature (Bartmann et al. 1992, Bishop et al. 2009), fawns that had greater mass at the time of capture experienced higher survival (Fig. 1.3).

Historically, in reaction to mule deer population declines, managers have been faced with increased pressure to implement immediate management actions. In many cases, this pressure is focused on predator control actions. While past research has demonstrated that predator control over large geographic areas has little effect on mule deer population performance (Bartmann et al. 1992, Hurley et al. 2011), this study provides evidence that an alternative strategy, habitat management, does have a positive effect on key population parameters. Ultimately, to be most informative to natural resource managers and to truly test the response of mule deer to habitat manipulation efforts, this study should be replicated using classical experimental designs. While finding access to large, untreated tracts of land will likely be a limiting factor, an experimental assessment of different mechanical disturbance techniques (i.e., roller-chopping and hydro-axing) will ultimately allow managers to learn which technique is ideal for different conditions and how to optimally invest limited resources. Similarly, future research should explore the longevity of treatment effects and the utility of repeated follow-up, additional treatments. These last 2 steps are of increasing importance as mule deer face expanding loss of habitat to different types of development.

MANAGEMENT IMPLICATIONS

This study provides a key piece of information that can be used to help wildlife and land managers justify the implementation of large-scale habitat treatments for the benefit of mule deer. In areas that are facing dramatic habitat loss, such as in areas of high urban development or in areas with high levels of natural resource extraction (i.e., oil, natural gas, coal or mineral extraction), this study can be used to help justify the use of mechanical and chemical habitat treatments as a tool to mitigate potential losses to mule deer populations.

Table 1.1. Comparison of size and treatment history of study units used to assess the effect of mechanical habitat improvement efforts on the overwinter survival of 6-month old mule deer fawns in southwest Colorado.

Study Unit	**Study Unit Type**	**Study Unit Size (km^2)**	**Area Treated (km^2)**	**Year Treated**
A –Sowbelly and Tatum Draws	Reference	94.4	0	
B – Peach Orchard Point	Advanced Treatment	50.7	4.5	2001
C – Cushman Mesa	Traditional Treatment	30.4	2.0	2001
D – Shavano Valley	Traditional Treatment	87.3	7.3	2004
E - Colona	Traditional Treatment	27.1	1.1	2003
F – McKenzie Buttes	Traditional Treatment	19.3	2.5	2004
G - Beaton Creek	Reference	23.4	0	
H - Billy Creek	Advanced Treatment	25.3	1.7	1998

Table 1.2. Model selection results of overwinter survival analysis of 6-month old mule deer fawns from different study units in southwestern Colorado. Model selection is based on Akaike's Information Criterion that has been corrected for small sample size (AIC$_c$). Models were constructed with an intercept (Int) and year (Yr) as a 3 parameter offset. Models could be comprised of effects including year, week, mass, traditional treatments (Trt), advanced treatments (Ad. Trt) and individual study units (Area).

Model #	**Model Structure**	**Δ AICc**	**AICc Weight**	**Model Likelihood**	***k***[a]
1	Int + Yr + Week + Mass + Ad. Trt	0.00[b]	0.376	1.00	29
2	Int + Yr + Week + Mass + Sex + Ad. Trt	1.34	0.193	0.51	30
3	Int + Yr + Week + Mass + Trt + Ad. Trt	1.91	0.145	0.38	30
4	Int + Yr + Week + Mass + Sex + Trt + Ad. Trt	3.17	0.077	0.21	31
5	Int + Yr + Week + Mass	3.18	0.077	0.20	28
6	Int + Yr + Week + Mass + Sex	4.66	0.037	0.10	29
7	Int + Yr + Week + Mass + Trt	4.83	0.034	0.09	29
8	Int + Yr + Week + Mass + Area	5.16	0.028	0.08	35
9	Int + Yr + Week + Mass + Sex + Trt	6.39	0.015	0.04	30
10	Int + Yr + Week + Mass + Sex + Area	6.73	0.013	0.03	36

[a] Accounting for parameters is as follows: Int = 1, Yr = 3, Week = 23, Mass = 1, Trt = 1, Ad. Trt = 1, Sex = 1, Area = 7

[b] AIC*c* value for the top model was 1404.77

Table 1.3. Cumulative weights for Akaike Information Criterion values, corrected for small sample size (AIC_c), for all covariates that were included in the suite of mule deer fawn survival models.

Covariate	**Cumulative AIC_c Weight**
Mass	0.999
Year	0.998
Week	0.997
Advanced Treatment	0.795
Sex	0.337
Traditional Treatment	0.272
Area	0.042

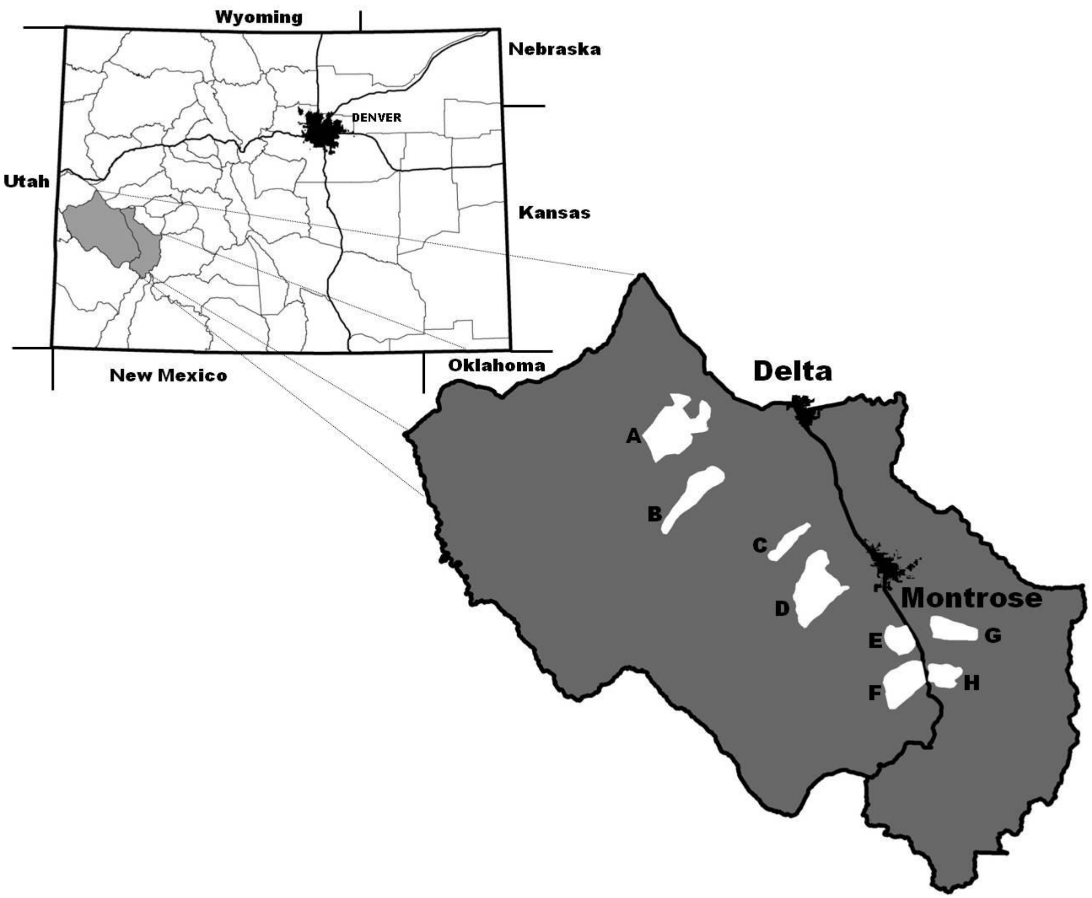

Figure 1.1. Map of Colorado depicting Data Analysis Unit (DAU) boundaries and the general study area located on the Uncompahgre Plateau and neighboring valleys in the San Juan Mountains in southwest Colorado. The general study area (solid gray DAUs), which encompassed the 8 study units (white polygons) is shown in relation to the surrounding communities of Delta and Montrose, Colorado (black polygons).

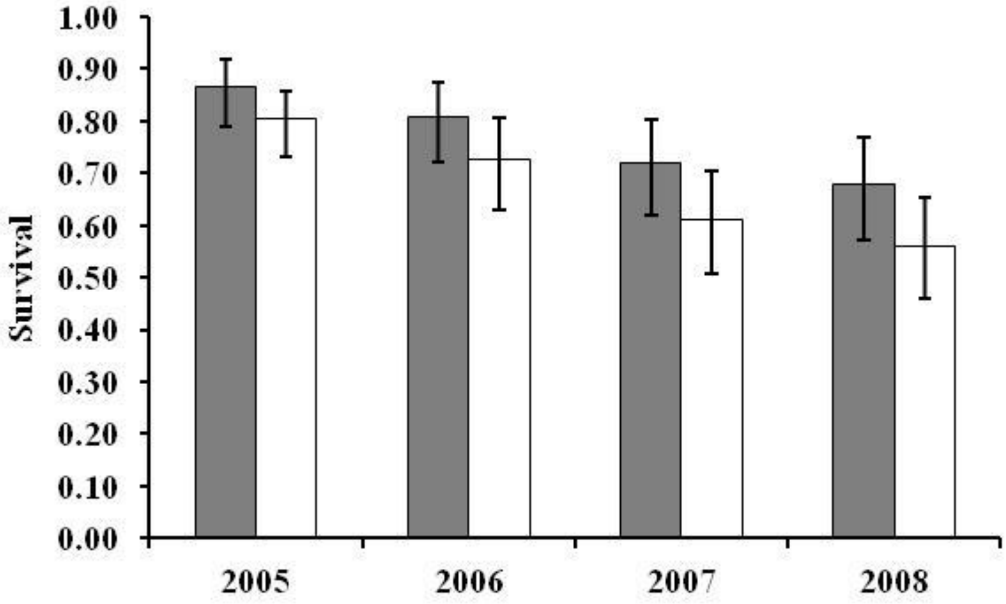

Figure 1.2. The difference in derived overwinter survival rates, with 95% confidence intervals, of 6-month old mule deer fawns from study units in southwestern Colorado. Dark gray bars reflect annual survival estimates of fawns from advanced treatment study units and white bars reflect survival estimates of fawns from traditional treatment and reference study units.

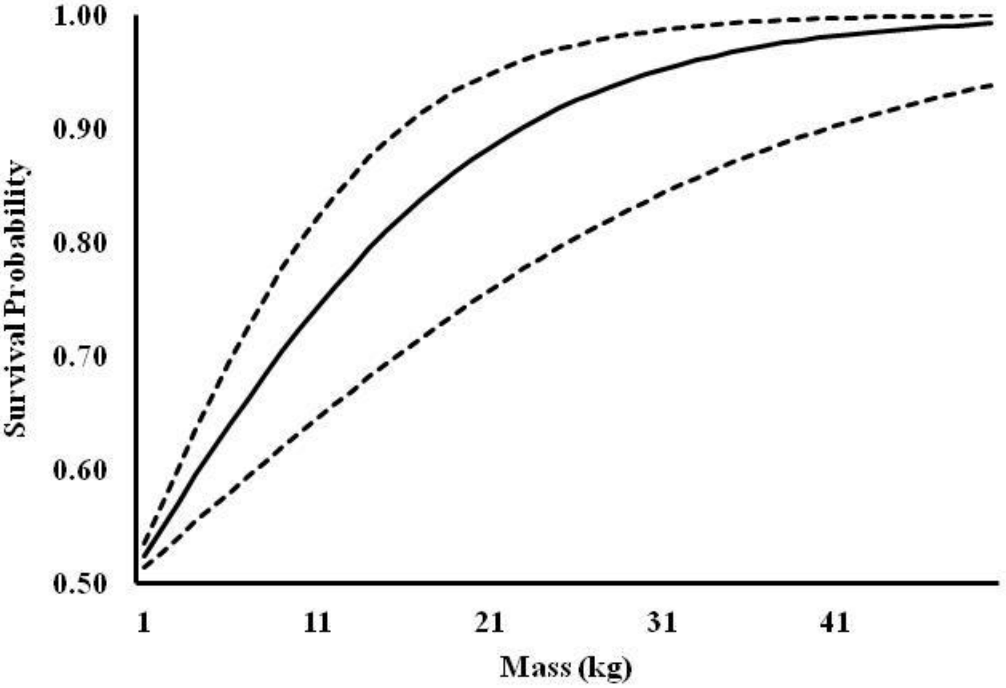

Figure 1.3. The effect of mass (with 95% confidence intervals) on overwinter survival of mule deer fawns between 2005 and 2008 in southwestern Colorado. Observed mass of fawns ranged between 21.4 kg and 48.6 kg. A consistent relationship between sex of fawn and survival was not observed.

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CHAPTER 2

Response of Mule Deer Density to Habitat Management in Colorado

The suite of demands competing for wildlife management funds necessitates direct assessment of management decisions, especially when these decisions have direct costs, as well as tangible opportunity costs. A specific example of such a decision includes habitat management for mule deer (*Odocoileus hemionus*), for which the opportunity cost of delivering habitat treatments may be the acquisition of new lands or conservation easements that increase the quantity of habitat. Estimating direct effects of management decisions on mule deer density has also been difficult. However, recent advancements in abundance estimation methodologies have made estimating abundance and density more reliable than in the past. I conducted a mark-resight study that estimated mule deer density across multiple study units that had been exposed to different intensities of habitat treatments on the eastern slope of the Uncompahgre Plateau and in neighboring drainages of the San Juan mountain range in southwest Colorado. My treatments were comprised of common habitat management techniques including hydro-axe and roller-chopper disturbances, as well chemical control of weeds and reseeding with desirable mule deer browse species. Reference study units received no habitat management treatments. Resighting probabilities (range 0.070–0.567) were best modeled as an interactive function of study unit and year, although sampling method was also important. Total deer densities varied between 20–84 deer/km^2 in southern study units and 4–12 deer/km^2 in northern study units. A consistent pattern of higher deer density on advanced treatment study units was not observed despite its being the primary hypothesis of the study. I recommend that if population density is to be used as a population response variable, it only be used in tandem with other, possibly more sensitive parameters, such as overwinter survival or late winter body condition.

INTRODUCTION

As wildlife managers implement management actions, assessing the impact of those actions on populations is desirable and necessary in order to improve the management process. However, knowing which population parameters will be most affected by management decisions is not always intuitive. As an example, habitat management has been a key consideration for wildlife, and specifically for mule deer (*Odocoileus hemionus*), for many decades (Leopold 1933, Wallmo 1981). However, assessment of habitat management efforts has not been routine. When assessment has occurred, it has typically focused on indirect response variables such as plant abundance, plant diversity or changes to mule deer distribution in treated areas (Barnitz et al. 1990, Kufeld 1983, Anderson 1969, Long et al. 2008) with impacts on deer density largely assumed or implied. While these earlier efforts have been informative, the suite of demands competing for wildlife management funds necessitates a more direct assessment of the effectiveness of habitat management actions.

In particular to Colorado, many wildlife managers, biologists, hunters and other user groups desire stable or increasing mule deer populations. However, as the quantity of mule deer habitat decreases due to a suite of factors (e.g., exurban development, development associated with energy extraction, or long-term plant community succession), wildlife managers and biologists have renewed interest in maximizing the quality of remaining habitat. This interest has become specifically focused on habitat treatments. Historically, treatments included burning and chaining (Kufeld 1983), but more recently have focused on hydro-axe and roller-chopper treatments (Watkins et al. 2007). However, implementation of habitat treatments is usually expensive. In the face of limited financial resources, delivery of habitat treatments also comes with the opportunity cost of acquiring new lands or implementing conservation easements that increase the quantity of habitat. To help inform decisions pertaining to this trade-off, Colorado's wildlife managers and biologists expressed interest in an evaluation of the effectiveness of current habitat management techniques.

While the most desirable population parameters for managers, and the easiest ones for use in dialog with hunters and other user groups, are density and abundance, assessments of vital rates (e.g., survival) are often more robust. Estimating abundance with a satisfactory level of precision is often cost, and time, prohibitive. Thus, many population management decisions have been tailored such that the decision process is informed by finer scale parameters such as reproductive rates, nesting rates, survival rates or population sex and age ratios while abundance is derived through a modeling approach (e.g., White and Lubow 2002). Of note, methodologies that allow abundance to be derived via population models are often poorly understood and commonly not trusted by interested user groups (e.g., Freddy et al. 2004). Thus, for harvest and population management decision making purposes, managers often rely on vital rate parameters and population modeling (e.g., White and Lubow 2002), yet for communication purposes managers primarily rely on abundance estimates (e.g., Freddy et al. 2004).

