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Habitat Relations

Habitat Management Influences Overwinter Survival of Mule Deer Fawns in Colorado

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ABSTRACT In the absence of natural or anthropogenic disturbance, many pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) woodland habitats reach late seral stages that encroach into forest openings. This encroachment typically occurs at the expense of browse species that are preferred by mule deer (*Odocoileus hemionus*). Wildlife managers often treat habitat management as a tool to bolster mule deer populations, but documented changes in deer vital rates in response to habitat manipulations are lacking. We evaluated the effects of different levels of habitat improvement on pinyon pine–Utah juniper winter ranges in Colorado on mule deer overwinter survival. Mule deer fawns that overwintered on areas that received both a traditional mechanical treatment as well as follow-up chemical treatments experienced increased survival ($\hat{S} = 0.768$, SE = 0.0851) over fawns on winter range that had only received traditional mechanical treatments or no habitat treatments ($\hat{S} = 0.675$, SE = 0.112). When treatment intensity was partitioned into 3 levels: no treatment, traditional mechanical treatments, and advanced treatments comprised of both mechanical and chemical treatments, mule deer fawns inhabiting winter range subjected to advanced treatments experienced higher survival ($\hat{S} = 0.768$, SE = 0.0849) than fawns on units that experienced only traditional mechanical treatments ($\hat{S} = 0.687$, SE = 0.108), which in turn experienced higher survival than fawns in areas that had received no habitat treatments ($\hat{S} = 0.669$, SE = 0.113). Our study provides evidence that habitat management on winter ranges can positively influence a key vital rate for mule deer in pinyon pine–Utah juniper ecosystems. We recommend that as habitat treatments are planned for benefit of mule deer, those plans include follow-up reseeding and weed control efforts.

KEY WORDS Colorado, fawn survival, habitat management, hydro-axe, mule deer, *Odocoileus hemionus*, roller-chop.

Wildlife managers often are compelled to identify and address the primary limiting factor to population growth. A key example of this challenge can be found in Colorado's mule deer (*Odocoileus hemionus*) population, which has demonstrated large fluctuations with several dramatic declines since 1900 (Workman and Low 1976, Unsworth et al. 1999, Gill 2001, Bergman et al. 2011). Mule deer are a valuable big game species and managers typically wish to increase mule deer abundance or population productivity; yet how to best achieve this outcome has been elusive. Thus, wildlife managers' challenges are 2-fold: understanding the underlying causes of mule deer population change and implementing management actions to moderate population fluctuations or offset population declines.

During the past 25 years, considerable effort and money have been invested in assessing the roles of predation and habitat quality as limiting factors for mule deer populations (Bartmann et al. 1992, Bishop et al. 2009, Hurley et al. 2011). Initial work conducted in Colorado used experimental manipulation to test the hypothesis of compensatory mortality (Bartmann et al. 1992, White and Bartmann 1998). Results from this work demonstrated that density played a primary role in population performance, with extant predators being a proximate source of mortality. More recently, collaborative research conducted by Colorado Parks and Wildlife (CPW) and Idaho Fish and Game identified overwinter fawn survival as playing a key role in population dynamics (Bishop et al. 2009, Hurley et al. 2011). In Idaho, predator removal had no effect on overwinter fawn survival or population trends (Hurley et al. 2011). In Colorado, experiments based on a treatment and control cross-over design showed deer supplemented with ad libitum pelleted food had improved overwinter fawn survival with correspondingly fewer predation events (Bishop et al. 2009). Thus, Bishop et al. (2009) concluded that overwinter nutrition was the primary factor limiting that population. Because of 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 is needed.

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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 and abundance of forbs. In particular, in many pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) woodland winter range habitats, pinyon pine, and juniper trees have encroached into forest openings and slowly replaced shrubland communities. Whereas this process increased escape and thermal cover for deer, these changes simultaneously may have reduced the nutritional carrying capacity of mule deer winter range via the loss of key forage species. In the absence of periodic fire and because wood products from these forests are of low economic value, mechanical disturbance is the primary approach to create and reset the vegetative structure of forest openings. Research on mule deer use of areas treated primarily via burning has demonstrated mixed results, with the majority of the response occurring during the 3-year period following treatment (Kie 1984, Long et al. 2008). However, research linking mule deer vital rates to habitat management, specifically mechanical disturbance, weed control, and reseeding, is lacking. 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 vital rates or deer population performance. Linking habitat management to mule deer population performance would provide managers with necessary information on the effectiveness of their habitat management strategies and efforts, thereby facilitating design and implementation.

