

Effect of Enhanced Nutrition on Mule Deer Population Rate of Change

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ABSTRACT Concerns over declining mule deer (*Odocoileus hemionus*) populations during the 1990s prompted research efforts to identify and understand key limiting factors of deer. Similar to past deer declines, a top priority of state wildlife agencies was to evaluate the relative importance of habitat and predation. We therefore evaluated the effect of enhanced nutrition of deer during winter and spring on fecundity and survival rates using a life table response experiment involving free-ranging mule deer on the Uncompahgre Plateau in southwest Colorado, USA. The treatment represented an instantaneous increase in nutritional carrying capacity of a pinyon (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) winter range and was intended to simulate optimum habitat quality. Prior studies on the Uncompahgre Plateau indicated predation and disease were the most common proximate causes of deer mortality. By manipulating nutrition and leaving natural predation unaltered, we determined whether habitat quality was ultimately a critical factor limiting the deer population. We measured annual survival and fecundity of adult females and survival of fawns, then estimated population rate of change as a function of enhanced nutrition. Pregnancy and fetal rates of adult females were high and did not vary in response to treatment. Fetal and neonatal survival rates increased in response to treatment, although the treatment effect on neonatal survival was marginal. Overwinter rates of fawn survival increased for treatment deer by 0.16–0.31 depending on year and fawn sex, and none of the 95% confidence intervals associated with the effects overlapped zero. Overwinter rates of fawn survival averaged 0.905 (SE = 0.026) for treatment deer and 0.684 (SE = 0.044) for control deer. Nutritional enhancement increased survival rates of fetuses to the yearling age class by 0.14–0.20 depending on year and fawn sex; 95% confidence intervals slightly overlapped zero. When averaging estimates across sexes and years, treatment caused fetal to yearling survival to increase by 0.177 (SE = 0.082, 95% CI: 0.016–0.337). Annual survival of adult females receiving treatment ($\hat{S} = 0.879$, SE = 0.021) was higher than survival of control adult females ($\hat{S} = 0.833$, SE = 0.025). Our estimate of the population rate of change ($\hat{\lambda}$) was 1.165 (SE = 0.036) for treatment deer and 1.033 (SE = 0.038) for control deer. Increased production and survival of young (i.e., fetal, neonatal, and overwinter fawn survival) accounted for 64% of the overall increase in $\hat{\lambda}$, whereas adult female survival accounted for 36% of the increase in $\hat{\lambda}$. The effect of nutrition treatment on overwinter fawn survival alone accounted for 33% of the overall increase in $\hat{\lambda}$.

We documented food limitation in the Uncompahgre deer population because survival of fawns and adult females increased considerably in response to enhanced nutrition. We found strong evidence that enhanced nutrition of deer reduced coyote (*Canis latrans*) and mountain lion (*Puma concolor*) predation rates of ≥ 6 -month-old fawns and adult females. Our results demonstrate that observed coyote predation, by itself, is not useful for evaluating whether coyotes are negatively impacting a deer population. Our results also indicate that mountain lions may select for deer in poorer condition under some circumstances, suggesting that mountain lion predation may not always be an additive source of mortality. Disease mortality rates of adult females did not decline in response to enhanced nutrition. Winter-range habitat quality was a limiting factor of the Uncompahgre Plateau mule deer population. Therefore, we recommend evaluating habitat treatments for deer that are designed to set-back succession and increase productivity of late-seral pinyon–juniper habitats that presently dominate the winter range. (WILDLIFE MONOGRAPHS 172:1–28)

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El Efecto de la Nutrición Aumentada en la Tasa de Cambio Poblacional de Venados Bura (*Odocoileus hemionus*)