Despite the high cost and high level of effort associated with estimating abundance, several advancements have been made in abundance estimation methodologies during the past 3 decades. These advancements, tied to the merger of new analytical techniques with more efficient computing, have led to a situation in which biologists and managers are now presented with many different approaches to estimate abundance. With respect to large mammals, mark-resight models (McClintock and White 2007, Keech et al. 2011), sightability models (Samuel et al. 1987, Ackerman 1988, Anderson and Lindzey 1996, Walsh et al. 2009), population quadrat sampling (Gill 1969, Kufeld 1980) and distance sampling (Schmidt et al. 2012) have struck a balance between cost of implementation and the desired level of precision. As can be expected, and depending on objective, different methods of abundance estimation are better suited to different situations. Mark-resight and other capture-mark-recapture methodologies have proven to be most useful when the opportunity to have a meaningful proportion of marked individuals in the population is possible.

In an attempt to provide an assessment of habitat management actions on a mule deer population, I conducted a study that estimated mule deer abundance and density across multiple study units that had been exposed to different intensities of habitat treatments. Habitat treatments ranged in intensity from repeated treatment efforts in some units to no treatments in other units. Congruent with results from other research on the same system, I predicted that the more productive population vital rates detected in habitat treatment units (see Chapter 1) would translate to higher deer densities in those same study units as compared to reference units.

STUDY AREA

I conducted this research on the eastern slope of the Uncompahgre Plateau and in neighboring drainages of the San Juan mountain range in southwest Colorado (Fig. 2.1). A total of 8 study units were identified for inclusion in this study (Table 2.1). Study units fell between 38° 15’ N and 38° 49’ N latitudes and between 107° 41’ W and 108° 28’ W longitudes. Elevations on my study units ranged between 1,670– 2,380 m. All study units were comprised of pinyon pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) forests interspersed with open meadows. Forest openings typically held browse and grass species (sagebrush (*Artemesia spp.*), cliffrose (*Purshia mexicana*), antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus spp.*), rabbittbrush (*Ericameria spp.*), western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), Indian ricegrass (*Achnatherum hymenoides*) and bluegrass (*Poa spp.*)). Closed canopy forests were typically late-seral stage with little or no understory vegetation. Depending on habitat treatment history (discussed below), vegetation in open canopy settings varied between late-seral stage, browse dominated habitats to early-seral stage, browse-grass-forb communities. All study units were centered on public lands (U.S. Bureau of Land Management and State Wildlife Areas) although most study units had privately owned land at their lower elevations.

METHODS

Study Unit Selection

Specific study units were selected based on their habitat treatment history, with all study units being categorized as reference units (no history of habitat management), traditional treatment units (units that received a single habitat treatment effort) or advanced treatment units (units that received a traditional habitat treatment as well as a follow-up treatment effort). Habitat treatments were comprised of mechanical disturbance in the form of rollerchopper and hydro-axe treatments. Rollerchopper treatments were delivered by pulling a large drum affixed with perpendicular blades behind a tracked bulldozer. As part of the rollerchopping process, the bulldozer uprooted trees and other vegetation and subsequently pulled the drum over the newly downed vegetation, breaking it into smaller pieces. Rollerchopper treatments were effective at treating larger areas, but at a less refined scale (Watkins et al. 2007). Hydro-axe treatments were delivered by a boom-mounted mulching blade affixed to a reticulated, wheeled tractor. A hydro-axe was capable of mulching individual, living trees to ground level and thus capable of a more refined approach to treating the landscape than rollerchopping (Watkins et al. 2007). Advanced habitat treatment efforts included vegetative reseeding and chemical control of weeds on the same piece of ground that had received a traditional habitat treatment.

In the case of traditional and advanced habitat treatment units, initial habitat treatments were delivered within the previous 2–8 years (see Chapter 1). I deliberately elected to not incorporate study units that had received mechanical treatments within the previous 1–2 years due to uncertainty about time lags in the vegetative response following mechanical disturbance. For advanced treatment units, follow-up treatments were implemented at the same time as the deer population monitoring efforts in this study. In order to more accurately assess the effectiveness of habitat treatment efforts, and to help control for spatial variation in landscape features and weather patterns, advanced treatment units were spatially paired with reference units. In particular, *a priori* knowledge regarding lower annual precipitation at northern latitudes in the greater study area influenced this stratification (Fig. 2.1). Two study units were paired in the northern portion of the greater study area. The northernmost of these, Sowbelly, was a reference unit and Peach Orchard Point (Peach) was an advanced treatment study unit. A third study unit, Transfer Road (Transfer), was also located in the northern portion of the greater study area (Fig. 2.1) and was a traditional treatment study unit. All remaining study units were located in the southern portion of the greater study area. Shavano Valley (Shavano), Colona Tract (Colona) and McKenzie Buttes (McKenzie) were all traditional treatment study units (Fig. 2.1). The southernmost study unit was Billy Creek State Wildlife Area (BCSWA; Fig. 2.1). BCSWA was the southern advanced treatment study unit for which Buckhorn Mountain (Buckhorn) was the paired reference study unit. Mule deer abundance and density were estimated in Sowbelly, Peach, BCSWA and Buckhorn during 4 consecutive years (2006–2009). Abundance and density were estimated on the Shavano, Colona, McKenzie and Transfer study units during 2006, 2007, 2008, and 2009, respectively.

Winter severity data were collected from the Natural Resource Conservation Service (NRCS) National Water and Climate Center (NWCC). Mean daily snow depth data for the month of March from 2 sites, Columbine Pass (2004–2009) and Red Mountain Pass (1999–2009), were used as relative indicators of annual winter severity on my study units. Both weather stations were located within the same drainage but at higher elevations than my study units. Snow data from the site located at Columbine Pass were used as an indicator for my 3 northern study units, whereas data from Red Mountain Pass were used as an indicator for my 5 southern study sites.

Deer -Marking

Mule deer were captured and marked as part of a larger research project (see Chapter 1). All deer were captured either by helicopter net-gunning (Webb et al. 2008, Jacques et al. 2009) or baited drop-nets (Ramsey 1968, Schmidt et al. 1978, White and Bartmann 1994). Capture, handling and radio-collaring procedures for all aspects of this study were approved by the Institutional Animal Care and Use Committees at Colorado Parks and Wildlife (protocol #10-2005) and Colorado State University (protocol #08-2006A).

The marked sample of deer available for my resighting flights included 6-month old fawns as well as adult females. All marked deer came from 1 of 3 different subsets of animals. The first subset was comprised of 6-month old fawns. At the onset of each winter (late November through early December), 25 fawns were captured and fitted with VHF radio collars (Lotek, Inc., Newmarket, ON, Canada) on each study unit. All radio collars were constructed with tan canvas belting. To enhance visual detection by observers, either white or yellow rubber neckband material was sewn to the sides and top of each radio collar. The second subset of marked animals was comprised of adult female mule deer that were captured in early March of each winter for body condition scoring purposes (E. Bergman, Colorado Parks and Wildlife, unpublished data). Thirty adult females were captured on each of 2 study units each winter. During the first winter (2006), these deer were captured on the Sowbelly and BCSWA study units. During the final three winters (2007–2009), these deer were captured on the Buckhorn and BCSWA study units. During the winters of 2006 and 2007, adult females were fitted with VHF radio collars similar to those deployed on mule deer fawns. During the winters of 2008 and 2009, adult females were fitted with temporary neckbands that were either yellow (2008) or blue (2009) in color. The final subset of marked animals was comprised of residual animals from earlier research projects (Bishop et al. 2009, Lukacs et al. 2009). This final subset of animals was unique to the Colona and Shavano study units. Some animals that had been fitted with VHF collars as part of these completed projects were still alive and relocated on these study units. Regardless of which subset animals came from, and regardless of which study unit animals were located on, marks could not be individually identified by observation during resighting flights. Thus, all deer that were encountered on flights were classified as either marked or unmarked.

Due to concerns regarding the assumption of population closure, the total number of VHF marked deer that were available to be seen on each study unit during each aerial survey was determined for each day that a survey occurred. For adult females fitted with neckbands, a similar determination could not be made so I assumed that these deer were available to be seen during each survey. Based on published survival rates of adult female deer in this area (Bishop et al. 2009, Lukacs et al. 2009), the daily survival rate of these animals was likely high ($\hat{S}$ = 0.999), lending support to this assumption. Likewise, the mid-winter immigration and emigration rates of deer on these study units, based on the radio collared subset of deer, was negligible (see Chapter 1), lending support to the assumption that departure from the study units did not occur following capture.

Aerial Surveys

Each year, aerial surveys were conducted during the last 2 weeks of March using a Bell 47-Soloy helicopter with a pilot and 2 observers. Study units were surveyed 3–6 times each year. All surveys were flown at 55–80 km/hour and 15–45 meters above the ground. Surveys were typically conducted on consecutive days, although due to weather delays and other conflicts this was not always possible. The same pilot and main observer were used on all flights. The second observer varied among years and occasionally among flights within a year. The sampling boundaries for each study unit were defined on a yearly basis by relocation data collected from radio-collared deer. If less than 1 hour of flight time was needed to survey an entire study unit, then the entire unit was sampled on each flight. Four of my study units—Sowbelly, Peach, Transfer, and McKenzie—were too large to be completely surveyed within 1 hour. For these units, a random flight path within the study unit was generated. Random flight paths were created by overlaying each study unit with a grid composed of 1 km^2 cells. To generate random flight paths, 10 cells were randomly selected, without replacement, and a flight path that efficiently incorporated each of these cells was then generated. Because the entire flight path was within the defined sampling area, all observed deer were classified, regardless if they fell within a random cell or not. Random flight paths were used for 1 flight and then replaced by new random flight paths for each subsequent flight. Due to the random process used to generate flight paths over the larger study units, all marked animals had an equal probability of being available under each flight path. Due to the different sampling procedures, resighting probabilities were not immediately comparable among study units. For smaller study units, every marked animal had the opportunity to be observed during each flight. For larger study units that were sampled using random flight paths, resighting probabilities were the product of the probability of being available for detection under a flight path and the probability of being detected.

Data Analysis

All data were analyzed using mark-resight models (McClintock and White 2011) in Program MARK (White and Burnham 1999). Mark-resight models largely replicate the results of the joint hypergeometric maximum likelihood estimator utilized in program NOREMARK (White 1996), but also provide the ability to model resighting probabilities and the ability to compare model results using model selection theory (Burham and Anderson 2002). Logit-normal models were used for all analyses due to the fact that the exact number of marked animals on each study unit was either known or assumed to be known with a high degree of confidence. However, marked animals could not be individually identified during aerial surveys. Due to the fact that marked deer could not be individually identified, the parameter used to estimate the variance of individual heterogeneity (σ^2) in resighting probability (p) was fixed at 0 for all models. A single abundance estimate was calculated for each study unit during each winter. Logit-normal models allow for a high degree of flexibility in the estimation of resighting probabilities. To explore this aspect of mark-resight abundance estimation, I built a model set composed of 19 models. For the simplest model, a single estimate for resighting probability was utilized (i.e., no spatial or temporal patterns were incorporated). More complex models allowed resighting probabilities to vary among years, study units and flights within a single year. Models were also structured to allow resighting probabilities to vary based on sampling method (i.e., smaller study units were completely surveyed during each flight, whereas larger study units were only partially surveyed using random flight paths). In order to make comparisons about the relative importance of the different factors that influenced resighting probability on my flights, all possible combinations of additive models and multiplicative interaction models were built, as suggested by Doherty et al. (2012).

RESULTS

Mean daily snow depth during March at Columbine Pass, for the period on record (2004–2009), was 1.297m (SD = 0.278m). For the 2006–2009 time period, March snow depths were below average every year except for 2008, during which the mean daily snow depth was 0.215m more than the 6-year average (Fig. 2.2). The 10-year (2000–2009) mean snow depth at Red Mountain Pass was 1.644m (SD = 0.285m). As was the case with Columbine Pass, mean daily snow depths at Red Mountain Pass were below the long-term average for 2006–2009 except for 2008 when the snow depth was 0.528m more than the 10-year mean (Fig. 2.2).

Over the course of 4 years, late winter abundance and density estimates were calculated for the 8 different study units. During the first winter of the study, sampling effort was less than during subsequent years (Table 2.1). Based on estimates from the first winter, sampling effort (i.e., the number of helicopter resight flights) was increased in all study units to improve the precision of estimates (Table 2.1). The area surveyed, as dictated by deer relocation data collected each winter, showed moderate variation among years (Table 2.1). The area surveyed for my southern study unit pairing (BCSWA and Buckhorn) varied between 19–27 km^2, whereas my northern study unit pairing (Peach and Sowbelly) varied between 47–94 km^2. Comparison among years for the remaining study units was not possible as these units were only surveyed during a single year (Table 2.1). Based on the above average snowpack during 2008, a reduction in area sample was expected in all sites, especially the northern sites, but the only site where a reduction was observed was Sowbelly.

My top two models of resighting probabilities were most supported by my data (AIC_c weight = 0.471 and AIC_c weight = 0.466, respectively; Table 2.2). The first model modeled resighting probability as an interactive function of study unit and year. The second model modeled resighting probability as an interactive function of sampling method, year, and flight and had an additional 19 parameters (Table 2.2). Year, sampling method, study unit and flight had cumulative AIC_c weights of 1.000, 0.517, 0.483, and 0.475 respectively.

Model-averaged resighting probabilities showed a high level of variation among units and years (Fig. 2.3). Estimated values ranged between 0.070–0.567. Within this, resighting probabilities tended to be lower in my northern study units (0.070–0.310) than in my southern study units (0.151–0.567, Fig. 2.3). However this result was largely driven by the different sampling methods used in large and small study sites. Based on the results from the model that only accounted for sampling method, resighting probabilities for large study units ($p = 0.203$, SE = 0.012) were less than those from smaller study units ($p = 0.414$, SE = 0.011). If the resighting probability from my smaller study units is considered to be an applicable resighting estimate for large study estimates, the probability that deer would fall within the random resight paths that were used to survey large units can be derived. Under this assumption, the probability of a deer being included in the flight path is $p = 0.490$. Finally, models built with multiplicative interaction structures consistently outperformed models with only additive effects (Table 2.2).

Total deer densities in my southern study units varied between 20–84 deer/km^2 (Fig. 2.4). Despite the fact that my southern study units tended to have more marked deer available for resighting, the large number of deer in each southern unit resulted in a relatively low proportion of marked individuals. The mean estimate of the proportion of marked individuals varied between 0.016–0.146 for my southern study units. The coefficient of variation for density estimates in my southern study units ranged between 0.053–0.294. I observed a consistent trend of higher mule deer density in my reference study units than in my advanced treatment and traditional treatment study units (Fig. 2.4). This result was in stark contrast to my *a priori* predictions that advanced treatment study units would have higher deer densities and greater overall abundance.

Deer densities on my northern study units varied between 4–12 deer/km^2. The mean estimate of the proportion of marked individuals in the northern study units varied between 0.044–0.096. The coefficient of variation for density estimates in my northern study units ranged between 0.107–0.417. Density estimates for the traditional treatment study units, located between the northern and southern unit pairings varied between 5.775–36.949 deer/km^2 (Fig. 2.4). The trend of higher deer density in my reference study units on southern study units was not as evident in my northern units (Fig. 2.4). Overall, my *a priori* hypotheses were not supported by my results.

DISCUSSION

As expected, resighting probabilities differed between large and small study units. For large study units, the estimated resighting probabilities were the product of the probability of being available to be observed and the probability being observed (i.e., the probability that an animal was present under a random flight path and was then seen). As study unit size transitions from large to small, the probability of an animal being under the randomly generated flight path should increase. This pattern can generally be observed in McKenzie and Cushman which had respectively larger areas surveyed (Table 2.1) and respectively smaller resighting probabilities

(Fig. 2.3). Based on published visibility results, my resighting probabilities aligned with rates reported for smaller group sizes of animals and higher percentage of vegetation cover (Samuel et al. 1987).

Based on patterns of deer density in my study units, density of mule deer on reference units appeared to be more dynamic than on units that had been exposed to habitat treatment efforts. This result may be more appropriately viewed as a stabilization of winter range deer density that stemmed from habitat management efforts. However, a consistent pattern of higher deer density on advanced treatment study units was not observed, as I had hypothesized.

A general trend in deer density among my northern study units was difficult to infer (Fig. 2.4). During the 2007 and 2009 winters, no apparent difference in mule deer density occurred between my reference and advanced treatment study units (Fig. 2.4). An increase in density was observed on my reference study unit during 2008, as compared to other years and other study units (Fig. 2.4), but this was likely due to a reduction in winter range availability caused by the above average snowpack (Fig. 2.2).

A more distinct pattern in density was observed in my southern study units (Fig. 2.4). However, this pattern did not follow the prediction that higher densities would be observed in my advanced treatment study units (Fig. 2.4). As was the case in my northern study units, I believe the above average snowpack during 2008 caused a spike in deer density on my southern reference unit. If this data point is viewed as a stochastic outlier, a declining trend in deer density on my southern reference unit can be observed.