To partially address this knowledge gap, we measured the overwinter survival of 6-month-old mule deer fawns across 3 types of study units: traditional treatment units, advanced treatment units, and reference units, wherein traditional treatment units were disturbed and reseeded simultaneously, advanced treatment units were traditional treatments that subsequently received follow-up weed control and additional reseeding, and reference units received no habitat manipulation. Our objective was to determine if overwinter survival of deer increased on mule deer winter range that had received habitat manipulation. Our prediction was that 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

We conducted this research on the southeastern portion of the Uncompahgre Plateau and in neighboring drainages of the San Juan mountain range in southwest Colorado (Fig. 1). We identified 8 study units, composed of mule deer winter range, for inclusion in this study (Table 1, Fig. 1). Study units were between 38° 15′ N and 38° 49′ N latitudes and between 107° 41′ W and 108° 28′ W longitudes with an elevation range of 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). Maximum winter (Dec–Feb) temperatures ranged between 3.7°C and 7.1°C and minimum temperatures ranged between −9.1°C and −5.7°C (Western Regional Climate Center 2011). Mule deer winter range across the study area and all study units was composed of pinyon pine–Utah juniper 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. The management objectives for D-19 and D-40 were similar. Both DAUs were managed for 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. The DAUs were delineated to capture both summer and winter range for deer and although deer used separate and distinct portions of winter range, a high level of mixing and spatial overlap occurred on summer range. Desired post-hunt sex ratios were 25–35 adult males per 100 adult females for these DAUs. All study units were centered on and primarily composed of public lands (U.S. Bureau of Land Management and State Wildlife Areas), although most study units had private land at lower elevations. Elk (*Cervus elaphus*) were present at all study units, although spatial overlap with deer was nominal because elk tended to use higher elevations.

METHODS

We classified study units into 2 treatments or untreated. Traditional treatment units were disturbed and reseeded simultaneously and advanced treatment units were also reseeded with browse species and received weed control efforts at a later date. For a portion of winter range to be labeled as a treated unit it had to have received some form of mechanical treatment within the previous 3–6 years. Incorporating a time lag between delivery of mechanical treatments and initiation of survival monitoring was a deliberate decision based on the lack of information regarding vegetative response to disturbance. To safeguard against the potential that habitat quality may decline immediately following treatment until browse species establish and grow (Young et al. 1985; Bates et al. 1998, 2000; Miller et al. 2000), we deliberately incorporated a 3–6-year time lag to increase the likelihood of detecting a survival response in deer.

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 treatments with less uniform shapes. A roller-chopper consisted of a large drum, affixed with perpendicular blades,