RESUMEN Preocupaciones sobre disminuciones poblacionales de venados bura (*Odocoileus hemionus*) durante los años noventa han incitado esfuerzos de investigación para identificar y entender los factores claves limitantes de los venados. Semejante a disminuciones pasadas de los venados, la prioridad alta de las autoridades estatales era evaluar la importancia relativa del hábitat y la depredación. Por lo tanto, evaluamos el efecto de la nutrición aumentada de venados durante invierno y primavera en las tasas de fecundidad y supervivencia utilizando un experimento de respuesta de tabla de vida involucrando venados bura silvestres de la Meseta de Uncompahgre en el sudoeste de Colorado. El tratamiento representó un aumento instantáneo en la capacidad nutricional en una área invernal dominado por piñón (*Pinus edulis*) y enebro de Utah (*Juniperus osteosperma*), y fue pretendido simular la calidad óptima del hábitat. Estudios previos en la Meseta de Uncompahgre indicaron que la depredación y la enfermedad fueron las causas más comunes de la mortalidad de venados. Determinamos si la calidad del hábitat fue últimamente un factor limitante crítico de la población de venados por manipular la nutrición y dejar la depredación como fue. Medimos fecundidad y la supervivencia anual de hembras adultas y la supervivencia de los cervatos, entonces estimado la tasa de cambio poblacional en función de nutrición aumentada. El embarazo y las tasas fetales de hembras adultas eran altos y no variaron en respuesta al tratamiento. Las tasas de supervivencia fetales y neonatales aumentaron en respuesta al tratamiento, aunque el efecto del tratamiento sobre supervivencia neonatal fuera marginal. La supervivencia de cervatos por invierno fue considerablemente más alto entre venados del tratamiento que venados de control. La supervivencia de invierno incrementó por 0.16–0.31, dependiendo del año y sexo de cervato, y ninguno de los intervalos de confianza de 95% asociado con el efecto incluyó 0. La supervivencia de cervatos por invierno promediado 0.905 (EE = 0.026) para venados de tratamiento y 0.684 (EE = 0.044) para venados de control. El tratamiento de nutrición aumentada incrementó la supervivencia de fetos a la edad añal por 0.14–0.20 dependiendo de año y sexo de cervato, aunque los intervalos de confianza de 95% asociado con el efecto apenas incluyó 0. Al promediar las estimaciones a través de sexos y años, el tratamiento causó supervivencia de fetos a la edad añal incrementar por 0.177 (EE = 0.082, IC 95%: 0.016, 0.337). Supervivencia de venados hembras recibiendo el tratamiento ($\hat{S} = 0.879$, EE = 0.021) fue más alto que la

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supervivencia de venados controles ($\hat{S} = 0.833$, $EE = 0.025$). Nuestra estimación de la tasa de cambio poblacional, $\hat{\lambda}$, fue 1.165 ($EE = 0.036$) para venados tratados y 1.033 ($EE = 0.038$) para venados controles. La supervivencia por invierno de crías (i.e., supervivencia fetal-neonatal-ciervos pro invierno) explicó 64% del aumento global en $\hat{\lambda}$, mientras que la supervivencia de los venados hembras adultas explicó 36% del aumento en $\hat{\lambda}$. El efecto del tratamiento de nutrición en la supervivencia de ciervos por invierno solo explicó 33% del aumento global en $\hat{\lambda}$.

Documentamos limitación de alimento en la población de venados de la Uncompahgre porque la supervivencia de los ciervos y las venados hembras incrementó considerablemente en respuesta a la nutrición aumentada. Encontramos evidencia fuerte que nutrición aumentada de venados redujo depredación por coyotes (*Canis latrans*) y pumas (*Puma concolor*) en ciervos ≥ 6 meses de edad y en venados hembras. Nuestros resultados demuestran que depredación por coyotes observada, sola, no es útil para evaluar si los coyotes impactan negativamente a una población de venados. Nuestros resultados indican también que las pumas pueden seleccionar venados en peor condición bajo algunas circunstancias, sugiriendo que depredación por pumas no siempre puede ser una fuente aditiva de la mortalidad. Las tasas de mortalidad por enfermedad de venados hembras no disminuyeron en respuesta a la nutrición aumentada. Calidad del hábitat en el área invernal fue un factor limitante de la población de venados bura de la Meseta Uncompahgre. Por lo tanto, recomendamos evaluar tratamientos del hábitat para venados que son diseñados para retrasar la sucesión y incrementar la productividad de los habitats del piñon-enebro en etapas avanzadas de sucesión los cuales actualmente dominan la área invernal.

Effet d'un Complément d'Alimentation sur le Taux de Croissance d'une Population de Cerfs Mulet