As noted, my initial prediction was that habitat treatment management actions would result in greater densities of deer on treated landscapes. This prediction largely paralleled the predictions and results of simultaneous research (see Chapter 1). This simultaneous research, which was conducted on the same study units during the same time frame as my mark-resight density estimation flights, showed a 1.15× magnitude increase in overwinter survival rates of mule deer fawns on advanced treatment study units (see Chapter 1). This documented increase in survival was directly linked to the advanced habitat treatment management actions and was expected to result in higher densities of deer. However, the specific management actions that defined advanced treatment units were only implemented as part of this research project during the summer of 2006 in Peach and during the summers of 2006 and 2007 in BCSWA. If increases in overall density were to occur, they likely would have been easier to detect after the increased survival of fawns had been allowed to compound for a longer period of time.

Alternatively, if the downward trend in density observed on the Buckhorn reference study unit during 2006, 2007 and 2009 (Fig. 2.4) reflected a true population trajectory, the lack of a similar trend on BCSWA may be important. If habitat management can lead to a local stabilization in density in light of concurrent declines in neighboring areas, this may have important management implications.

While not predicted, the large annual variation in density estimates from individual study units demonstrates that large fluctuations in density do occur between years. However, this variation appeared to be dampened in advanced treatment study units (Fig. 2.4). This phenomenon may be attributable to habitat management efforts. Likewise, annual variability in winter severity likely explains the spike in density observed on my reference units during 2008. The relationship between increasing snow depth at higher elevations and the concentration of animals on limited, lower elevation habitat has been established for several species (Gilbert 1970, Bruggeman et al. 2009). Presumably, as conditions at higher elevations were less accommodating during the 2008 winter, overall density should have increased on all study units as deer moved to lower elevations. As my data suggest, this did occur on my reference study units, but not on my advanced treatment study units. I speculate that deer that traditionally spent winter on study units that had experienced habitat improvement efforts did not face the same food limitation stress as deer that wintered on reference units and thus moved regardless of winter severity. A similar phenomenon with spring migration has been observed in that various species follow the spring plant phenologic progression of green-up (Mysterud et al. 2001). The behavior I believe to be occurring as part of the downward migration is driven by a building snowpack that forces animals out of summer and transition ranges. Specifically, deer that overwinter on habitat that offers poorer quality, and less abundant forage, are more reluctant to move down in elevation (i.e., leave summer and transition range) and only do so when confronted with extreme conditions. Individuals that anticipate high quality habitat and abundant forage will move prior to being forced off of summer range.

Ultimately, the use of density as a population response parameter for habitat assessment, as my results demonstrate, may not be ideal. Similar conclusions have been reached in the past (Van Horne 1983, Hobbs and Hanley 1990). In particular, simulation models presented by Hobbs and Hanley (1990) provide an explanation that aligns well with my results as well as from other research in my study system (see Chapter 1). Hobbs and Hanley (1990) demonstrated that animals living in habitat with lower resource quality may subsequently experience a lower level of reproductive output. For populations to be maintained under these conditions, a higher density of productive animals is necessary. As demonstrated by my earlier results (see Chapter 1), overwinter survival of 6-month old mule deer fawns was lower in my reference study units. When lower juvenile survival rates and higher overall densities are considered in tandem, they can be viewed as evidence that my reference study units may have been near their local carrying capacity. This conclusion may be further validated if the potential downward trend in density on my southern reference study unit is viewed as an actual population trajectory and not a spurious effect.

Evaluation of habitat management actions, especially when financial resources are limited, is important to judge the effectiveness of actions and dollars invested. Within this, a simultaneous assessment of different population parameters is prudent. Despite a relatively high level of effort, as well as a relatively high financial cost, the density and abundance estimation procedures I employed were not particularly sensitive. My results likely would have improved had this study been extended to include additional years of data collection. Likewise, inference from my study is limited by the fact that I had a functional sample size of 2 study areas. Replication over additional reference and advanced treatment study unit pairings would have been beneficial, but difficult to achieve with appropriate spatial scales and available finances. Similarly, my level of precision would have improved had I been able to individually identify marked deer as part of the resighting process. Overall, my results suggest that finer scale response variables (e.g., survival of young or overall body condition) may be most appropriate for assessing the wildlife population-habitat relationship versus density estimation.

MANAGEMENT IMPLICATIONS

For population management purposes, the use of change in ungulate density as a metric for assessing impacts to the environment is often desired. Examples of such scenarios may include population response to urban development and expansion, response to natural resource extraction (i.e., mining), and more recently, population response to climate change. Despite this desire, abundance and density may not be appropriate response variables. My research did not conclusively link the response of deer density to habitat change. Ultimately, if population abundance and density are to be used as population response variables, I encourage their use in tandem with other fine scale population response variables such as survival rates and body condition.

Table 2.1. The number of marked mule deer (with number of resight flights) that were utilized to estimate abundance and density in each of 8 study units on the Uncompahgre Plateau in southwest Colorado. The number of marked animals in each unit could decrease between flights due to mortality. The number of available marks increased between observation surveys as additional animals were captured as part of a separate research project. The area surveyed (km^2) for each study unit varied among years.

Unit	2006	2007	2008	2009
Sowbelly	10 & 40 (5)[a]	43 (6)	20 (6)	28 (5)
Area Surveyed	67 km^2	85 km^2	47 km^2	94 km^2
Peach	20 (5)	24 (6)	22 (6)	19 & 18 (5)[b]
Area Surveyed	52 km^2	51 km^2	84 km^2	82 km^2
Transfer				18 (4)
Area Surveyed				49 km^2
Shavano	23 (3)			
Area Surveyed	27 km^2			
Colona		64 (5)		
Area Surveyed		15 km^2		
McKenzie			20 (5)	
Area Surveyed			31 km^2	
Buckhorn	18 (3)	47 (5)	61 (5)	24 (4)
Area Surveyed	20 km^2	19 km^2	19 km^2	27 km^2
BCSWA	24 & 23 (3)[c]	68 & 65 (5)[d]	76 & 75 (5)[e]	54 (4)
Area Surveyed	23 km^2	19 km^2	19 km^2	24 km^2

[a] 10 marks available on Flights 1 through 3, 40 marks available on flights 4 and 5

[b] 19 marks were available on Flight 1, 18 marks available on flights 2 through 5

[c] 24 marks available on flight 1, 23 marks available on flights 2 and 3

[d] 68 marks were available on Flights 1 through 3, 65 marks available on flights 4 and 5

[e] 76 marks were available on Flight 1, 75 marks available on flights 2 through 5

Table 2.2. Model selection results for the 7 best mark-resight abundance estimation models for mule deer (*Odocoileus hemionus*) from 8 study units on the Uncompahgre Plateau and neighboring drainages in southwest Colorado. Model evaluation is based on Akaike's Information Criterion that has been corrected for small sample size (AIC$_c$). Variation in model structure relates to the estimation of resighting probabilities (*p*). The Year covariate allowed for annual variation in *p*. The Sampling Method covariate accounted for the different sampling strategies used in large and small study units. The Study Unit and Flight covariates allowed *p* to spatially and temporally vary, respectively.

Model	ΔAIC$_c$[1]	AIC$_c$ Weight	Model Likelihood	K[2]
Study Unit * Year	0.00	0.471	1.000	40
Sampling Method * Year * Flight	0.02	0.466	0.988	59
Sampling Method * Year	4.46	0.051	0.108	28
Study Unit + Year + Flight	7.94	0.009	0.019	36
Study Unit + Year	10.54	0.002	0.005	31
Sampling Method + Year + Flight	14.09	0.001	0.001	30
Sampling Method + Year	17.15	0.000	0.000	25

[1] AIC$_C$ for the top model was 4208.33

[2] All models have 20 parameters dedicated to abundance

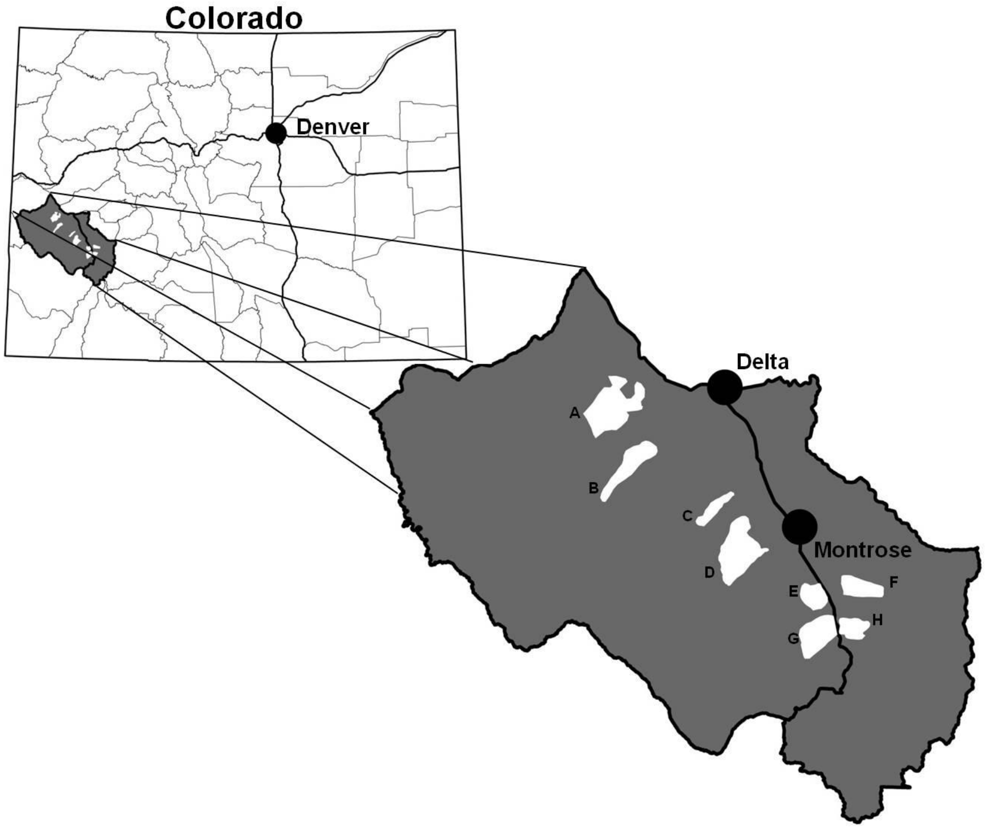


Figure 2.1. Map of Colorado depicting Data Analysis Unit (DAU) boundaries and the greater study area located on the Uncompahgre Plateau and neighboring valleys in the San Juan Mountains in southwest Colorado. The greater study area (solid gray DAUs), which encompassed the 8 study units (white polygons), is shown in relation to the surrounding communities of Delta and Montrose, Colorado (black circles). From north to south, study units included Sowbelly (A), Peach (B), Transfer (C), Shavano (D), Colona (E), Buckhorn (F), McKenzie (G), and Billy Creek State Wildlife Area (H).

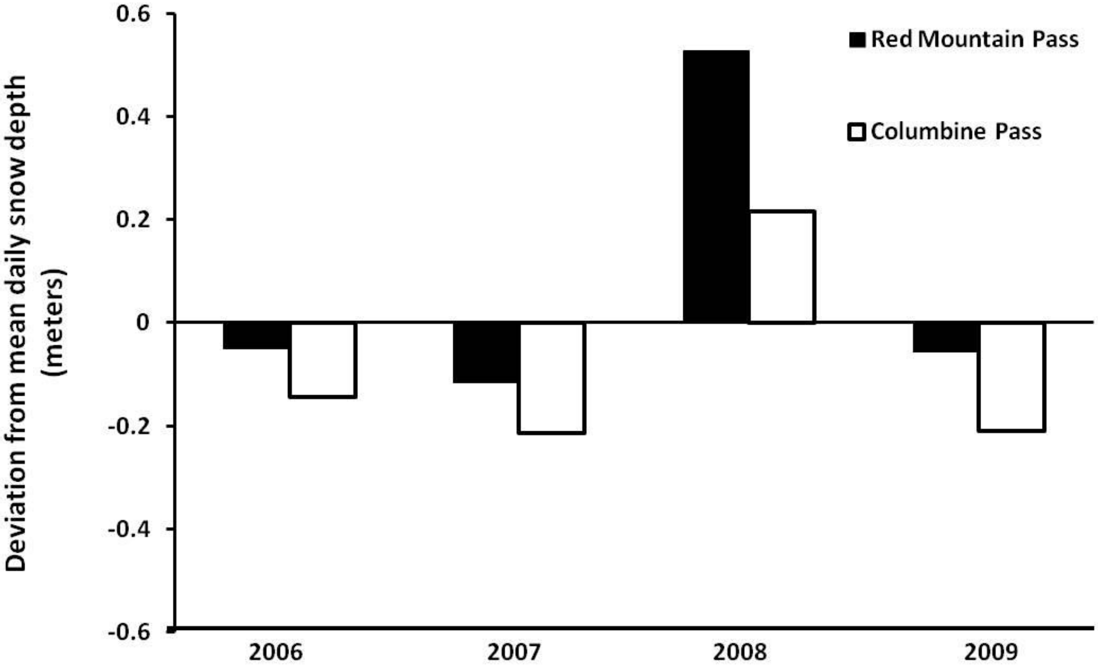


Figure 2.2. Deviation from long-term mean daily snow depths for the month of March from 2 high elevation sites near study units in southwest Colorado. Data at Red Mountain Pass during 2000–2009 (black columns) are viewed as a relative indicator of winter severity for southern study units, whereas data at Columbine Pass during 2004–2009 (white columns) are viewed as a relative indicator of winter severity for northern study units.

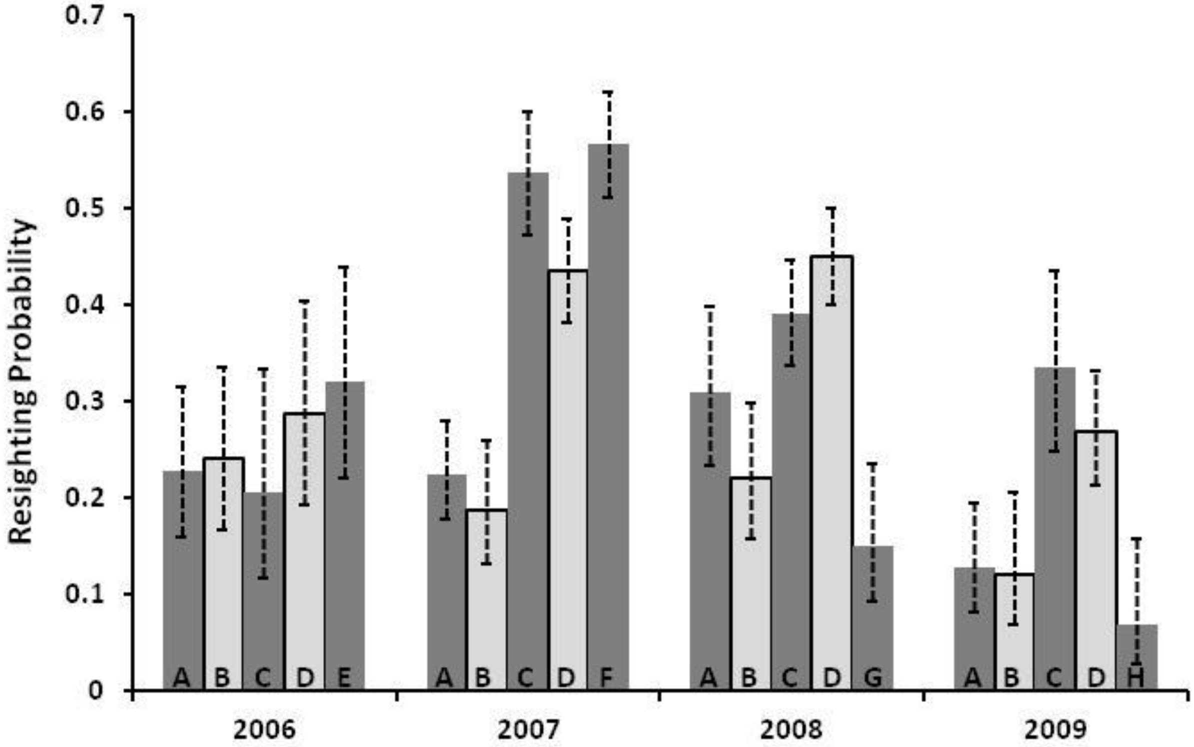
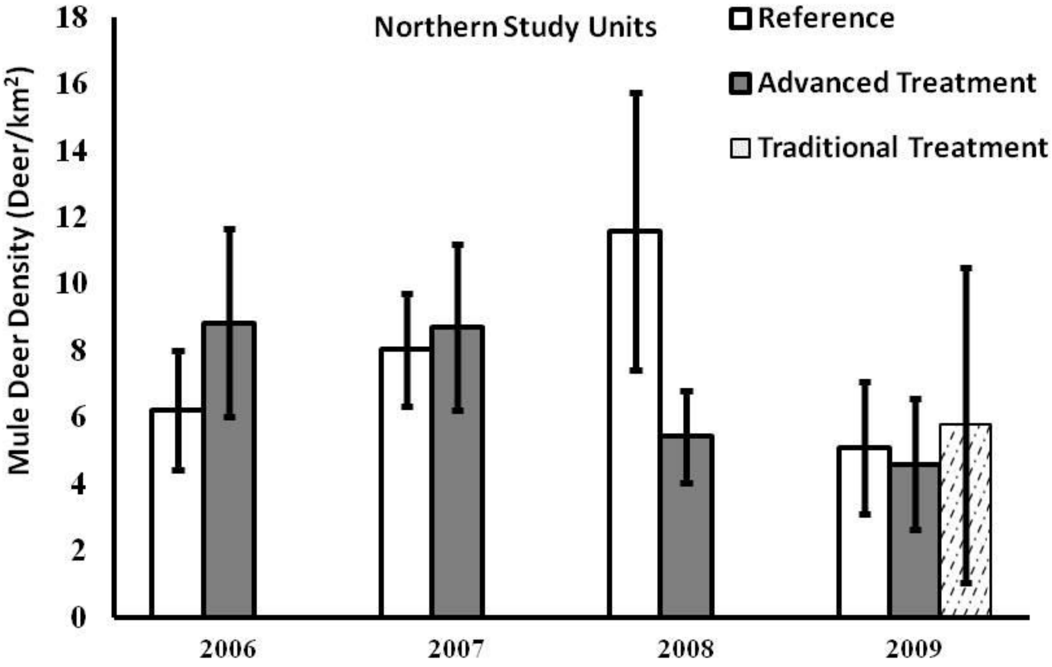


Figure 2.3. Model-averaged mark-resight resighting probabilities for Mule deer (*Odocoileus hemionus*), with 95% confidence intervals, from study units on the Uncompaghre Plateau and in neighboring drainages of the San Juan mountains in southwest Colorado. Resighting probabilities were estimated for Sowbelly (A), Peach (B), Buckhorn (C) and BCSWA (D) study units each year. Resighting probabilities were estimate for Shavano (E), Colona (F), McKenzie (G) and Transfer (H) study units during 2006, 2007, 2008 and 2009, respectively. All study units were located on low density, pinyon pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) woodland winter range.