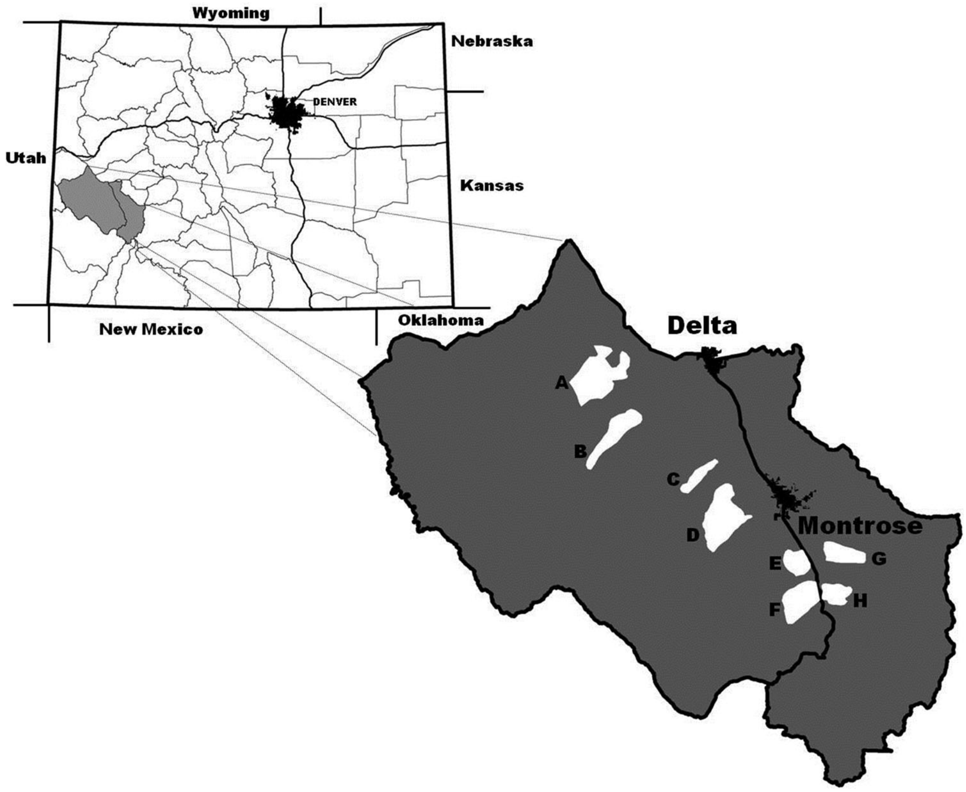

Figure 1. Map of Colorado depicting Data Analysis Unit (DAU) boundaries and the general study area located on the Uncompahgre Plateau and neighboring valleys in the San Juan Mountains in southwest Colorado. The general study area (solid gray DAUs), which encompassed the 8 study units (white polygons) is shown in relation to the surrounding communities of Delta and Montrose, Colorado (black polygons). From northwest to southeast, study units included Sowbelly (A), Peach (B), Transfer (C), Shavano (D), Colona (E), McKenzie (F), Buckhorn (G), and Billy Creek (H).

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 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. Mechanical disturbance efforts were intended to create forest openings that were conducive to shrub species growth but also to maintain nearby access to closed forest habitats that provided escape and thermal cover.

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 had an additional treatment that included reseeding and weed control efforts 2–4 years after the traditional mechanical disturbance. The follow-up reseeding efforts used seed mixes composed of desirable browse species for mule deer (bitterbrush, cliffrose,

Table 1. Comparison of size and timing of habitat treatments on 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	Reference	94.4	0	
B: Peach	Advanced treatment	50.7	4.5	2001[a]
C: Transfer	Traditional treatment	30.4	2.0	2001
D: Shavano	Traditional treatment	87.3	7.3	2004
E: Colona	Traditional treatment	27.1	1.1	2003
F: McKenzie	Traditional treatment	19.3	2.5	2004
G: Buckhorn	Reference	23.4	0	
H: Billy Creek	Advanced treatment	25.3	1.7	1998[b]

[a] Advanced treatment reseeding and herbicide applications occurred during summer 2006.
[b] Advanced treatment reseeding and herbicide applications occurred during summers 2006 and 2007.

sagebrush, serviceberry [*Amelanchier alnifolia*], and four-wing saltbush [*Atriplex canescens*]). Follow-up weed eradication, via application of the herbicides Plateau® (imazpic), Milestone® (aminopyralid), and glyphosate, targeted cheatgrass (*Bromus tectorum*) and jointed goatgrass (*Aegilops cylindrica*). 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. 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

We selected 8 study units based on their habitat treatment history. Further, because of the potential variation in weather patterns, we stratified the area by latitude and first selected a reference unit and a paired advanced treatment unit in both the northern (study units A and B) and southern halves (study units G and H) of the study area (Table 1, Fig. 1). Paired units were 5 km (southern pairing) and 8 km (northern pairing) apart to minimize the movement of animals between study units. Both advanced study units were located on State Wildlife Areas, whereas each of the reference study units were located on lands primarily administered by the Bureau of Land Management. Although land management was potentially confounded with the study objectives, differences between study unit pairings were subtle. The study area had a 6.7% difference in conifer-pine tree cover and a 5.7% difference in shrubland between the advanced treatment and reference study unit pairing in the north. Differences in percent cover were 1.7% and 5.7% for conifer-pine and shrubland, respectively, in the southern unit pairing. Overall, grazing pressure from domestic livestock was minimal on all study units, with the majority of grazing occurring as livestock producers moved animals from summer range pastures to private pastures on the valley floor. Grazing intensity from domestic livestock was strongest on the northern study unit pairing, but the reference study unit and the advanced treatment study units were not different.