RÉSUMÉ L'inquiétude concernant le déclin des populations de cerf mulet (*Odocoileus hemionus*) durant les années 1990 a orienté les efforts de recherche vers l'identification et la compréhension des facteurs limitant ces populations. Lors des précédents déclin, l'une des priorités des agences d'état en charge de la faune sauvage a porté sur l'évaluation de l'importance relative de l'habitat et de la prédation. C'est pourquoi nous avons évalué l'impact d'un complément d'alimentation en hiver et au printemps sur les taux de fécondité et de survie, grâce à une analyse démographique impliquant des cerfs muets en liberté sur le Plateau Uncompahgre, dans le sud-ouest du Colorado. Le complément de nutrition peut être considéré comme un accroissement immédiat de la capacité d'accueil de l'aire d'extension hivernale dont l'habitat est composé de pins du Colorado (*Pinus edulis*) et de genévriers (*Juniperus osteosperma*). Ce traitement visait à simuler un habitat de qualité optimale. Des études préliminaires sur le Plateau de Uncompahgre ont montré que la prédation et les maladies sont les principales causes immédiates de mortalité du cerf mulet. En manipulant la nutrition et en laissant la prédation inchangée, nous avons déterminé si la qualité de l'habitat constituait un facteur limitant la performance de la population. Nous avons mesuré la fécondité et la survie annuelle des femelles adultes et la survie des faons. Nous avons ensuite utilisé ces paramètres pour estimer le taux de croissance de la population en présence ou non de complément alimentaire. Les taux de gestation et le nombre moyen de foetus des femelles adultes étaient élevés et ne variaient pas dans la réponse au traitement. Le taux de survie foetale et néonatale a augmenté en réponse au traitement, bien que l'effet du traitement sur la survie néonatale ait été marginal. Le taux de survie hivernale des faons était nettement plus élevé pour les cerfs ayant reçu l'apport nutritionnel que pour les cerfs ayant servi de témoin. La survie hivernale des faons a augmenté de 0.16–0.31, suivant l'année et le sexe du faon, et aucun des intervalles de confiance à 95% associés à l'effet n'incluait 0. La survie hivernale des faons était en moyenne 0.905 ($SE = 0.026$) pour les cerfs de traitement et 0.684 ($SE = 0.044$) pour les cerfs de contrôle. L'amélioration nutritionnelle a augmenté le taux de survie des foetus âgés de 1 an de 0.14?0.20, suivant l'année et le sexe, bien que l'intervalle de confiance à 95% incluait 0. En faisant une moyenne des estimations sur les sexes et les années, le traitement d'apport nutritionnel a permis une augmentation de la survie depuis le stade foetal jusqu'à deux ans de 0.177 ($SE = 0.082$, 95% CI: 0.016, 0.337). Le complément alimentaire a également eu un effet positif sur la survie des femelles adultes. La survie des femelles ayant reçu le traitement ($\hat{S} = 0.879$, $SE = 0.021$) était supérieure à la survie des individus témoins ($\hat{S} = 0.833$, $SE = 0.025$). Notre estimation du taux de multiplication de la population $\hat{\lambda}$ est égale à 1.165 ($SE = 0.036$) pour les cerfs ayant reçu le traitement et 1.033 ($SE = 0.038$) pour les cerfs témoins. L'augmentation de survie des jeunes (i.e., survie fétale, néonatale et survie hivernale des faons) expliquait 64% de l'augmentation totale de $\hat{\lambda}$, contre 36% pour l'augmentation de survie des femelles adultes. L'effet du traitement nutritionnel sur la survie hivernale des faons représentait à elle seule 33% de l'augmentation totale de $\hat{\lambda}$.

L'augmentation de $\hat{\lambda}$ en réponse à un supplément alimentaire nous a permis de mettre en évidence que la croissance de la population de cerfs de l'Uncompahgre est limitée par la ressource en nourriture. Nous avons montré que l'amélioration de la nutrition réduit les taux de prédation par le coyote (*Canis latrans*) et le puma (*Puma concolor*) sur les femelles adultes et les faons de plus de 6 mois. Nos résultats montrent que l'observation de prédation les coyotes n'est pas en soi utile pour déterminer si cette prédation a ou non un impact négatif sur une population de cerfs. Nos résultats indiquent également que, sous certaines circonstances, les pumas pourraient sélectionner les cerfs en mauvaise condition, ce qui suggère que la prédation par les pumas n'est probablement pas toujours une source de mortalité additive. Le taux de mortalité par maladie des femelles adultes n'a pas diminué en réponse à l'amélioration de la nutrition. La qualité de l'habitat dans l'aire de répartition hivernale est un facteur limitant la population de cerfs muets du Plateau de Uncompahgre. Par conséquent, nous recommandons l'évaluation de traitements visant au retour des successions végétales et à l'accroissement de la productivité des habitats non-climatiques de pins/genévriers, lesquels dominent actuellement la répartition hivernale du cerf-mulet.