Northern Study Units
Reference
Advanced Treatment
Traditional Treatment
Mule Deer Density (Deer/km²)
0
2
4
6
8
10
12
14
16
18
2006
2007
2008
2009

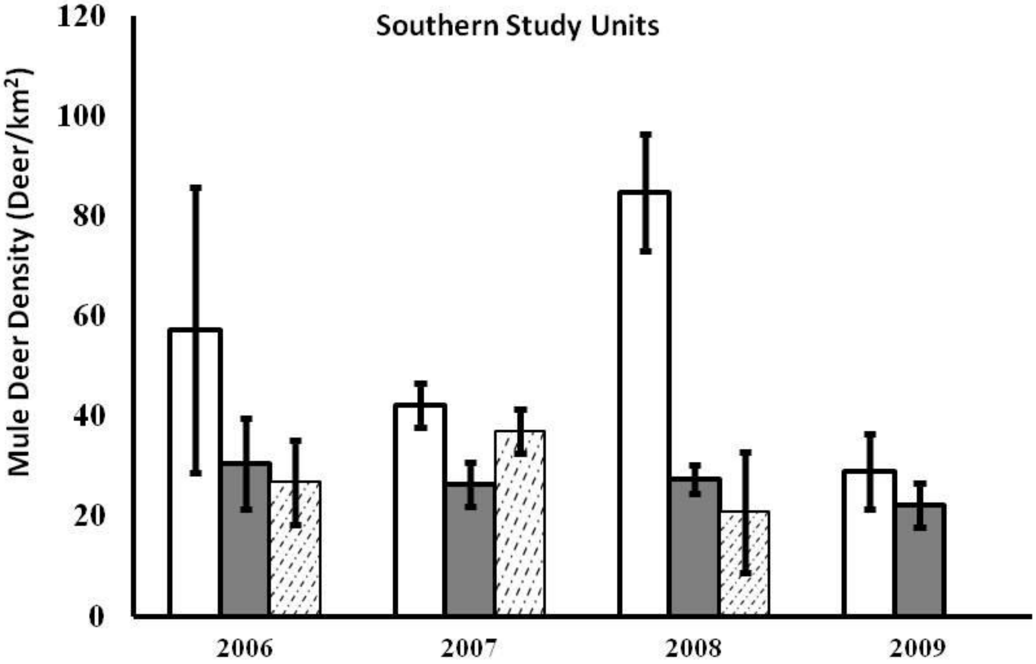

Southern Study Units
Mule Deer Density (Deer/km²)
0
20
40
60
80
100
120
2006
2007
2008
2009

Figure 2.4. Mule deer (*Odocoileus hemionus*) density estimates, with 95% confidence intervals, for 8 study units on the Uncompahgre Plateau in southwest Colorado. Northern study units (Sowbelly, Peach and Transfer) are depicted in panel A, whereas southern study units (Shavano, Colona, McKenzie, Buckhorn and BCSWA) are depicted in panel B. Note the difference in scale between panels.

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CHAPTER 3

Response of Mule Deer Body Condition to Habitat Manipulation in Southwest Colorado

The relationships between habitat, body condition and life history characteristics are tightly interwoven and of interest to wildlife managers as they strive to better understand the role that habitat plays in regulating population dynamics. With the increased availability of portable ultrasound machines and the refinement of hormonal assays, assessment of ungulate body condition has become a more accessible monitoring strategy. I employed body condition scoring, estimation of % ingesta-free body fat (%IFBF) and assessment of thyroid hormones (FT4 and FT3) as metrics to determine if landscape-level habitat manipulation affected body condition of adult (≥1.5 years old) female mule deer (*Odocoileus hemionus*). All body condition related metrics were measured on 2 study areas — a reference area that had received no habitat treatments and a treatment study area that had received mechanical removal of pinyon pine (*Pinyon edulis*) - Utah juniper (*Juniperus osteosperma*) forest, chemical control of weeds and reseeding with browse species. A consistent trend of higher %IFBF was observed in the treatment study area ($\widehat{\%\mathrm{IFBF}} = 7.100$, SE = 0.455) than in the reference study area ($\widehat{\%\mathrm{IFBF}} = 6.566$, SE = 0.455), although variation of estimates weakened my ability to draw strong conclusions. A similar pattern was observed with higher concentrations of thyroid hormone consistently being observed in the treatment study area, but large amounts variation with concentration estimates made it difficult to conclusively distinguish between study areas. Population-level impacts stemming from my observed differences in body condition parameters were likely nominal, although the consistent pattern of higher body condition related estimates in my treatment study area prevents complete dismissal of my methods as viable population monitoring strategies.

INTRODUCTION

Monitoring populations is a fundamental component of ungulate management. Monitoring can be focused on estimating sex and age ratios among years (White et al. 2001, Solberg et al. 2010, Bergman et al. 2011), measuring survival rates (Lukacs et al. 2009, White et al. 2011), and less commonly, the estimation of abundance (see Chapter 2, Freddy et al. 2004). Population monitoring has also been extended beyond wildlife parameters to monitor habitat as an index to population status (Seaton et al. 2011). The trophic effect of declining habitat quantity or quality on ungulate abundance and life history parameters has been a central topic of research and discussion for several decades. In such bottom-up systems, the predicted sequence of density-dependent effects experienced by mammals, as their populations saturate a landscape and reach the local carrying capacity, were succinctly predicted by Eberhardt (1977a, 1977b) and have subsequently been reiterated by others (Gaillard et al. 1998, Gaillard et al. 2000). Of these predictions—reduced survival of juveniles, delay of first pregnancy, reduced neonatal and parturition rates and reduced survival of adults—all but the first are directly related to body condition of adult females (≥1 year old). Thus, the relationships between habitat, body condition and life history characteristics are tightly interwoven and of interest to researchers, biologists and managers as they strive to better understand the role that habitat plays in regulating population dynamics (e.g., Keech et al. 2000, Bishop et al. 2009a).

Stemming from interest in the relationship between ungulates and their vegetative environment, assessing ungulate body condition has evolved to include new technologies and methodologies. What was historically assessed using subjective metrics (Cheatum 1949, Riney 1960) has been expanded to include quantifiable parameters such as estimated total body fat (Stephenson et al. 1998, Cook et al. 2001, Cook et al. 2010). In particular, the increased availability of portable ultrasound machines, coupled with the development and validation of robust body condition estimation models, has made the assessment of ungulate body condition an accessible monitoring strategy. Likewise, thyroid hormone concentrations, collected via blood serum, also tend to reflect the current condition of ungulates (Watkins et al. 1982, Watkins et al. 1983, Bishop et al. 2009b).

Total body fat and thyroid hormones can be viewed as metrics for the same general trait, overall deer health; however, they are parameters for different processes. In particular, total body fat estimates reflect the energetic reserve that individual deer carry with them. Alternatively, thyroid hormone concentrations reflect the ability of deer to utilize body fat reserves. The T4 hormone is a product of the thyroid gland and is a precursor to the T3 hormone (Feldman and Nelson 1987, Meyer and Harvey 2004). T3 is generated by the loss of an iodine atom from a T4 molecule (Feldman and Nelson 1987, Meyer and Harvey 2004). The T3 hormone plays a direct role in regulating the basal metabolic rate and thermal regulation within animals (Feldman and Nelson 1987, Meyer and Harvey 2004). Measurements of these 2 hormones typically occur in 2 forms, total hormone concentrations (T4 and T3) and free hormone concentrations (FT4 and FT3). Free hormone concentrations reflect the amount of each hormone available for immediate use by the animal, whereas total hormone concentrations also include hormone molecules that are bound to protein molecules which are thereby inhibited from use (Feldman and Nelson 1987, Meyer and Harvey 2004). Variation in hormone concentrations is indicative of physiological adjustment to changes in the environment.

In Colorado, estimating the response of mule deer body condition to changes in habitat conditions has been identified as a priority by biologists. In particular, as biologists and managers implement habitat management actions, or as they consider alternative large scale changes to habitat (e.g., habitat response to wildfire or habitat alteration due to development), they often wish to know if ungulate populations have been affected. Experimental research conducted by Bishop et al. (2009a) demonstrated a strong connection between maternal condition, pregnancy rates, as well as neonatal survival and juvenile survival, when food was supplemented. However, the work of Bishop et al. (2009a) was designed to explore an ecological process, not to test a practical management scenario. In particular, Bishop et al. (2009a, 2009b) relied on ad libitum pelleted food as a mechanism to experimentally manipulate body condition of free-ranging mule deer. In an attempt to replicate the results of Bishop et al. (2009a, 2009b) using common habitat management techniques, I conducted a study that assessed late-winter body condition of adult female mule deer with respect to such management techniques. I employed body condition scoring, estimation of total body fat and assessment of thyroid hormones as metrics to determine if landscape-level habitat manipulation affected body condition of adult (≥1.5 years old) female mule deer. I hypothesized that estimates of late winter condition parameters for adult females on the treatment study area would be consistent with animals in better overall condition, although I also hypothesized that my parameter estimates would be lower than the experimentally elevated estimates reported by Bishop et al. (2009a, 2009b) because increasing browse availability to similar ad libitum levels was not a realistic expectation for my habitat management techniques.

STUDY AREA

I conducted this research on 2 study areas near the southeastern tip of the Uncompahgre Plateau in southwest Colorado. One study area (Buckhorn) was maintained as a reference area, whereas the second study area (Billy Creek State Wildlife Area – BCSWA) was a treatment area. The study areas were deliberately located in close proximity to one another to minimize spatial variation and Buckhorn was located approximately 8.5 km north of BCSWA. Each study area was located on pinyon pine (*Pinyon edulis*)- Utah juniper (*Juniperus osteosperma*) forest winter range. These forests were late-seral stage, typified by open understory with occasional sagebrush (*Artemesia spp.*), cliffrose (*Purshia mexicana*), antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus spp.*), or rabbitbrush (*Ericameria spp.*) plants. Grasses included western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), Indian ricegrass (*Achnatherum hymenoides*) and bluegrass (*Poa spp.*).

Both study areas fell within Colorado Parks and Wildlife's Data Analysis Unit (DAU) 40. This 2,437 km^2 DAU was managed for a post-hunt population size of 13,500–15,000 mule deer. Each of these study areas was centered on public lands, although Buckhorn had private land at lower elevations. Likewise, both study areas declined in elevation from east to west. Mule deer arrival on each study area each winter was believed to have been heavily influenced by the building snowpack at higher elevations. Grazing pressure from domestic livestock was minimal on both study areas, with the majority of grazing occurring as livestock producers moved animals from summer range pastures to private pastures on the valley floor.

Due to the proximity of the study areas to one another, and to the overall topography, a high degree of spatial overlap on summer range occurred between the deer that used these 2 distinct winter range segments (E. Bergman, Colorado Parks and Wildlife, unpublished data). Due to this mixing on summer range, I assumed that no discernible difference in body condition occurred between deer prior to their arrival on my winter range study areas. A common, but untested, assumption in Colorado deer management is that summer and transition range habitat quality is sufficiently high to allow animals to reach peak physical condition each year, prior to downward migration to winter range.

METHODS

Habitat Treatments

For my research, habitat treatments occurred on BCSWA in 2 stages. The first stage occurred in 1998, during which 1.7 km^2 (~8%) of the study area was exposed to mechanical roller-chopper treatments. Roller-chopper treatments consisted of a large drum, affixed with perpendicular blades, that was pulled behind a bulldozer (Watkins et al. 2007). Standing trees and taller vegetation were uprooted by the bulldozer and subsequently broken into smaller pieces by the drum. On BCSWA, roller-chopper treatments ranged in size between 6.8–24.7 hectares and were intended to open up the forest canopy and increase the edge/area ratio. Treatments also created a mulched ground cover that was beneficial for holding moisture. The second stage of habitat treatment efforts was reseeding and weed control efforts that occurred concurrently with my study (2006–2008). Reseeding efforts specifically targeted desirable browse species for mule deer (bitterbrush, cliffrose, sagebrush, serviceberry (*Amelanchier alnifolia*), four-wing saltbush (*Atriplex canescens*)). Weed eradication, via herbicide application, targeted cheatgrass (*Bromus tectorum*) and jointed goatgrass (*Aegilops cylindrica*). The delay between the first stage of habitat treatments and the initiation of mule deer body condition monitoring was a deliberate decision to allow time for vegetation to grow post-treatment. In particular, I suspected that during the 1–2 year period following mechanical disturbance, browse quality and abundance may have been lower than pre-treatment conditions. Thus, by allowing a time lag I afforded browse species the opportunity to regrow under more open conditions.

Field Methods

During early March of each winter (2007–2009), 30 adult female deer were captured via helicopter net-gunning (Webb et al. 2008, Jacques et al. 2009). Upon capture, all deer were immediately blind-folded, hobbled and ferried to a central processing site (≤3.2 km). At the field processing site, deer were weighed, age was estimated via tooth eruption and wear patterns (Severinghaus 1949, Robinette et al. 1957, Hamlin et al. 2000) and blood was drawn via jugular venipuncture. At the processing site, I also measured the maximum subcutaneous fat thickness (cm) on the rump and the thickness of the longissimus dorsi muscle (cm) using a Sonovet 2000 (Universal Medical Systems, Bedford Hills, NY) portable ultrasound machine and a 5-MHz linear transducer (Stephenson et al. 1993, Stephenson et al. 1998, Stephenson et al. 2002, Cook et al. 2001). To facilitate ultrasound measurement, an appropriately sized patch of skin was plucked free of hair and lubricated to ensure that air pockets did not occur between the skin and the transducer. I also determined a body condition score for each animal by palpating the rump (Cook et al. 2001, Cook et al. 2007, Cook et al. 2010). Capture, handling and radio-collaring procedures for all aspects of this study were approved by the Institutional Animal Care and Use Committees at Colorado Parks and Wildlife (protocol #10-2005) and Colorado State University (protocol #08-2006A). Body condition scores were combined with ultrasound measurements to generate a scaled estimate of the total percent of the body that was ingesta-free body fat (%IFBF) of each animal (Cook et al. 2010). At the time of capture, pregnancy was determined via transabdominal ultrasonography (Smith and Lindzey 1982, Houston et al. 2001, Vahtiala et al. 2004) or via pregnancy-specific protein B concentrations (Wood et al. 1986) from blood serum samples (Biotracking, LLC, Moscow, ID). Blood serum samples were also submitted to the

Diagnostic Center for Population and Animal Health at Michigan State University (East Lansing, MI) for estimation of T4, FT4, T3, and FT3 concentrations.