Whereas we focused our efforts on the paired reference and advanced treatment areas each year, we also included a different traditional treatment study unit each year of our 4-year study. These 4 traditional treatment units (study units C–F; Table 1) were identified prior to the start of the study and we randomly selected the year that each was included without replacement. We incorporated the traditional treatment study units to extend the inference to which results could be applied. As such, our hypothesis was tested on 8 study units (2 reference units, 2 advanced treatment units, and 4 traditional treatment units) over a 4-year period.

Fawn Capture and Monitoring

We determined a sample size of 25 mule deer fawns per study unit, per year, would provide the necessary power to detect a 20% difference in survival between reference units and advanced treatment study units during the 4-year study, based on power analysis using $\alpha = 0.05$, $\beta = 0.30$, and long term overwinter fawn survival estimates of 0.44 (SD = 0.217; Unsworth et al. 1999).

Because of the remote location of several study units, helicopter net-gunning (Webb et al. 2008; Jacques et al. 2009) was the primary method of capturing deer. In study units that were easily accessible from roads, we also used baited drop nets (Ramsey 1968, Schmidt et al. 1978, White and Bartmann 1994) for capture. We fitted all captured fawns with temporary very high frequency (VHF) radiocollars that were designed to drop off after 6 months (LOTEK Wireless, Inc., Newmarket, ON, Canada). All radiocollars were equipped with mortality sensors, which would increase the pulse rate of transmitted signals after remaining motionless for 4 hours. We weighed fawns and recorded sex at the time of capture. Captures occurred between 1 December and 1 January. Capture, handling, and radiocollaring procedures 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).

We routinely monitored all radiocollared deer between the time of capture and 15 June of each year. Routine monitoring included ground monitoring 2–4 times per week. However, we could not reliably detect all radiocollared deer via ground monitoring. Thus, we also conducted weekly monitoring flights to ensure that we determined the live or dead status of each deer at least once per week. When detected, we investigated mortalities within 1–2 days to improve estimates of the date of death and to determine cause of death.

Statistical Analysis

We conducted survival analyses using the known-fate data type in Program MARK (White and Burnham 1999) and model selection and variable weighting strategies followed the methods of Burnham and Anderson (2002). We based model selection on differences in Akaike's Information Criterion that was corrected for small sample size (AIC_c) between models. To remove potential bias from survival estimates from capture related mortalities and stress of the capture process, deer did not enter the survival analysis for the first week following capture. We built models that allowed deer survival to vary by study unit, treatment intensity, week, and year. Models that accounted for treatment intensity partitioned all study units into 3 categories (reference units, traditional treatment units, and advanced treatment units; Table 1). In addition to study unit variation, we also built models that partitioned data by sex and mass. Following the suggestion of Doherty et al. (2010), we built all possible combinations of additive models. 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. Inherent in this model building comparison strategy was inclusion of models that omitted any aspects of habitat treatments. We used model averaging of this model set for parameter estimation.

For a posteriori exploratory purposes, we evaluated several additional models. First, we assessed a highly parameterized, multiplicative interaction model that allowed survival to vary within a single year and between different years. Likewise, based on initial model results, we built a subset of models to assess the role of treatment history. These models did not differentiate between traditional treatment and advanced treatment units. As opposed to the original model structures, the exploratory treatment history models partitioned all study units into 2 treatment categories: treated units (e.g., traditional treatment and advanced treatment units pooled), and reference units. We did not include any of the exploratory models in the cumulative model weights or final model comparisons.