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INTRODUCTION

Mule deer (*Odocoileus hemionus*) populations apparently declined during the 1990s across much of the western United States and present numbers are well below peak population levels documented during the 1940s–1960s (Unsworth et al. 1999, Gill et al. 2001, Heffelfinger and Messmer 2003). An understanding of limiting factors is necessary to understand why populations may have declined and to guide management efforts aimed at increasing deer numbers (Gill et al. 2001, de Vos et al. 2003). Factors limiting growth of mule deer populations are difficult to understand because they are numerous, interacting, and subject to variability. Climatic variation can cause wide population fluctuations and may be the primary reason for observed changes, yet managers are concerned with factors that can be manipulated through management actions. Predation and habitat have typically received the most attention from wildlife agency administrators, biologists, and sportsmen. Predation is routinely identified as the most common proximate cause of deer mortality. Habitat quality is believed to have declined across much of the western United States because of altered fire regimes and associated plant successional changes, invasion of noxious weeds, overgrazing,

energy development, and habitat loss caused by urban development (Lutz et al. 2003, Watkins et al. 2007).

Identification of principal limiting factor(s) is necessary to make informed management decisions. Some mule deer populations may be driven by extreme environmental variation that is primarily density independent, in which case the preferred management strategy may be to monitor populations, or perhaps climate variables, and make responsive harvest decisions (Mackie et al. 1998). However, in less-variable environments, determining whether habitat or predation is most limiting has substantial management implications because the 2 factors represent divergent limitation scenarios.

The relationship between habitat quality and deer population size is heavily rooted in density-dependence theory. As populations approach or exceed nutritional carrying capacity (NCC) of a given environment, fecundity and survival are expected to decline. Nutritional carrying capacity refers to the number of animals that can be supported on a specified landscape given animal nutrient requirements relative to nutrient availability (McLeod 1997). Density-dependent effects have been demonstrated in body condition (Gaillard et al. 1996, Stewart et al. 2005, Kjellander

et al. 2006), fecundity (Clutton-Brock et al. 1987, Stewart et al. 2005), and survival (Clutton-Brock et al. 1987, Bartmann et al. 1992, Singer et al. 1997, White and Bartmann 1998) of ungulates. Gaillard et al. (2000) provided a detailed review of density-dependent effects in fecundity and survival of ungulates. If a population is limited by NCC and demonstrating density-dependent feedback, wildlife managers have 2 main options for improving fawn production and survival. One option is to increase adult female harvest to reduce adult female density and increase fawn production and survival. Under this option, the management goal is to optimize age and sex ratios to increase the number of adult males available for harvest (McCullough 1979, 2001). A second option is to improve habitat quality for deer to increase total deer numbers.

When deer populations are below NCC, predation will more likely be a source of additive mortality and biological concern (Ballard et al. 2001). If a population is limited by predation, wildlife managers should pursue management options different than those mentioned above. First, adult female harvest should be minimized, or at least conservatively managed, to maximize production and survival of young. Second, predator control or liberalized harvest of predator species may be considered to lessen mortality and increase deer numbers. Habitat treatments and predator control can be costly in terms of both economic and social capital. Neither option should be pursued without adequate justification.

To determine the importance of different limiting factors, a specific effect must be isolated, often in the context of considerable background variation (i.e., process variance). The relative importance of habitat quality versus predation can be ascertained by manipulating one factor and leaving the other unaltered in a field experiment. If habitat quality is ultimately limiting the deer population, such that further population growth is restricted by NCC, then we would expect observed predation to have minimal effect on population growth (Bartmann et al. 1992, Ballard et al. 2001). In contrast, if the population is below NCC and predation is a common proximate mortality cause, we might expect some threshold of predator removal to cause an increase in the deer population. Ideally, 2 field experiments should be conducted: one that manipulates predation and one that manipulates habitat. Hurley and Zager (2006) conducted an intensive predator control study in southeast Idaho, USA, measuring deer population parameters in response to reductions in coyote (*Canis latrans*) and mountain lion (*Puma concolor*) numbers. Coyote reductions caused an increase in neonatal deer survival during some years, although coyote predation on neonates was found to be partially compensatory. Coyote reductions had no measurable effect on 6-month-old fawn survival, adult female survival, or population size. Mountain lion reductions caused an increase in deer survival that resulted in a small increase in population size. We complemented Hurley and Zager's (2006) study by manipulating deer nutrition and not manipulating coyote and mountain lion predation.