Analytical Methods

Prior to building body condition models, I tested for correlation between response variables. Based on the results of correlation analyses, I modeled 3 of the 5 body condition measurements (%IFBF, FT4, and FT3) as a response to group covariates (study area and year) and to individual covariates (chest girth, hind foot length, pregnancy status, and age). For all analyses, model selection and evaluation was based on AIC_c (Burnham and Anderson 2002). For model comparison, conditional model averaging of estimates was conducted such that average parameter estimates were generated using all models. For models in which individual parameters did not appear, ß and standard error values of 0 were used. All possible combinations of additive multiple linear regression models were evaluated using the “MuMin”, “Stats”, and “AICcmodavg” packages in R (R Foundation for Statistical Computing, version 2.15.0. www.r-project.org, accessed 24 January 2013). While individual mass was collected for animals at the time of capture, these data were not directly used in the estimation process for %IFBF. For each of the 3 response variables, a total of 64 models were compared. To assess the role of habitat treatments, year, %IFBF, and age on pregnancy I modeled the probability of an individual deer’s pregnancy status using logistic regression in the “Stats” package in R. To determine if there was evidence for a delay in age of first pregnancy, or senescence in pregnancy, exploratory models allowing for quadratic effects were also built. Finally, I also conducted post hoc exploratory analyses that were intended to test the conclusions and recommendations drawn by Bishop et al. (2009b), regarding the utility of using blood serum thyroid concentrations to estimate %IFBF. In particular, Bishop et al. (2009b) reported that the T4 and FT4 hormones were effective at predicting %IFBF ($\widehat{\%\mathrm{IFBF}} = -4.8015 - 0.0946 \times \mathrm{T4} + 0.000603 \times \mathrm{T4}^2 + 0.1474 \times \mathrm{FT4} + 0.1426 \times \text{chest girth}, R^2 = 0.609$). Following the methods of Bishop et al. (2009b), second and third order polynomials were allowed to occur in these later models.

RESULTS

Estimated %IFBF was more correlated with T4 (0.25) and FT4 (0.18) than with T3 (0.07) and FT3 (0.09). However, the highest overall correlations were observed within categories of thyroid hormones. T4 and FT4 had the highest correlation (0.89), whereas the correlation between T3 and FT3 was slightly lower (0.70). Correlation of concentrations between the 2 T4 hormones and each of the 2 T3 hormones were consistently between 0.40–0.45. Correlation between predictor variables was low with the highest observed correlation occurring between individual chest girth and individual hind foot length (0.31).

The pooled, mean estimate of %IFBF for deer during the 3 year period of this study was 7.16% (SE = 1.78). The observed mean value for BCSWA ($\overline{\%\mathrm{IFBF}} = 7.38, \mathrm{SE} = 1.31$) was slightly higher than Buckhorn ($\overline{\%\mathrm{IFBF}} = 6.95, \mathrm{SE} = 2.14$). Overall, the effect of year was an important component to model structure for all hormones (Table 3.1). When %IFBF was compared among years, the mean estimate observed in 2007 ($\overline{\%\mathrm{IFBF}} = 6.82, \mathrm{SE} = 1.96$) was less than that observed in 2008 ($\overline{\%\mathrm{IFBF}} = 7.48, \mathrm{SE} = 1.78$) or 2009 ($\overline{\%\mathrm{IFBF}} = 7.19, \mathrm{SE} = 1.56$). The observed pattern of higher %IFBF in BCSWA was observed during all 3 years (Table 3.2). A similar pattern of higher concentrations of the T4 hormones in BCSWA was also observed during all years (Table 3.2). Alternatively, patterns of concentration of the T3 hormones were inconsistent between the 2 study areas (Table 3.2).

The difference in %IFBF between study areas and years was subtle, with wide overlap in the estimates of variance (Fig. 3.1). The overall best model incorporated study area, year and individual chest girth (Table 3.3). Models that included each of these covariates were consistently ranked among the best (Table 3.3). Cumulative AIC_c weights from %IFBF models highlighted the importance of these 3 covariates (Table 3.1). In particular, the effect of annual variation in %IFBF was weak, although higher estimates were observed during 2008 (Fig. 3.1). While estimates of %IFBF was higher in BCSWA than in Buckhorn, when pooled over the 3-year period, estimates of %IFBF from BCSWA reflected a 1.08× magnitude increase over Buckhorn. The best model for %IFBF, based on AIC_c, also accounted for individual chest girth. Based on cumulative AIC_c weights, the remaining covariates of interest (pregnancy status, hind foot length and age) contributed little to overall model results (Table 3.1).

Linear regression models for FT4 were similar to those of %IFBF. The best model for each of these parameters was composed of study area, year, age, and pregnancy status (Table 3.4). As was the case with %IFBF, estimated concentrations of FT4 for Buckhorn were consistently lower than those estimated for BCSWA (Table 3.2). However, while the highest %IFBF was estimated during the second year of the study (2008), FT4 concentrations were highest during the first year of the study. The model-averaged parameter estimate for pregnancy status in FT4 models was negative ($\hat{\beta} = -1.739, SE = 0.754$), but a common factor in many of my top models (Tables 3.1 and 3.4). The morphometric measurements of chest girth and hind foot length had weak overall effects. Although present in a few of my top FT4 models (Table 3.4), the cumulative AIC_c weights for these covariates were near 0.50 (Table 3.1).

The best linear regression model for FT3 deviated from the patterns established by %IFBF and FT4. Whereas model selection procedures showed a clear distinction between study areas for the previously discussed body condition indices, the role of year and age appeared to have the greatest influence on model performance for FT3 (Tables 3.1 and 3.5). Concentration of FT3 was lower during 2008 and 2009, following the pattern observed for FT4.

Based on AIC$_c$, as well as model-averaged parameter estimates, when pregnancy status was treated as a dependent variable there was no evidence that the probability of an adult female deer being pregnant varied between study areas or during years. Little difference in pregnancy rates was observed between BCSWA and Buckhorn during the 3 year period (BCSWA = 0.877 (SD = 0.329), Buckhorn = 0.862 (SD = 0.345)). When study area was ignored, observed mean pregnancy was lower during 2008 than that observed in 2007 and 2009 (2007: 0.896 (SD = 0.307), 2008: 0.833 (SD = 0.376), 2009: 0.883 (SD = 0.324)). For my analyses, probability of being pregnant was best predicted by the model $\widehat{\text{Pregnant}} = 3.354 - 0.2739 \times \text{Age}$. With the exception of age, 95% confidence intervals included 0 for all covariates. The effect of age on pregnancy was negative ($\hat{\beta} = -0.311$, SE = 0.109), although the evidence for late age senescence was not strong (Fig. 3.2). Exploratory models that were structured with second and third order quadratic expressions in an attempt to accommodate delayed age of first pregnancy or late age senescence did not improve on the simpler additive models.

Results of my exploratory analysis in which %IFBF was modeled using thyroid hormones did not mirror Bishop et al.'s (2009b) results. For my analyses, %IFBF was best predicted by the model $\widehat{\%\text{IFBF}} = 1.911 + 0.1814 \times \text{TT4} - 0.002 \times \text{TT4}^2 + .000007 \times \text{TT4}^3$. However, the predictive ability of my model was quite low ($R^2 = 0.106$). When Bishop et al.'s (2009b) model ($\widehat{\%\text{IFBF}} = -1.359 + 0.075 \times \text{TT4} - 0.0003 \times \text{TT4}^2 - .050 \times \text{FT4} + 0.058 \times \text{Chest Girth}$, $R^2 = 0.120$) was fit to my data, the model only received 2.6% of the model weight and had low predictive ability.

DISCUSSION

The patterns reflected in my results tend to support my hypothesis that late-winter body condition of adult female deer was elevated in my treatment study area as compared to my reference area. Both total fat reserves (%IFBF) and the metabolic capacity to utilize those reserves (FT4) appeared to be higher in treatment deer than in reference deer. However, despite these patterns, consideration of the variation surrounding those estimates greatly weakens any conclusions.

For both %IFBF and FT4 results, study area and year were consistently among the most important covariates. In the case of FT4, models including both of these covariates accounted for >99% of the cumulative model weight (Table 3.2). In the case of %IFBF, the single covariate that carried most of the cumulative model weight was chest girth. Due to the fact that body mass was not included in the %IFBF estimation process, the improvement within models that had a body size relative parameters was not surprising. Specifically, these body size related variables helped distinguish between large bodied animals that had low %IFBF and small bodied animals that had high %IFBF. Annual variability in body condition among winters was expected to be an important factor in assessing late winter body condition, although its importance relative to habitat management efforts was difficult to predict prior to my study. This expectation was met as yearly variation never carried less than 82% of the cumulative AIC_c weight. I suspect that had I been able to increase the positive effects of habitat treatments, the importance of yearly variation may have been diminished. However, the treatments delivered as part of my research reflect those commonly utilized by land management agencies. Thus, it is reasonable to conclude that while the effect of habitat management techniques are positive, thereby elevating the late winter body condition of mule deer, the magnitude of those effects are subtle and not strong enough to eliminate the role of yearly variation.

In comparison to the results of Bishop et al. (2009a), my hypotheses were generally met. In particular, the mechanical habitat treatments utilized as part of my research did mirror the pattern stemming from the pelleted food ration provided by Bishop et al. (2009a). However, as expected, the magnitude of my treatment effect was substantially lower and more tenuous when variation in estimates was considered. Bishop et al. (2009a) reported %IFBF estimates of 10.21%–13.90% in treatment units and 6.64%–7.60% in control units, reflecting a ~1.61× magnitude increase. I detected a 1.08× magnitude increase using common habitat management techniques. In regards to predictive ability, Bishop et al. (2009b) found a higher level of correlation and attributed a stronger ability of the T4 and FT4 hormones to predict %IFBF than what I found in my research. My results do not support the recommendation that thyroid hormones should be used to estimate %IFBF as even my best predictive model did not attain a satisfactory level of performance and my overall correlation between %IFBF and hormones were low. My inability to validate the results of Bishop et al. (2009b) is noteworthy as it places a caveat on my ability to generate distinctions between areas based on body condition alone.

Population-level impacts stemming from the differences in body condition on my study areas were likely nominal. For example, I did not detect a meaningful difference in pregnancy rates between the 2 study areas. Likewise, while my study did not assess neonatal rates I do not think the number of fetuses produced in the treated area was greater than that in the reference area. However, I note that I did not actively seek low quality habitat to serve as my reference area. Rather, the reference area was defined by pinyon-juniper winter range that had not received vegetative treatments. This allowed me to test the hypothesis that habitat manipulation and improvement could be used to improve winter range in terms of late winter body condition. The magnitude of improvement in body condition could be expected to be amplified, relative to pre-treatment levels, if habitat treatments were applied to poor quality habitat. Given that neither of my study areas were intentionally located on poor quality habitat, the pattern reflected in my data on mule deer body condition is noteworthy.

In parallel research (see Chapter 1), the overwinter survival of mule deer fawns was measured on these, and other, study areas at the same time as this study. I found a 1.15× increase in fawn survival on treated study areas such as BCSWA (see Chapter 1). Likewise, I measured mule deer abundance and density on both BCSWA and Buckhorn from 2007–2009 and observed a possible downward population trend in Buckhorn but a stable, albeit less dense, population in BCSWA (see Chapter 2). I speculated that habitat treatments on BCSWA had prevented a population decline in deer on that study area (see Chapter 2).

When considered in tandem, my results from other work (see Chapters 1 and 2) and these results can be used to evaluate the first two hypotheses of Eberhardt (1977a, 1977b). In particular, Eberhardt (1977a, 1977b) predicted that survival of young would be the first population parameter to reflect a response under habitat limited scenarios. My results support this conclusion (see Chapter 1). The second sequential effect predicted by Eberhardt (1977a, 1977b) was the delayed onset of first pregnancy. Based on my results, this did not appear to have occurred on my study areas. While speculation is limited by small sample size, my results indicate that the nutritional plane on both study areas was adequate for all age classes of mature female deer to become pregnant. Thus, despite a truncated evaluation, the sequence of density-dependent effects predicted by Eberhardt (1977a, 1977b) were likely correct. If so, overall habitat quality on my reference study area remained high enough that negative population-level effects stemming from poor quality habitat were only reflected in the most sensitive population parameter.

MANAGEMENT IMPLICATIONS

For mule deer population management purposes, my research demonstrates the cascade effect of landscape-level, vegetative manipulations on individual deer body condition. However, my research also demonstrates that adult female body condition parameters are not overly sensitive and inferring population level impacts exclusively from body condition parameters may be difficult. However, by targeting the most depleted portions of mule deer winter range habitat for habitat treatments, land managers may be able to improve body condition of animals.

Table 3.1. Regression coefficients (β_i) and Akaike's Information Criterion cumulative model weights (ω_i) for body condition predictor variables from multiple linear regression models for adult female mule deer. Data were collected in southwest Colorado during early March, 2007–2009.

Predictor Variable		Response Variables %IFBF	 FT4	 FT3
Unit	ω_i	0.722	1.000	0.265
	$\widehat{\beta_\iota}$ (SE)	-0.385 (0.191)	-3.433 (0.614)	0.010 (0.028)
Year	ω_i	0.823	1.000	0.999
2008	$\widehat{\beta_\iota}$ (SE)	0.745 (0.273)	-3.447 (0.756)	-0.108 (0.130)
2009	$\widehat{\beta_\iota}$ (SE)	0.267 (0.267)	-5.115 (0.743)	-0.872 (0.128)
Chest	ω_i	0.966	0.412	0.317
	$\widehat{\beta_\iota}$ (SE)	0.089 (0.028)	0.035 (0.028)	0.003 (0.003)
Age	ω_i	0.363	0.890	0.982
	$\widehat{\beta_\iota}$ (SE)	-0.025 (0.024)	-0.351 (0.138)	-0.082 (0.026)
Foot	ω_i	0.293	0.533	0.504
	$\widehat{\beta_\iota}$ (SE)	0.017 (0.027)	-0.170 (0.109)	-0.026 (0.018)
Pregnant	ω_i	0.260	0.827	0.452
	$\widehat{\beta_\iota}$ (SE)	-0.016 (0.103)	-1.739 (0.754)	-0.094 (0.071)

Table 3.2. Observed mean estimates (with standard error) for 5 body condition variables from adult female mule deer in southwestern Colorado. Data were collected during early March in a treatment study area (Billy Creek State Wildlife Area – BCSWA) and a reference study area (Buckhorn Mountain). Variables include scaled percent ingesta-free body fat (%IFBF), as well as concentrations for the thyroid hormones: T4 (nanomole/L), T3 (nanomole/L), FT4 (picomole/L), and FT3 (picomole/L).

Year	Unit	%IFBF	T4	FT4	T3	FT3
2007	BCSWA	6.82 (1.51)	88.23 (15.53)	14.8 (3.98)	1.55 (0.53)	2.1 (0.7)
	Buckhorn Mountain	6.81 (2.36)	78.07 (22.34)	13.1 (4.66)	1.42 (0.31)	2.07 (0.56)
2008	BCSWA	7.91 (1.24)	94.3 (20.71)	13.37 (4.59)	1.17 (0.28)	1.98 (0.59)
	Buckhorn Mountain	7.05 (2.12)	56.17 (23.32)	8.37 (3.91)	1.17 (0.58)	2.13 (1.16)
2009	BCSWA	7.4 (0.94)	74.63 (14.61)	11.33 (3.46)	1.22 (0.32)	1.41 (0.52)
	Buckhorn Mountain	6.98 (1.99)	54.77 (19.34)	6.83 (3.17)	1.26 (0.35)	1.14 (0.44)

Table 3.3. Multiple linear regression model output for the top 5 models predicting scaled percent ingesta-free body fat for adult female mule deer captured in southwest Colorado. Data were modeled using study area (Area), year (Year), individual pregnancy status (PRG), chest girth (Chest), age (Age) and hind foot length (Foot).

Model	$\Delta\mathrm{AIC}_c^a$	ω_i^b	K^c	R^2
Area + Year + Chest	0	0.222	6	0.096
Area + Year+ Chest+ Age	1.52	0.104	7	0.099
Area + Year+ Chest+ Foot	1.89	0.086	7	0.098
Area + Year + Chest + PRG	2.17	0.075	7	0.096
Year + Chest	2.55	0.062	5	0.072

[a] Model comparisons are made using Akaike's Information Criterion that has been corrected for small sample size (AIC_c)

[b] AIC_c model weight

[c] Number of estimated parameters

Table 3.4. Multiple linear regression model output for the top 5 models predicting concentrations for the FT4 thyroid hormone in adult female mule deer captured from southwest Colorado. Data were modeled using study area (Area), year (Year), individual pregnancy status (PRG), chest girth (Chest), age (Age) and hind foot length (Foot). Model comparisons are made using Akaike's Information Criterion that has been corrected for small sample size (AIC$_c$).