RESULTS

We captured 498 6-month-old mule deer fawns. Because of radiocollar malfunction ($n = 9$) and mortalities ($n = 13$) that occurred within 1 week of capture, we left-censored 22 of these deer from the survival analyses. We right-censored 8 additional animals during the study, 1 because of a mid-winter movement from a study unit to a neighboring unit and 7 because of premature shedding of radiocollars. During the 4-year study, 2 deer died during the 7–14-day postcapture window, and 2 deer died during the 14–21-day postcapture window. Of these 4 mortalities, 2 were due to predation, 1 was due to malnutrition, and 1 was due to unknown causes. Although these deaths were possibly influenced by the capture process, we did not find a cause-and-effect relationship. We included those mortalities in the survival analysis to minimize any artificial inflation of survival rates due to censoring. Post censorship, average sample size for each study unit and each year was approximately 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 candidate models, 10 were within 7.0 AIC_c units and accounted for >99.5% of the total model weight (Table 2). The remaining models had ΔAIC_c values >11.0 and accounted for <0.5% model weight. Fawn sex consistently entered into several of the best models, but models that neglected sex consistently received more support than otherwise identical models (Table 2). Based on the estimates from our best model, we found a positive effect of mass on survival probability ($\hat{\beta} = 0.096$, SE = 0.021; Fig. 2). Three variables were consistently included in the 10 best models. In particular, year (AIC_c cumulative weight = 0.998) and week (AIC_c cumulative weight = 0.997) effects were always present (Tables 2 and 3). Likewise, individual mass at capture (AIC_c cumulative weight = 0.999) consistently appeared in all of the 10 best models (Tables 2 and 3). Of note, in only 2 of the 10 best models did individual study units (AIC_c cumulative weight = 0.042) appear in the model structure (Tables 2 and 3). The best of these 2 models had a ΔAIC_c value of 5.16 and accounted for only 2.8% of the total model weight (Table 2). Alternatively, models that accounted for advanced treatments (AIC_c cumulative weight = 0.795) and traditional treatment (AIC_c cumulative weight = 0.272) comprised the 4 best models (Tables 2 and 3). The model best supported by our data ($\omega_i = 0.376$) was comprised of an intercept term, year, week, mass, and advanced treatment structures. Thus, this model did not

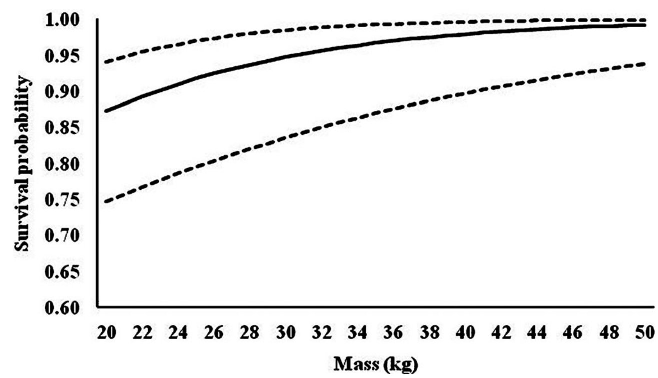

Figure 2. The effect of mass, with 95% confidence intervals, on overwinter survival of mule deer fawns between 2005 and 2008 in southwestern Colorado. Observed mass of fawns ranged between 21.4 kg and 48.6 kg. We did not observe a consistent relationship between sex of fawn and survival.

Table 2. Log likelihood values and model selection results of overwinter survival analysis of 6-month-old mule deer fawns from different study units in southwestern Colorado, 2005–2008. Model selection is based on Akaike's Information Criterion that has been corrected for small sample size (AIC_c). We constructed models 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). The intercept term includes the treatment effect for reference study units.

Model	Model structure	ΔAIC_c	ω_i[a]	Log (L)	K[b]
1	Int + Yr + Week + Mass + Ad. Trt	0.00[c]	0.376	−671.43	29
2	Int + Yr + Week + Mass + Sex + Ad. Trt	1.34	0.193	−703.06	30
3	Int + Yr + Week + Mass + Trt + Ad. Trt	1.91	0.145	−671.25	30
4	Int + Yr + Week + Mass + Sex + Trt + Ad. Trt	3.17	0.077	−671.88	31
5	Int + Yr + Week + Mass	3.18	0.077	−670.74	28
6	Int + Yr + Week + Mass + Sex	4.66	0.037	−674.90	29
7	Int + Yr + Week + Mass + Trt	4.83	0.034	−673.85	29
8	Int + Yr + Week + Mass + Area	5.16	0.028	−674.01	35
9	Int + Yr + Week + Mass + Sex + Trt	6.39	0.015	−667.72	30
10	Int + Yr + Week + Mass + Sex + Area	6.73	0.013	−673.66	36

[a] AIC_c model weight.
[b] Accounting for parameters is as follows: Int = 1, Yr = 3, Week = 23, Mass = 1, Trt = 1, Ad. Trt = 1, Sex = 1, Area = 7.
[c] AIC_c value for the best model was 1,404.77.

Table 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, southwestern Colorado, 2005–2008.