Model	ΔAIC$_c$	ω_i^a	K^b	R^2
Area + Year + PRG + Age	0.00	0.233	7	0.360
Area + Year + PRG + Age + Foot	0.14	0.217	8	0.367
Area + Year + PRG + Age + Foot + Chest	0.38	0.192	9	0.374
Area + Year + PRG + Age + Chest	1.44	0.114	8	0.362
Area + Year + Age	3.50	0.041	6	0.339

[a] AIC$_c$ model weight

[b] Number of estimated parameters

Table 3.5. Multiple linear regression model output for the top 5 models predicting concentrations for the FT3 thyroid hormone in adult female mule deer captured from southwest Colorado. Data were modeled using study area (Area), year (Year), individual pregnancy status (PRG), chest girth (Chest), age (Age) and hind foot length (Foot). Model comparisons are made using Akaike's Information Criterion that has been corrected for small sample size (AIC_c).

Model	ΔAIC_c	ω_i^a	K^b	R^2
Year + Age	0.00	0.141	5	0.269
Year + Age + Foot	0.29	0.122	6	0.277
Year + Age + PRG	0.40	0.115	6	0.277
Year + Age + Foot + PRG	0.48	0.111	7	0.285
Year + Chest + Age + Foot	1.30	0.073	7	0.282

[a] AIC_c model weight

[b] Number of estimated parameters

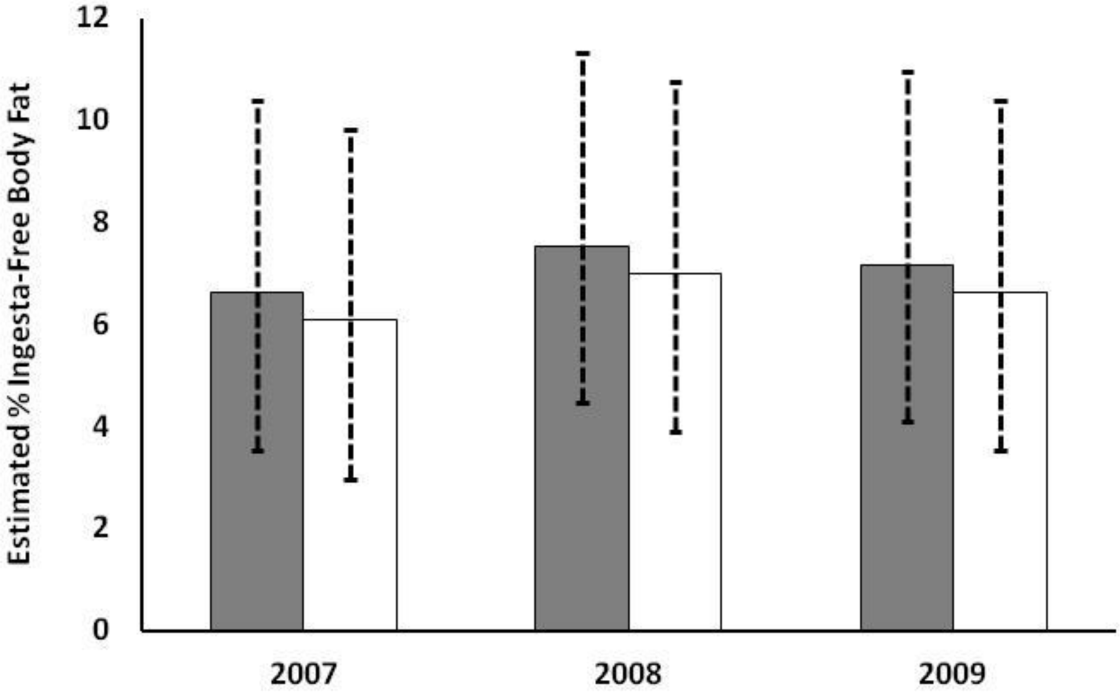

Figure 3.1. Scaled estimates of late winter percent ingest free body fat (%IFBF), with 95% predicition intervals, for adult female mule deer (*Odocoileus hemionus*) in southwest Colorado. Solid gray bars reflect estimates for my treatment study area (Billy Creek State Wildlife Area) and white bars reflect estimates for my reference study area (Buckhorn Mountain). Estimates and prediction intervals were generated according to the model $\widehat{\%\mathrm{IFBF}} = -2.159 - 0.534 \times \mathrm{Buckhorn} + 0.905 \times \mathrm{Year}^{2008} + 0.539 \times \mathrm{Year}^{2009} + 0.092 \times \mathrm{Chest}$ in which chest girth was held constant at the observed mean of 95.476 cm and coefficient estimates have been model averaged based on model results.

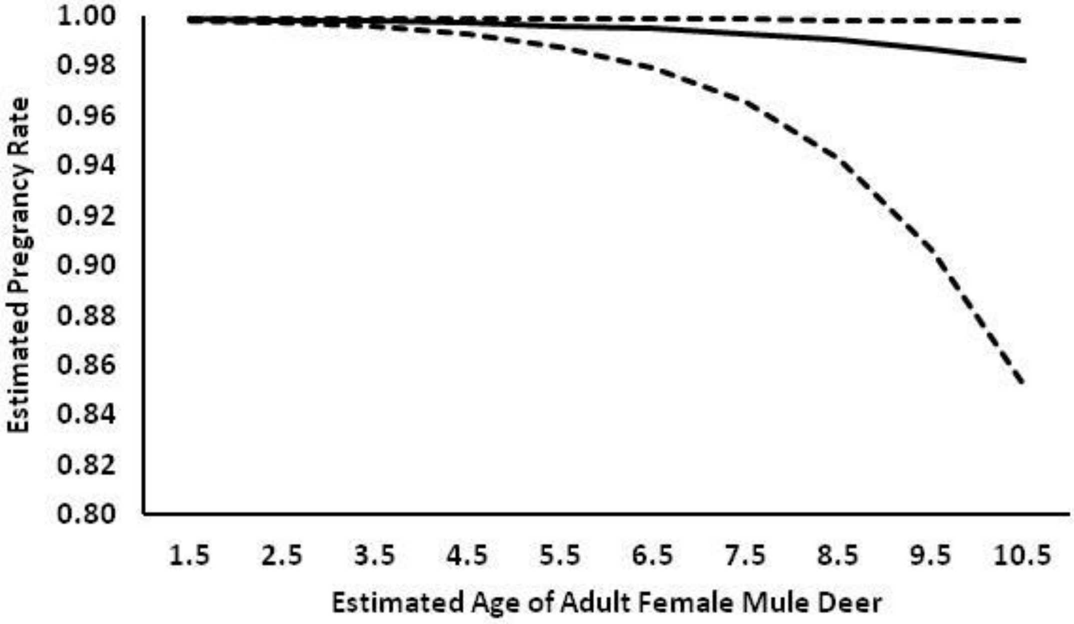

Figure 3.2. Probability of pregnancy, with 95% confidence intervals, for adult mule deer (*Odocoileus hemionus*) in southwest Colorado. No discernable difference in probability of pregnancy between my treatment and reference study areas was observed.

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CHAPTER 4

Density Dependence in Colorado's Mule Deer

Biologists, managers and hunters have expressed concern over a recent decline in some western Colorado mule deer (*Odocoileus hemionus*) herds, but whether this decline is part of a regional pattern or unique to Colorado is unclear. Similarly, the underlying cause of this decline is yet to be determined. In response to this management concern, a review of scientific evidence on Colorado's mule deer population dynamics is warranted. To be most beneficial, such a review should be done in the context of a conceptual model that portray population growth as a function of population size, per-capita growth rate and population carrying capacity. Similar declines that occurred during the 1960s and early 1990s resulted in similar reviews that also identified future research and management studies that would benefit mule deer. These topics included: harvest, predation, intraspecific competition, disease, interspecific competition, and habitat loss and degradation. Between the late 1990s and present time, many of these topics have been addressed with research, but the new knowledge and information has not been compiled in a review. The conventional working hypothesis in Colorado is that mule deer herds are limited by winter range habitat. However, I identify new gaps in knowledge and suggest potential, future research topics. These topics include density reduction experiments to address competition and focused experiments to address the role of mountain lion and black bear predation.

INTRODUCTION

Colorado's mule deer population has demonstrated several dramatic shifts in abundance during the past 6–7 decades (Colorado Parks and Wildlife, unpublished data: Fig. 4.1). Typically these fluctuations have mirrored regional mule deer population dynamics (Workman and Low

1976, Gill 2001). However, biologists, managers, and hunters have expressed concern over a recent decline in some western Colorado mule deer herds (A. Holland, Colorado Parks and Wildlife, personal communication). Whether this recent decline is part of a broader, regional pattern or a Colorado-specific phenomenon is unclear. In response to this decline, a review of scientific evidence on Colorado's mule deer population dynamics may help guide decisions as different management actions and research objectives are considered.

Historical declines in mule deer populations have resulted in similar reviews (Workman and Low 1976, Gill 2001). In particular, a decline in mule deer populations during the late 1960s and early 1970s resulted in a regional symposium that was focused specifically on identifying potential causes of that decline (Workman and Low 1976). After a period of population increase during the late 1970s and 1980s, mule deer populations declined again during the early and middle portions of the 1990s. While this second decline was also observed at the regional scale, it was the impetus for a Colorado-centric symposium in 1999, resulting in a report to Colorado's legislature that called for a renewed focus on mule deer research and increased population monitoring activities (Gill 2001). A product of both symposia was the identification of several recurring potential causes for mule deer population decline: habitat loss, habitat degradation, predation, disease, interspecific competition (i.e., with elk (*Cervus elaphus*) and livestock) and intraspecific competition (i.e., increased density or overabundance of mule deer relative to available habitat). For these causes, the definition of habitat was primarily concentrated on browse availability and browse condition, and to a lesser extent escape and thermal cover provided by vegetation. In particular to Colorado, the review by Gill (1999) identified shortcomings in the collective knowledge base, and thereby indirectly provided a recipe for research, management experiments, and population monitoring that would benefit deer management. Many of these studies have been completed, yet a collective review of research results has not occurred as this new evidence has been published.

TERMINOLOGY AND ASSUMPTIONS

In order to provide a review of scientific evidence and to make an assessment of key characteristics of a population, terminology must be clearly defined. A key component of many population models, especially those pertaining to vertebrate species, is that populations are limited (i.e., unlimited population growth is not feasible). Under this constraint, eventually the number of deaths equals the number of births, resulting in no population growth. While the factors setting this upper limit to populations are debated and commonly researched, the notion that an upper limit exists (i.e., carrying capacity – K) is fundamental to other population attributes. For example, the terms “regulation” and “limitation” can easily be confused. For the purposes of this paper, and following the distinctions drawn by Messier (1991) and Boutin (1992), I define a regulating factor as any factor that has the ability to bring a population back into equilibrium after perturbation. The strength of a regulating factor is dependent on overall deer density and population size relative to K. Stronger regulating effects occur at higher deer densities when populations are near K. Regulatory effects are weaker when populations and deer densities are lower. Alternatively, a limiting factor is defined as the single factor that prevents populations from increasing beyond a threshold. Removal or adjustment of the limiting factor would result in a population that is capable of reaching a new, presumably higher, threshold. The rate at which a population achieves this new threshold is dictated by regulating factors.

Population regulation and population limitation can also be expressed as part of theoretical population growth models. In a generic form, population growth can be written as

$$\frac{dN}{dt} = f(N, r, K)$$

in which the change in population size (*dN*) occurs during a discrete time interval (*dt*). This rate of population growth is a function (*f*) of the current population size (*N*), the intrinsic rate of increase (*r*), and carrying capacity for the population (*K*). The value $\frac{dN}{dt}$ is a population's growth rate. The function relating population size, population growth rate and carrying capacity can take many forms (e.g., logistic growth, theta-logistic growth) and can be expanded to include harvest (Williams et al. 2001). Such derivations have been extensively explored (Ricker 1954, Hassell 1975, Hassell et al. 1976, Williams et al. 2001, Gotelli 2008). While the major differences between different theoretical population growth models are often manifest when populations are below carrying capacity, with each model having a different set of ecological circumstances under which it is most useful, any single mathematical function is of nominal consequence to this review. Expanding my theoretical model to accommodate the per-capita rate of change (*R*)

$$R = \frac{\left(\frac{dN}{dt}\right)}{N}$$

reveals a value that can be easily confused with the intrinsic rate of increase (*r*). As noted above, whereas r is a constant value, R changes depending on population size (*N*). In keeping with the definitions of population regulation and population limitation, the strength of regulating factors manifest in *R* are dependent on current population size (*N*). Limiting factors are those that influence carrying capacity for the population (*K*).

Regardless of how population models are conceptualized, several noteworthy assumptions and simplifications are commonly made. First, the perspective that populations have a single limiting factor is a common oversimplification. This simplification facilitates both communication and study design. In reality, populations may be limited by an interaction of factors, such as habitat condition and weather severity; interactions that are partially driven by random processes that complicate scientific and management endeavors. Another common oversimplification for many conceptual models is that *K* is assumed to be known and fixed. In applied settings, neither of these assumptions is valid. A simple demonstration of how *K* can change over short time intervals can be found by considering the influence of weather on browse availability. During harsh winters during which the snowpack greatly exceeds normal depths and temperatures are lower than those traditionally experienced, winter browse for deer can be buried under thickly crusted snow layers, rendering it unavailable for immediate use. Under these extreme conditions, the quantity of available food is reduced. If deer are food limited on the winter range that is experiencing these conditions, *K* is reduced. Alternatively, during mild winters in which snow depths are below average and temperatures are higher than traditionally expected, access to plant resources on winter range is unrestricted and *K* is increased. Similarly, extended periods of drought or abundant moisture can change the long term trajectory of available browse, and subsequently *K*. Due to the dynamic nature of browse availability, managers rarely know how many deer can be supported by current conditions. A similar assumption that is commonly made for simplification purposes is that all mule deer browse is of equal quality. As demonstrated by Hobbs and Swift (1985), forage quality is often inversely related to forage quantity. Thus, traditional range food supply/animal food requirements models require a simplification that fails to accommodate the interaction between *K* and the nutritional status of animals. One final oversimplification that is commonly made when considering *K* is that all animals have an equal competitive advantage, a similar nutritional response, and an equal likelihood of facing mortality when *K* is reached. However, an extensive body of literature has demonstrated that adult mule deer are more robust in terms of survival than fawns (e.g., Unsworth et al. 1999, Lukacs et al. 2009, Bishop et al. 2009). In particular studies that have assimilated mule deer survival data over broad spatial and temporal scales have demonstrated that the variation in fawn survival exceeds that of adult survival (Unsworth et al. 1999, Lukacs et al. 2009). Similarly, other studies have provided evidence that adults have a competitive advantage over fawns (Garrott and White 1982, Bishop et al. 2005, Bergman et al. 2011). Ultimately, this can be viewed as evidence that *K* is different for adults and fawns.

Much of the research on mule deer population dynamics has also investigated the principals of additive and compensatory mortality (e.g., Bartmann et al. 1992, Bishop et al. 2009). Compensatory mortality is a phenomenon that is dependent on a population being above *K*, implying that by the end of an annual cycle the number of individuals exceeding that threshold will have necessarily died. The portion of the population that will have necessarily died has been referred to as the “doomed surplus” (Errington 1934, Kokko and Lindström 1998, Boyce et al. 1999). For simplicity in communication, all of the doomed individuals will die from causes related to the limiting factors for the population. However, this scenario is not necessarily the case and is unlikely. A hypothetical example can be found in a nondescript deer population that is limited by winter habitat, but is also exposed to sport harvest. In this example, the available habitat is capable of supporting no more than 500 individuals during the winter months and annual sport harvest is 25 individuals. During some years far more than 500 animals arrive on winter range, such as 600, but harvest may remain static at 25 individuals. Under this scenario, 100 individuals are expected to die, presumably of malnutrition (i.e., the doomed surplus is 100 individuals). If 25 individuals die due to sport harvest and 75 still die of malnutrition, harvest-caused mortality is completely compensatory with malnourishment-caused mortality. During years in which fewer than 500 animals arrive on winter range, yet 25 animals are harvested, those 25 deaths can be considered completely additive as resources were available to support those animals had they not been harvested. These 2 scenarios represent opposite ends of a mortality spectrum, thereby also creating a false dichotomy in the illusion that mortality is either always additive or always compensatory. A final derivation of this example can be found during years in which slightly more than the carrying capacity of deer arrive on winter range, such as 510, with harvest remaining static at 25 deer. During these years, partially additive mortality is expected as the loss of 10 deer can be considered compensation between harvest and starvation, yet the loss of 15 extra deer is additive. While these scenarios are for a hypothetical example, they reflect the driving principals of harvest management programs in which harvest objectives are based on the desire for sport harvest to be compensatory, and to accommodate the relationships between density dependence, mortality and timing of harvest (Kokko and Linsdström 1998, Boyce et al. 1999).