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

distinguish between individual study units, but it demonstrated an effect of treatment intensity (i.e., it distinguished advanced treatment units from all other units). The slightly more complex model that included fawn sex did not capture the variation within the data quite as well ($\Delta AIC_c = 1.34$; $\omega_i = 0.193$). Also within ΔAIC_c of 2.0 was the third best model that included both traditional treatment effects and advanced treatment effects ($\Delta AIC_c = 1.91$; $\omega_i = 0.145$). As opposed to the best model, this model accounted for treatment intensity on all levels (i.e., traditional treatment units, advanced treatment units, and references were all distinguished from one another). Survival estimates also were consistent between these models in that the effect of both habitat treatment types on survival was positive. For the best model, the effect of advanced habitat treatments ($\hat{\beta} = 0.409$, SE = 0.183) was strong. For the model in which both types of treatments were included (the AIC_c third best model), advanced habitat treatment effects ($\hat{\beta} = 0.432$, SE = 0.196) were stronger than traditional treatment effects ($\hat{\beta} = 0.070$, SE = 0.222). We observed a consistent pattern within models that were structured similarly in that models that accounted for all 3 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, Table 2). However, the beta estimates for traditional treatments and advanced treatments were positive in all models. The best model that did not account for habitat treatment intensity was marginally competitive ($\Delta AIC_c = 3.18$), but it accounted for considerably less model weight (7.7% of total model weight). The remaining covariates of interest accounted for less than 50% of the cumulative AIC_c weight (Table 3), indicating that they were only present in the least supported models and did not meaningfully contribute to the overwinter survival of fawns.

Annual survival declined during the study regardless of treatment intensity (Fig. 3). Nonetheless, survival rates were high during all 4 years of the study. Estimated survival rates, based on our best model, for advanced treatment units declined 21.7% from 0.866 (SE = 0.0320) to 0.678 (SE = 0.0512) during the 4-year study period. Similarly, based on our third best model, estimated survival rates for traditional treatment study units declined 29.4% from 0.813 (SE = 0.0463) to 0.574 (SE = 0.0687) and survival rates in the reference units declined 31.1% from 0.801 (SE = 0.0432) to 0.552 (SE = 0.0557).

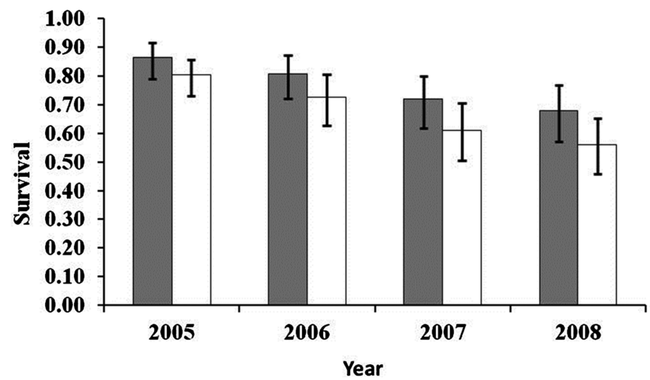

Figure 3. Estimated overwinter survival rates, with 95% confidence intervals, of 6-month-old mule deer fawns from study units in southwestern Colorado. Model estimates stem from the best performing survival model. Dark gray bars reflect annual survival estimates of fawns from advanced treatment study units and white bars reflect pooled survival estimates of fawns from traditional treatment and reference study units.

Exploratory model results helped elucidate the appropriate level of complexity and structure that could be supported by our data. Although 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 have had negligible support ($\Delta AIC_c = 47.38$). For the exploratory models in which survival was modeled based on treatment intensity (i.e., data from traditional treatment units and advanced treatment units were pooled), the magnitude of the advanced treatment effect was diluted. Because of the pooling of data, the resulting standard error was improved ($\hat{\beta} = 0.299$, SE = 0.171), but this was an artifact of the larger sample size.