The biological feedback mechanisms experienced by populations as they reach *K* have been a topic of interest to ecologists and managers for several decades (Eberhardt 1977). In particular, among many taxa, predictions of the sequence and role of density-dependent feedback mechanisms are surprisingly consistent — density-dependent effects are predicted to impact populations sequentially in the order of reduced juvenile survival, increased age of first reproduction, declines in the reproductive rates of adult females, and reduced survival of the adult age class (Eberhardt 1977, Gaillard et al. 1998, Gaillard et al. 2000). The perspective that populations demonstrate shifts in life history characteristics as overall abundance nears carrying capacity is a logical extension of the objectives of Hobbs and Swift (1985). Hobbs and Swift (1985) demonstrated that when the interaction of forage quality and forage quantity was considered in carrying capacity models, they could predict the maximum number of animals that could maintain a diet of a specified quality, or they could predict the maximum quality of diet for a specified number of animals. However, despite the foundational premise of density dependence and the repetition of predictions, the effect of density on the dynamics of free-ranging ungulate populations is difficult to demonstrate.

A REVIEW OF EVIDENCE – POTENTIAL LIMITING FACTORS

Due to the uncertainty surrounding the geographic extent of this most recent decline, but also to the certainty that it has occurred in Colorado, I will primarily focus this review on research and analyses that are particular to mule deer herds in Colorado. I also note that research and collaboration among Colorado and other western states is common, and I have expanded this review to include those pieces of scientific evidence. I will also include pertinent literature from outside Colorado, and from other North American ungulates, to gain insight on ecological processes that have not been the focus of research in Colorado. In particular, this review will focus on harvest, predation, intraspecific competition, disease, interspecific competition, and habitat loss and degradation.

Harvest

Many harvest management systems are based on the premise that a doomed surplus, or harvestable surplus, of animals exist in the population. As described above, this surplus occurs when populations are at or near K. The most publicized of these systems pertains to harvest of waterfowl in North America (Burnham and Anderson 1984, Nichols et al. 1995, Nichols et al. 2007). However, similar examples can found in the ungulate literature (Wallmo 1981, Swenson 1985). Alternative harvest management strategies also exist. A well-known example of one of these alternatives, which was embraced by marine fishery managers during the 1950s, is based on the desired outcome of maximizing a sustained yield (Hilborn et al. 1995). The principal of maximum sustained yield is that populations can be held below *K* in order to maximize production and recruitment of new individuals into the population (Williams et al. 2001). From a numerical perspective, the same number of individuals recruited into the population can be harvested with no change in overall abundance (Williams et al. 2001). These 2 harvest management philosophies represent opposite ends of a continuum — the harvestable surplus strategy assumes harvest is completely compensatory while the maximum sustained yield strategy assumes harvest is completely additive — yet both philosophies are based on the premise of density dependence. The fundamental difference between the 2 strategies is that they exploit different aspects of *R*, a population's per-capita rate of change. These 2 strategies also create a false dichotomy as managers rarely know how many animals are in a population, what *K* is for a system, or if *K* is changing. This is particularly evident for mule deer when considering that harvest recommendations are set and harvest occurs prior to winter. Winter is commonly the period in which *K* can be stochastically suppressed by deep snow depths and low temperatures. In the face of this uncertainty, the potential for harvest to drift between being completely additive, partially additive and completely compensatory is high. The most complete documentation of this harvest management dilemma for large ungulate systems stems from moose (*Alces alces*) management in Alaska, where multiple harvest objectives are placed on a system that is subjected to periodic and harsh environmental fluctuations, as well as a rich predator assemblage (Gasaway et al. 1983, Gasaway et al. 1992, Boertje et a. 2009, Young and Boertje 2011).

This diversity in harvest management strategies can also be found in Colorado's deer herd management plans (Andy Holland, Colorado Parks and Wildlife, personal communication). For example, many of Colorado's deer herds are managed with the objective of maximizing *N* (abundance). While the total number of animals that can be supported in these herds remains unknown, the approach to herd management reflects the principals of a harvestable surplus. Specifically, summer and fall abundance of these herds are believed to exceed winter range *K*. Thus, harvest is intended to capture this surplus, making it a compensatory source of mortality. Alternatively, a few select herds that experience harsh winter events at more frequent intervals are managed such that *N* is preferentially kept below *K* as set by those extreme winter conditions. During mild winters when range capacity is less restricted, this approach to herd management reflects sustained yield principles. The last example stemming from Colorado's deer herd management pertains to an entirely separate objective that is geared towards providing individual hunters with a high quality hunting experience. High quality hunting experiences are typically comprised of herds that have high adult male:adult female ratios, the opportunity for hunters to encounter deer that have reached older age classes and thus have more developed antler structure, but also lower encounter rates with other hunters.

Two evaluations of Colorado's harvest management decisions have occurred (Bishop et al. 2005, Bergman et al. 2011). Each of these was an evaluation of restrictions to deer hunting, and primarily within this, restrictions on the hunting of adult male deer. In each case, as harvest was restricted, an increase in adult male:adult female ratios was observed. In particular, ratios increased by as many as 4.52 adult males per 100 adult females in one study (Bishop et al. 2005) and by as many as 21.86 adult males per 100 adult females in the other study (Bergman et al. 2011). However, simultaneous declines in fawn:adult female ratios were observed as part of each study. Declines were as high as 6.96 fawns per 100 adult females (Bergman et al. 2011) and 7.51 fawns per 100 adult females (Bishop et al. 2005). While neither study was a direct experimental evaluation of intraspecific competition or density dependence, both studies provide circumstantial evidence that increasing the proportion of adult male deer in the population came at the expense of population productivity. If lowered fawn:adult female ratios can be interpreted as an indicator of suppressed population growth, the studies of Bishop et al. (2005) and Bergman et al. (2011) may provide evidence that harvest decisions that change the sex and age structure of deer herds to favor mature animals may have a regulating effect — thereby slowing the rate of population growth ($\frac{dN}{dt}$) by reducing the per-capita rate of change (R) in my conceptual model.

The effect of hunting on wildlife species also extends beyond population management. In particular, the indirect effect of hunters on ungulates, specifically movement patterns and animal behavior, has received recent attention (Conner et al. 2001, Vieira et al. 2003, Ciuti et al. 2012). Similarly, the effect of trophy-focused hunting pressure on large ungulates, and the subsequent effect on trends in antler size, has also been the focus of recent research (Allendorf and Hard 2009, Monteith et al. 2013).

Predation

The role of predation in shaping ungulate population dynamics is a common research topic with many different conclusions being possible, depending on individual circumstances. In the Rocky Mountain West, the motivation to study coyote (*Canis latrans*) predation on mule deer is several-fold. First, encounter rates between coyotes and hunters (i.e., observation of coyotes and coyote tracks, hearing coyote howls, and finding coyote kill sites) are likely higher than those for any other predator of deer. Stemming from this, an intuitive reaction by hunters is often that coyote predation has a stronger effect on deer population dynamics than other sources of predation. Thus, pressure from the public for a more complete understanding of the impact of coyote predation on deer populations has frequently been articulated (Willoughby 2012). Secondly, investigations into the causes of mortality of mule deer have consistently identified coyote predation as a common source of mortality (Bartmann et al. 1992, Whittaker and Lindzey 1999, Pojar and Bowden 2004, Bishop et al. 2009). Stemming from this demand and from these patterns, the effect of coyote predation on mule deer has been more thoroughly investigated than other sources of predation. Experimental manipulation of coyote density as a treatment effect on deer population dynamics has occurred as part of 2 studies. Research conducted by Bartmann et al. (1992) in northwest Colorado evaluated the effectiveness of coyote control as a management strategy to increase productivity within a deer herd. While the annual removal of 47–93 coyotes from the 140 km^2 winter range study area reduced coyote predation, a simultaneous increase in starvation rates occurred and no overall increase in survival rates was detected. This switch between mortality causes, with no increase in survival, was viewed as strong evidence that coyote predation was compensatory with starvation. Specifically, if this were a top-down system in which coyotes were limiting (i.e., predation determined K), removal of coyotes should have increased K, translating to an increase in R as the deer population responded. No change in R was observed.

More recently, research conducted by Hurley et al. (2011) in southeast Idaho also tested the effectiveness of coyote removal from deer winter range as a management strategy to improve mule deer population performance. Hurley et al. (2011) removed an average of 53.3 coyotes/1,000 km^2 per year during a 6-year period. Coyote removal did result in increased neonate survival during years in which lagomorph populations were low; however, the increase in survival was temporary. Subsequent December fawn:adult female ratios showed no population level increase stemming from coyote control efforts. No effect of coyote removal was observed during years of normal lagomorph abundance. As was the case with Bartmann et al. (1992), no change in R was observed.

In addition to these large scale predator manipulation studies, several other studies have quantified coyote predation on mule deer in Colorado. In particular, work by Bishop et al. (2009) reported coyote-caused mortality rates for 2 groups and age classes of deer. In the first group, comprised of animals that had received a nutrition enhancement, fawns had a coyote-caused overwinter mortality rate of 0.04 (SE = 0.01) and adults had an annual coyote-caused mortality rate of 0.01 (SE = 0.01). Alternatively, fawns that had not received the nutrition enhancement experienced an overwinter coyote-caused mortality rate of 0.12 (SE = 0.03) and adults experienced an annual coyote-caused mortality rate of 0.02 (SE = 0.01).

Other, non-experimental, research has also been conducted in Colorado. Work conducted by Whittaker and Lindzey (1999) assessed the frequency of coyote predation on mule deer neonates (≤30 days old) on Colorado’s Front Range. Whittaker and Lindzey (1999) reported a 30-day survival rate of 0.66 for mule deer neonates during a 2-year study, with coyotes accounting for 79% of the mortality. When compared to other neonatal survival data during the first 30 days of life (Pojar and Bowden 2004), the survival rates reported by Whittaker and Lindzey (1999) appear to be slightly lower, with coyotes accounting for a higher proportion of the mortality. In the case of each study, coyote predation diminished after the first 30 days of life, highlighting the role of prey vulnerability in the predation process. While this example links vulnerability to age and immaturity, vulnerability can also be associated with malnourishment (Bartmann et al. 1992) or landscape features (Bergman et al. 2006). Because neither the study conducted by Whittaker and Lindzey (1999), nor the study conducted by Pojar and Bowden (2004) measured survival to the stage of recruitment into the adult age class, determining if the predation they documented was additive or compensatory is not possible. However, if the deer herds studied by Whittaker and Lindzey (1999) and Pojar and Bowden (2004) were above *K*, predator caused neonate mortality during the first 1–3 months of life would be compensatory with winter fawn mortality that would be linked to malnutrition.

Other research in Colorado assessed the secondary impact of coyote removal, for livestock protection purposes, on mule deer (Harrington and Conover 2007). Based on sex ratio data, Harrington and Conover (2007) found that coyote control efforts had no effect on deer herd productivity. An extensive literature review conducted by Ballard et al. (2001) resulted in several general conclusions about predation. First, as noted by studies from Colorado, coyote predation can be a significant mortality factor for mule deer. However, Ballard et al. (2001) also noted that discerning the role of coyote predation on deer population dynamics was often confounded by other factors such as weather and habitat condition. This confounding between mortality factors highlights the necessity of discerning between proximate and ultimate mortality causes.

While the role of coyote predation has been the focus of deliberate research, in Colorado there have been no studies that have directly assessed the effect of increased mountain lion (*Puma concolor*) harvest, or mountain lion removal, on mule deer population dynamics. However, the research conducted by Hurley et al. (2011) in Idaho also provides experimental evidence on this topic. Hurley et al. (2011) found that overwinter mortality of adult mule deer decreased and fawn:adult female ratios increased in areas of intense mountain lion removal, indicating that mountain lion predation may be partially additive. Despite these patterns, no significant change in population trend was documented. This result was partially attributed to the conclusion that winter severity was the most significant factor limiting mule deer population growth (Hurley et al. 2011). Thus, the process variation in K stemming from weather had a stronger influence on deer population dynamics than predation. In Colorado, Pojar and Bowden

(2004) reported a 3.2% mountain lion caused mortality rate for mule deer ≤6 months old. Also in Colorado, Bishop et al. (2009) reported a mountain lion caused mortality rate of 0.5% for adult female deer that had received a nutrition enhancement and 3.2% for adult females that had not received the enhancement. While Bishop et al. (2009) found that felid predation comprised nearly 15% of all mortality for deer ≥6 months old, predation on deer that had received a nutrition enhancement was greatly reduced. This was interpreted as evidence that mountain lions selected for animals in poorer condition, which can also be interpreted as that mountain lion predation was at least partially compensatory with starvation.

The role of bear bear (*Ursus americanus*) predation on mule deer population dynamics has not received focused attention in Colorado or elsewhere in the Rocky Mountain West. While bear predation on neonates has been reported in numerous studies (Pojar and Bowden 2004, Bishop et al. 2009), this predation appears to be highly synchronous with birth pulses. Specifically, predation by bears peaks shortly after the peak in parturition before quickly waning during the subsequent 3–5 week period. This pattern has largely lent itself to the perspective that bear predation is not likely a limiting factor in mule deer population dynamics. Literature reviews conducted by Ballard (1992) and Zager and Beecham (2006) identified conditions under which the pulse in bear predation following parturition was most likely additive. In particular, bear predation appeared to be additive when bear densities, particularly black bear densities, were high and ungulate densities were low. However, this evidence was largely specific to brown bear (*Ursus arctos*) and black bear predation on moose in Alaska and Canada (Stewart et al. 1985). More recent evidence provided by Barber-Meyer et al. (2008) has extended this perspective to elk populations as well. Pojar and Bowden (2004) reported a bear-caused mortality rate of 4.0% for mule deer fawns ≤6 months old, although the bulk of this mortality appeared to occur between early June and the middle of August. Bishop et al. (2009) reported low bear-caused mortality rates for adult female deer (0.0%–0.8%), with bear predation probabilities that quickly decayed from a maximum of 0.20 during the first 100 days of life for newborn fawns. Thus, while black bear predation likely does not affect K, it could affect R. However, if herds are winter habitat limited, black bear predation during this period would be compensatory with overwinter malnutrition related deaths.

Intraspecific Competition

The research projects that have addressed intraspecific competition on mule deer in Colorado can be broken into 3 broad categories: stocking experiments, density reduction experiments, and habitat manipulation studies. Of note, with the exception of general management studies, all of these research projects were focused on winter range. Bartmann et al. (1992) used deer-proof fenced pastures, stocked with different densities of deer, to test the effect of intraspecific competition on overwinter fawn survival. Three pastures, ranging from 0.66–1.69 km^2 were stocked with mule deer during 3 separate winters. Deer densities in the pastures were 44, 89, and 133 deer/km^2. Bartmann et al. (1992) found that overwinter survival of fawns was inversely related to density during all years of the study, although malnourishment was the primary cause of mortality in all 3 pastures. The fact that malnourishment related mortality occurred in even the lowest density pasture was considered to be evidence that food limitation was occurring on this winter range. No coyote predation was reported.

The effect of deer density and intraspecific competition was tested under free-ranging conditions as part of 2 different studies. Each of these studies relied on a reduction in deer density as a treatment effect. The first of these utilized deer removal from a non-fenced, winter range study area in order to conduct the previously described stocking experiment (Bartmann et al. 1992). During a 2-year study period, overwinter mule deer density on a treatment study unit was reduced by 22% and 16%, whereas density was left unaltered on control units. Despite these reductions in density, no difference in overwinter survival of fawns was observed between the treatment and control study units. Bartmann et al. (1992) concluded that density reductions were not high enough to induce a treatment effect on overwinter survival of fawns. No differences in mortality causes were observed between treatment and control study units, although as winter severity increased, the percent of fawns that died due to malnourishment increased. Following this initial project, a second density reduction experiment was conducted in which hunter harvest was increased in a treatment study unit, whereas no increased harvest occurred in a control study unit (White and Bartmann 1998). Building on the results of Bartmann et al. (1992) in which reductions in density of 22% and 16% resulted in no detectable treatment effect, desired reduction in density for this second study was >50% (White and Bartmann 1998). Conducted over a 4-year period, the increased harvest resulted in a 76% reduction in density. The reduction in density resulted in increased fawn survival from 0.31 to 0.77 during the treatment period, an increase of 0.46, whereas an increase of 0.29 was observed in the control unit. Despite the fact that an increase in survival occurred in both the treatment and control study units, the higher survival that occurred in the treatment area — the area with lower deer density — can be viewed as evidence that population regulating effects were occurring.

As an alternative to reducing the density of deer, recent research has focused on habitat alteration as a mechanism to increase the finite supply of food. The first of these studies was an experimental manipulation of winter resource availability delivered via pelleted food (Bishop et al. 2009). Using a cross-over study design, Bishop et al. (2009) delivered ad libitum food to mule deer on 2 winter range experimental study units. Average overwinter survival of fawns on the treatment study unit was 0.905, whereas it was 0.684 on control units. Increases in adult survival, pregnancy rates and neonatal survival rates were also detected, ultimately leading to a projected population rate of change of 1.17 on treatment study units, versus 1.03 on control study units. The increases in survival rates and productivity were viewed as evidence that *K* for mule deer was set by nutritional limitation. I extended the results of Bishop et al. (2009) by replacing pelleted food with mechanical habitat treatments on mule deer winter range (see Chapters 1, 2, and 3). While the treatment effect on the overwinter survival of fawns was smaller, I documented a 1.15 times magnitude increase in survival in study units that had received mechanical disturbance treatments, reseeding, and chemical control of weeds over study units that hadn't received any treatments (see Chapter 1). This increase in survival translated to an increase in the projected finite population growth rate from 1.10 in untreated study units to 1.15 in treated study units. However, I failed to conclusively demonstrate an effect when determining if habitat treatments extended to overall abundance (see Chapter 2). This lack of effect, in regards to abundance, was attributed to insensitivity of the abundance estimation procedures, annual variation in weather patterns that periodically forced additional animals on to study units, but also to a lag effect between increased survival of fawns and an attending increase in abundance.

Disease

Research on disease within Colorado's mule deer population, especially during the past 15 years, has primarily focused on Chronic Wasting Disease (CWD). However, the focus of much of this research has been on the spatial ecology of the disease (Conner and Miller 2004, Farnsworth et al. 2006) and mechanisms for reducing the prevalence of the disease in deer herds (Wolfe et al. 2004, Conner et al. 2007). Extension of CWD research to deer population dynamics has largely been based on simulation. Results from these simulation efforts have been variable, although Gross and Miller (2001) demonstrated that population growth and productivity could be strongly influenced by low infection rates, implying a potentially regulating influence. However, extension of simulation results to field assessment has demonstrated weaker effects. In particular, Dulberger et al. (2010) concluded that while effects were present, the influence of CWD on recruitment was weak and could be ignored when considering the effects of the disease on population growth rates. Part of the difficulty in making conclusions about the population level impact of CWD on mule deer is imbedded in the evidence that infected deer are more vulnerable to predation (Miller et al. 2008, Krumm et al. 2009). The fact that mountain lions have demonstrated the ability to select for CWD positive deer demonstrates that compensation between predation and disease-related mortality occurs.

Other diseases, particularly bluetongue and Epizootic Hemorrhagic Disease (EHD), also occur in Colorado. However, outbreaks of these diseases tend to be spatially localized and unpredictable in occurrence. Thus, the frequency and magnitude of outbreaks have remained undocumented. However, Thorne et al. (1988) estimated that 1,000 mule deer died during a bluetongue outbreak in Wyoming, providing evidence that while outbreaks are unpredictable, their impacts may not be trivial. In such cases, disease outbreaks would likely impact N, but not K or R.

Interspecific Competition

Competition between mule deer and other species has received research attention since the 1950s (e.g., McKean and Bartmann 1971). Within this, the majority of competition research, when focused on other wild ungulates, has focused on elk (Beck and Peek 2005, Torstenson et al. 2006). In consideration of domestic livestock, the majority of research has focused on competition between mule deer and cattle (Beck and Peek 2005, Torstenson et al. 2006). A common trend among all of these research projects has been the quantification of dietary and spatial overlap between different species. Studies have consistently concluded that in regards to dietary overlap between mule deer, elk, and cattle, mule deer demonstrate a high degree of diet partitioning as compared to the other 2 species (Beck and Peek 2005, Torstenson et al. 2006). Although not in Colorado, Beck and Peek (2005) recently also found evidence of moderate (45%–59%) diet overlap between mule deer and elk during summer months. Torstenson et al. (2006) reported similar overlap (45%) between these 2 species during spring, although mule deer showed preference for forbs and shrubs, whereas elk showed preference for graminoids. In Colorado, research focused on range response to different stocking rates of mule deer, sheep, and cattle was conducted during the 1950s and 1960s (McKean and Bartmann 1971). This research also demonstrated variable preference for different species of plants by all 3 species. However, McKean and Bartmann (1971) concluded that only under higher density stocking rates of multiple species did deterioration of range conditions occur (McKean and Bartmann 1971). Unfortunately, research focused on competition between mule deer and other species has not been extended to population-level effects. Specifically, a robust evaluation of population-level effects with an estimation of how many mule deer may be replaced by other species in locations of range overlap, has not occurred. While the need for such research has been identified (Lindzey et al. 1997) the financial and logistic constraints to accomplish such work are high. While the research results noted above demonstrate that the direct effects of competition between mule deer and other species are likely low, the indirect effects such as displacement of deer from optimal foraging locations or periods, and the subsequent cascade effect on body condition and productivity can only be speculated.

Habitat Loss and Degradation

Loss of habitat for wildlife species is commonly a piecemeal process. Thus, unlike many other factors that have a negative impact on mule deer, the impact of habitat loss is subtle and effects may only be realized after many years of compounding. Evaluation of the impacts of habitat loss on wildlife populations thus becomes a long process in which repeated quantification of both impacts and populations is necessary. For example, Nellemann et al. (2003) studied the impacts of hydroelectric reservoir infrastructure development on reindeer (*Rangifer tarandus*) during a 10-year period. This effort required monthly surveys of reindeer, but subsequently documented an overall reduction to 8% of pre-development densities in areas within 4km of developed sites. Similar results for mule deer facing habitat loss due to energy development in Wyoming were reported by Sawyer and Nielson (2011). In the case of Sawyer and Nielson (2011), a 43% decline in mule deer abundance was observed in herds facing energy extraction and development, whereas a congruent decline of 23% was observed in nearby control areas. In each of these cases, habitat loss was slow (i.e., spread out over multiple years), but quick enough to be documented during a 10-year period. Habitat loss or habitat deterioration due to other causes, such as exurban and rural residential development, or vegetative succession to less desirable species, may occur over a time period spanning multiple decades. Documenting effects over such long time periods is increasingly difficult. Extension of historical trends into forecasts or predictions of future conditions is subsequently a difficult challenge to overcome. For example, Schwartz et al. (2012) linked projections of road density models with brown bear demographic criteria to estimate the loss of source habitat through 2020, and thus predicted that future exurban development would result in conversion of suitable habitat into sink habitat for brown bears. Similar efforts were made for mule deer in Oregon, although predictions about future habitat conditions were not extended to mule deer abundance (Kline et al. 2010). In addition to direct habitat loss, vegetative conversion within mule deer habitat to new, less desirable or less palatable species can also occur. While not quantified, a subtle example of such a conversion that has likely impacted mule deer in Colorado has been the conversion of mixed agricultural fields that included a higher non-native alfalfa (*Medicago sativa*) component to predominantly grass fields. While recognized as a management dilemma in Colorado, no assessment of mule deer habitat loss or habitat conversion has occurred. Modeling efforts initiated by Johnson et al. (2012) will be the first effort to quantify this habitat conversion by land type as well as by landowner (e.g., private lands, state owned lands and federally owned lands). Thus, while the effects of habitat and nutritional limitation on deer herd productivity are well documented, the effects of habitat loss and conversion on population size have not been quantified. However, the modeling work by Johnson et al. (2012) may ultimately provide a data-based link between $\frac{dN}{dt}$ and reductions in K.

DISCUSSION

Based on published evidence from Colorado and elsewhere, the working hypothesis continues to be that Colorado’s mule deer populations are limited by habitat, and more specifically, quality of winter range habitat. Refining this hypothesis leads to the conclusion that herds are limited by overwinter fawn survival, which in turn is a function of K for that winter. The preponderance of evidence, particularly the evaluations of winter nutrition and habitat management, but also evidence of compensation between predation and starvation support this position. However, some factors remain untested. Tightly interwoven with the view that populations are habitat-limited is the role of intraspecific competition. The theory of density dependence in mule deer is predicated on the assumption that mule deer herds have a finite amount of suitable habitat available for use. Even under optimal conditions, this finite amount of space is capable of supporting a finite number of deer. If the amount of habitat declines, or if the quality of habitat declines, the finite number of deer, *K*, that can be supported is reduced. If accurate, this assumption requires the thorough understanding of the principles of additive and compensatory mortality, but also the ability to discern when mortality is additive versus compensatory. Under the habitat limitation assumption, which assumes that a population is at or above *K*, the cause of mortality for deer is largely irrelevant as it pertains to the doomed surplus in a population; removal of one source of mortality would result in an increase in other mortality causes. Due to the partial dependence of *K* on weather and other stochastic events, even populations that are thought to be slightly below *K* may be subject to a doomed surplus if harsh or extreme conditions occur. Several of the key mule deer research projects discussed in this review demonstrate the phenomena of additive and compensatory mortality. This was particularly evident when coyotes were removed as part of the work conducted by Bartmann et al. (1992). A clear exception to this generalization, but an exception that also provides evidence in support of the working hypothesis, is the lack of compensation that occurred when Bishop et al. (2009) reduced the opportunity for malnutrition by providing pelleted food. In this case, survival rates increased. Bishop et al. (2009) also demonstrated a consistent pattern of higher predation occurring, in the absence of enhanced nutrition, regardless of treatment location. In the case of harvest management studies (Bishop et al. 2005 and Bergman et al. 2011), reductions in fawn:adult female ratios were observed following increases in the male component of different herds. While not direct evidence of a cause-and-effect relationship, these results were potentially indicative that resource limitation was occurring and competitive interactions between different sexes and age classes of deer resulted in shifts in population ratios. The reviewed research pertaining to density-dependence and winter range limitation on Colorado's mule deer herds has occurred at small spatial scales. To extend this knowledge to the field management level, a density reduction experiment at the herd level would be beneficial.

In line with the hypothesis that mule deer are limited by winter range habitat, the role of coyote predation on mule deer does not appear to be limiting. The experimental evaluation of coyote removal on deer population dynamics has been robust. However, to test the regulating effect of coyote predation on deer, a large scale deer density perturbation (i.e., density reduction) would again be beneficial. Evidence from a white-tailed deer and coyote predator-prey system provides evidence that coyote predation may have greater impact on deer populations, and thereby become additive in nature, when deer populations are at lower densities, although this result was confounded by the fact that predation rates on deer were also linked to densities of alternative prey, snowshoe hares (Patterson and Messier 2000). To date, there are insufficient data to make similar conclusions about the impacts of coyotes on low density mule deer populations in Colorado. Specifically, if coyote predation becomes additive at low deer densities, determining the density at which that switch begins to occur is currently impossible.

To date, the effect of mountain lion predation on adult female deer in Colorado is additive or compensatory remains unclear. However, it is possible the impact of this predation is variable, depending on other environmental factors such as deer density, winter severity, or CWD incidence. Based on the abundance of mountain lion habitat in Colorado, as well as conservative mountain lion harvest management strategies, assuming that mountain lion predation on Colorado's mule deer is weakly additive may be reasonable. The population-level effect of bear predation on mule deer neonates (≤2 months old) also remains unclear. Evidence from other predator-prey systems that are comprised of a more complex predator assemblage (e.g., grizzly bears, black bears, wolves and mountain lions) indicates that bear predation during this period is additive. Without more thorough, experimental evaluation, robust conclusions cannot be drawn about the effects of mountain lion and bear predation on Colorado's mule deer herds.

As noted above, other factors in Colorado's mule deer population dynamics also remain untested. For example, despite a large increase in Colorado's elk population between the 1960s and present time, interspecific competition between mule deer and elk has not been evaluated in Colorado. Based on the dearth of information on these competitive processes, Colorado's mule deer management would benefit from research on this topic. Specifically, when put in the context of harvest management and herd management plans, managers and biologists would benefit from a quantitative assessment of deer and elk population interactions. A specific example might include the experimental reduction in herd size of one species, with the desired outcome being a positive response in population parameters (e.g., young:adult ratios, survival rates or overall abundance) in the other species. Likewise, research focused on the roles of summer range, transition range and the role of annual variation in weather has not been conducted. Recent research on elk and summer range (Cook et al. 2004), but also on mule deer transition range (Sawyer and Kauffman 2011) has highlighted this important aspect of ungulate ecology, but remains deficient in Colorado's research program. Specifically, quantification of time spent in transition range and estimation of the nutritional benefits stemming from exposure to those vegetation types would provide biologists with data to confront any assumptions on the importance of transitional range. One final factor that warrants more thorough investigation, especially in North America, is the relationship between climate phenomena and population performance. While addressed more frequently for European and arctic ungulates, and North

Atlantic weather patterns (Post and Forchhammer 2002, Stien et al. 2012), the relationship between weather, climate and mule deer remains largely uninvestigated (but see Marshal and Bleich 2011). Particularly as they relate to shifts in abundance in Colorado, linking the contribution of El Niño and La Niña weather events to large declines in mule deer may prove to temper concerns over herd health.

Despite its apparent presence, the impact and cause of population cycling in mule deer is a neglected subject. This knowledge gap stems from 2 issues: first, most research projects tend to be short in duration (2–4 years) and have only been implemented during the previous 2–3 decades. Similarly, most population monitoring datasets do not extend far enough back in time to quantify any cycling in a robust manner. The second issue that has limited assessment of population cycling in mule deer rests in the fact that many population management decisions are focused on stemming the population decline phase of each cycle. Ultimately, population cycling may largely be viewed as a nuisance in the management process; a phenomenon that has been disrupted by individual differences among herd management objectives and no longer occurs in its traditional form.

As is the case with population cycling, the notion that multiple mortality causes may have an interactive effect on a population has been neglected. While winter browse availability and quality appears to set the upper limit for deer herds in Colorado (i.e., habitat is population limiting), a suite of other factors may regulate how quickly a deer herd reaches that limit. A hypothetical example can be constructed for Colorado’s Front Range where CWD prevalence is high. Krumm et al. (2009) and Miller et al. (2008) found that mountain lions are capable of selecting for CWD infected deer. However, mountain lion diets are diverse and also included non-infected deer. Similarly, due to private land ownership and limited hunter access, hunter harvest of mountain lions is typically low in this region, potentially leading to higher densities of mountain lions. The interaction of disease and predation, coupled with higher predator/prey ratios could conceivably have a strong regulatory effect on deer population growth. A similar example can be found in the vast body of research conducted on northern ungulate systems that are comprised of a more complex predator assemblage (Ballard 1992, Ballard and Van Ballenberghe 1998). Many of these studies have assessed the likely inflection points at which the effects of predation switch from being additive — typically at low prey densities — to compensatory — typically at high prey densities. On reflection of this, a more thorough understanding of predation rates by coyotes, mountain lions and bears, at different deer densities may be a satisfying contribution for hunters, biologists, managers and researchers.

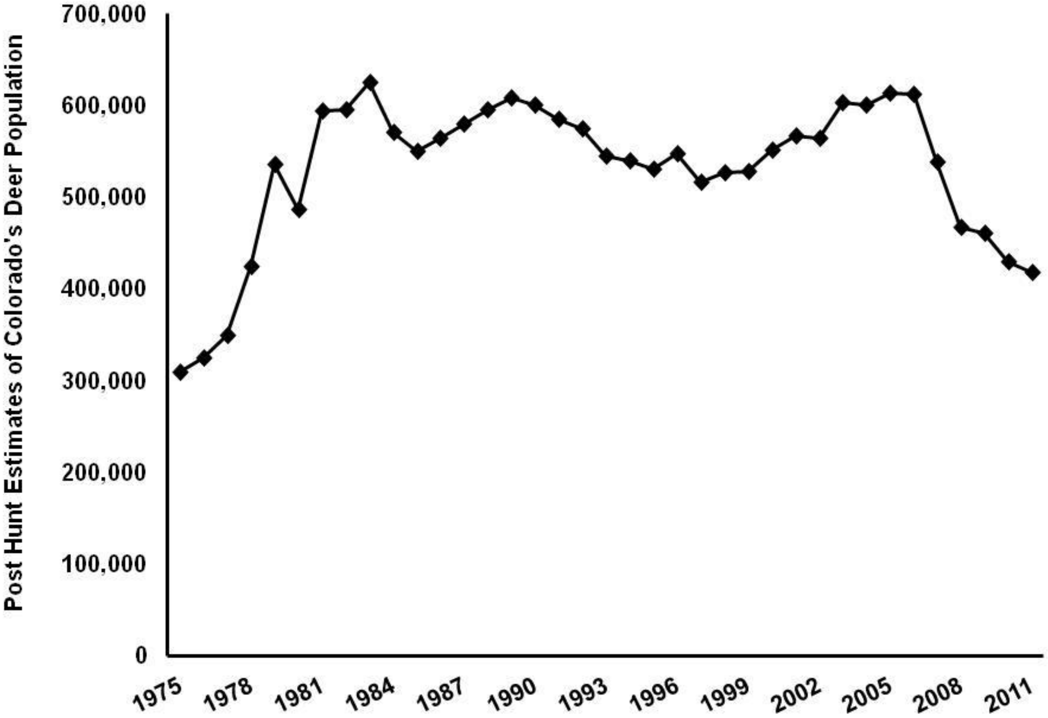

Figure 4.1. Historical (1975–2011) estimates of Colorado's deer population, based on pooled model estimates from throughout the state. The decline beginning in 2007 was the impetus for this review and evaluation of scientific evidence.

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