DISCUSSION

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 our 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). Nevertheless, our results provide evidence that landscape-scale habitat treatments can improve mule deer fawn survival. However, our modeling results demonstrate that follow-up reseeding and weed control are essential to realize the full benefits of mechanical disturbance. More specifically, although mechanical disturbance fills the crucial role of creating space and resources for shrubs by opening up the forest canopy and reducing vegetative competition with mature trees (Miller et al. 2000), initially the area likely had an inadequate native browse seed base to benefit mule deer (Lang and Halpern 2007). In particular, Miller et al. (2000) found that cover and diversity of herbaceous species declined in sagebrush associations as dominance of juniper increased. Lang and Halpern (2007) found a limited potential for meadow species to recover from the existing soil seed bank following removal of forest canopy. We acknowledge that our study did not assess mule deer survival immediately following mechanical disturbance. After treatments, we assumed that a time lag was needed for browse species to establish and grow. Fawn survival possibly increased initially in units following the traditional treatment with a subsequent decline; our 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 time since delivery of habitat treatments in the traditional treatment study units was 3–6 years. Alternatively, survival rates of fawns wintering in the traditional treatment study units may have never reached those observed in the advanced treatment units. Regardless of which scenario actually occurred, the 1.14× increase in survival in advanced treatment units over reference units highlights the importance of following-up on mechanical treatments. When data were not pooled and advanced treatment units were compared to both traditional treatment and reference units, this difference in survival reflects a 1.12× magnitude increase over traditional treatment units and a 1.15× magnitude increase over reference units. The minimal 1.03× magnitude effect of traditional habitat treatment practices in increasing survival over reference units further highlights the importance of follow-up treatments as part of planned habitat management for mule deer. Although the increase in survival between types of study units was not surprising, the lack of a true manipulative experimental design allows for other variables to be correlated with the various treatments. Specifically, randomization of treatment types and study units was not possible, leading to the location of all advanced treatment study units on State Wildlife Areas. These State Wildlife Areas were acquired primarily as mitigation offsets for development projects that occurred on nearby mule deer winter range and did not differ from the surrounding federally owned lands in topography, grazing intensity, or natural vegetation structure.

Advanced habitat treatment efforts provided a substantial boost to overwinter survival of mule deer fawns beyond that observed in traditional treatment and reference areas. In most cases, follow-up with reseeding or chemical control of undesirable species can easily be incorporated into habitat management plans. In many cases, especially on federally managed lands, the planning and implementation process for delivering mechanical habitat treatments includes acquiring National Environmental Policy Act and archaeological clearances as well as writing a formal Environmental Assessment. Extending treatments to include follow-up use of herbicide or reseeding would require minimal additional cost or time, as compared to the costs associated with initial treatments. Although traditional treatments were not as effective as advanced treatments, 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.

We observed a declining trend in annual survival rates during this study that was inconsistent with winter severity or late summer precipitation. Average snowpack was below average during the 2005, 2006, and 2008 winters but above average during the 2007 winter (National Water and Climate Center [NWCC] 2012). Likewise, late summer precipitation was above the long-term average during 2006 and 2007 but below average during 2005 and 2008 (NWCC 2012). The wide range in annual variation in survival rates during this study was not surprising. Both Lukacs et al. (2009) and Unsworth et al. (1999) concluded that even 10 years may not be enough time to capture all of the temporal variation that occurs within fawn survival. Thus, we did not expect habitat management efforts to reduce process variation in fawn survival, but we did expect the efforts to increase mean survival rate. This expectation was met (Fig. 3). Despite the fact that week was repeatedly observed in our best models, we did not observe a discernible trend across weeks. We did not observe an obvious biological processes that could explain the phenomenon and this result was likely a spurious effect within our data. Consistent with previous studies, mule deer fawns that had greater mass at the time of capture experienced higher survival (Bartmann et al. 1992, Bishop et al. 2009).

Managers often face pressure to quickly implement management actions that will prevent further decline of mule deer populations. In many cases, this pressure is focused on predator control. 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). In contrast, this study provides evidence that habitat management has a positive effect on a key population parameter. Because improvements to nutritional status can also increase population productivity (Bishop et al. 2009), the population effects related to improved fawn survival we demonstrate may be an underestimate of the full population response. If adult survival also increased, the overall population growth rate would be expected to increase at a far greater rate. To further evaluate habitat management as a population management tool, additional vital rates including adult survival and reproduction should also be evaluated. Additionally, direct evaluation of the time lag between delivery of habitat treatments and response in mule deer vital rates is necessary. Quantifying the responses of plant species to habitat treatments would also be beneficial. Finally, 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

In the absence of natural or anthropogenic disturbance, many pinyon pine–Utah juniper woodland habitats reach late seral stages that encroach into forest openings. This encroachment typically occurs at the expense of browse species that are preferred by mule deer. This study demonstrates that direct habitat management practices including mechanical disturbance of these forest habitats, followed by concerted reseeding of browse species and chemical control of weeds, can be used to improve the overwinter survival of mule deer fawns. Although follow-up treatments may not be necessary if native seed bases are established in treatment areas, follow-up treatments require minimal additional cost or time in comparison to mechanical disturbance. In the absence of site-specific information, we recommend that mechanical disturbances be followed with reseeding and weed control efforts.

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LITERATURE CITED

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121.

Bates, J. D., R. F. Miller, and T. Svejcar. 1998. Understory patterns in cut western juniper (*Juniperus occidentalis* spp. *Occidentalis hook*) woodlands. Great Basin Naturalist 58:363–374.

Bates, J. D., R. F. Miller, and T. J. Svejcar. 2000. Understory dynamics in cut and uncut western juniper woodlands. Journal of Range Management 53:119–126.

Bergman, E. J., B. E. Watkins, C. J. Bishop, P. M. Lukacs, and M. Lloyd. 2011. Biological and socio-economic effects of statewide limitation of deer licenses in Colorado. Journal of Wildlife Management 75:1443–1452.

Bishop, C. J., G. C. White, D. J. Freddy, B. E. Watkins, and T. R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Second edition. Springer, New York, New York, USA.

Doherty, P. F., G. C. White, and K. P. Burnham. 2010. Comparison of model building and selection strategies. Journal of Ornithology 152: S317–S323.

Gill, R. B. 2001. Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife Special Report Number 77, Fort Collins, USA.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178.

Jacques, C. N., J. A. Jenks, C. S. Deperno, J. D. Sievers, T. W. Grovenburn, T. J. Brinkman, C. C. Swanson, and B. A. Stillings. 2009. Evaluating ungulate mortality associated with helicopter net-gun captures in the Northern Great Plains. Journal of Wildlife Management 73:1282–1291.

Kie, J. G. 1984. Deer habitat use after prescribed burning in northern California. Research Note PSW-369. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Lang, N. L., and C. B. Halpern. 2007. The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. Canadian Journal of Botany 85:557–569.

Long, R. A., J. L. Rachlow, and J. G. Kie. 2008. Effects of season and scale on response of elk and mule deer to habitat manipulation. Journal of Wildlife Management 72:1133–1142.

Lukacs, P. M., G. C. White, B. E. Watkins, R. H. Kahn, B. A. Banulis, D. J. Finley, A. A. Holland, J. A. Martens, and J. Vayhinger. 2009. Separating components of variation in survival of mule deer in Colorado. Journal of Wildlife Management 73:817–826.

Miller, R. F., T. J. Svejcar, and J. A. Rose. 2000. Impacts of western juniper on plant community composition and structure. Journal of Range Management 53:574–585.

National Water and Climate Center. 2012. Natural Resources Conservation Service. National Water and Climate Center, Portland, Oregon, USA.

Pojar, T. M., and D. C. Bowden. 2004. Neonatal mule deer fawn survival in west-central Colorado. Journal of Wildlife Management 68:550–560.

Ramsey, C. W. 1968. A drop-net deer trap. Journal of Wildlife Management 32:187–190.

Schmidt, R. L., W. H. Rutherford, and F. M. Bodenham. 1978. Colorado bighorn sheep-trapping techniques. Wildlife Society Bulletin 6:159–163.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.

Watkins, B. E., C. J. Bishop, E. J. Bergman, B. Hale, B. F. Wakeling, A. Bronson, L. H. Carpenter, and D. W. Lutz. 2007. Habitat guidelines for mule deer: Colorado Plateau shrubland and forest ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Webb, S. L., J. S. Lewis, D. G. Hewitt, M. W. Hellickson, and F. C. Bryant. 2008. Assessing the helicopter and net gun as a capture technique for white-tailed deer. Journal of Wildlife Management 72:310–314.

Western Regional Climate Center (WRCC). 2012. WRCC homepage. <www.wrcc.dri.edu>. Accessed 1 March 2012.

White, G. C., and R. M. Bartmann. 1994. Drop nets versus helicopter net guns for capturing mule deer fawns. Wildlife Society Bulletin 22: 248–252.

White, G. C., and R. M. Bartmann. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. Journal of Wildlife Management 62:214–225.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Workman, G. W., and J. B. Low. , editors. 1976. Mule deer decline in the West: a symposium. Utah State University and Utah Agricultural Experiment Station, Logan, USA.

Young, J. A., R. A. Evans, and C. Rimbey. 1985. Weed control and revegetation following western juniper (*Juniperus occidentalis*) control. Weed Science 33:513–517.

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