We studied a deer population in southwest Colorado, USA, that declined during the decade preceding our research (B. E. Watkins, Colorado Division of Wildlife [CDOW], unpublished data); the decline was in part caused by a concurrent decline in December fawn recruitment (White et al. 2001). Anecdotal evidence

indicated that quality of winter-range habitat in the area declined during recent decades in response to fire suppression, long-term grazing practices, and a surge in urban and exurban development on winter range. Winter-range habitat predominantly comprised late-seral pinyon (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) woodlands with minimal understory vegetation and limited species diversity. In contrast, anecdotal evidence indicated summer range, which comprised mosaics of aspen (*Populus tremuloides*), mountain shrub, mountain big sagebrush (*Artemisia tridentata*), and Gambel oak (*Quercus gambelii*) with vigorous understory, was highly productive for deer. We hypothesized that poor habitat quality on winter range contributed to the observed decline of the deer population. Predation by coyotes and mountain lions was presented as a competing hypothesis as to why the population declined.

We implemented an instantaneous increase in NCC of winter range habitat and measured deer population responses. We did not manipulate predator numbers or any other potential limiting factor, and we conducted the entire study with free-ranging mule deer. Our research objective was to evaluate the effect of enhanced nutrition on a mule deer population in the context of a life table response experiment (Caswell 2001). Specifically, we evaluated the effect of enhanced nutrition on pregnancy rates and numbers of fetuses produced; fetal, neonatal, and overwinter fawn survival; and annual survival of adult females. We then used these estimates to quantify the effect of enhanced nutrition on population rate of change. Our ultimate goal was to determine whether habitat was limiting a deer population in which predation was the most common proximate mortality factor.

STUDY AREA

We conducted our research in southwest Colorado on the southern half of the Uncompahgre Plateau and in the adjacent San Juan Mountains (Fig. 1). Our winter range study area comprised 2 sites, or experimental units (EUs; Fig. 2): the Colona EU (38°21'N, 107°49'W) and the Shavano EU (38°27'N, 108°01'W). Winter-range EUs ranged in elevation from 1,830 m to 2,290 m and comprised pinyon–Utah juniper woodlands with interspersed big sagebrush adjacent to irrigated agricultural fields. During our study, annual precipitation averaged 22.3 cm and minimum temperature in January averaged -8.2° C in Montrose, Colorado, which is 60 m below the lowest winter range elevation in either EU (Western Regional Climate Center [WRCC] 2005). Deer occupied winter range EUs from November through April each year. Estimated deer densities varied between 31 deer/km² and 59 deer/km² in each EU during the study, with densities periodically reaching 85 deer/km² in portions of an EU when receiving nutritional enhancement treatment. We estimated deer densities in each EU using mark-resight surveys from helicopter on 4 occasions and from the ground on one occasion (C. J. Bishop, CDOW, unpublished data).

Summer range fell between 37°49'N and 38°28'N latitude and 107°26'W and 108°17'W longitude (Fig. 1). Elevations ranged from 1,830 m to 3,500 m, with most deer summering between 2,600 m and 3,000 m. Radiocollared deer from the 2 winter-range EUs were intermixed throughout most of the summer range,



Figure 1. Location of winter-range experimental units (EU; ●) and summer-range study area (diagonal lines) on the Uncompahgre Plateau and adjacent San Juan Mountains in southwest Colorado, USA, where we studied effects of enhanced nutrition on mule deer population performance, 2000–2004.

lessening potential confounding of summer-range habitat use on the effect of the winter-range nutrition treatment (Fig. 2). The notable exception was an area located 12 km directly southwest of the Shavano EU, which was used exclusively by deer from the Shavano EU.

Dominant habitat types on the summer range, from lower to higher elevations, were pinyon–juniper, Gambel oak, ponderosa pine (*Pinus ponderosa*), big sagebrush, aspen, and mixed forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Diverse habitat mosaics occurred at interfaces of each of the major habitat types. Snowberry (*Symphoricarpos* spp.) was a common understory shrub in Gambel oak, ponderosa pine, and aspen habitats and occasionally in sagebrush habitats. Annual precipitation averaged 57.4 cm and maximum temperature in July averaged 26.7° C at the Ouray weather station situated at 2,376 m elevation in the summer range (WRCC 2005).

Deer hunting was limited throughout our study area and hunting pressure was nearly constant during 2000–2004. Our study area comprised substantial portions of CDOW Game Management Units (GMUs) 61, 62, and 65. These 3 GMUs encompassed 7,700 km² with an estimated population of approximately 40,000 deer (B. E. Watkins, unpublished data).

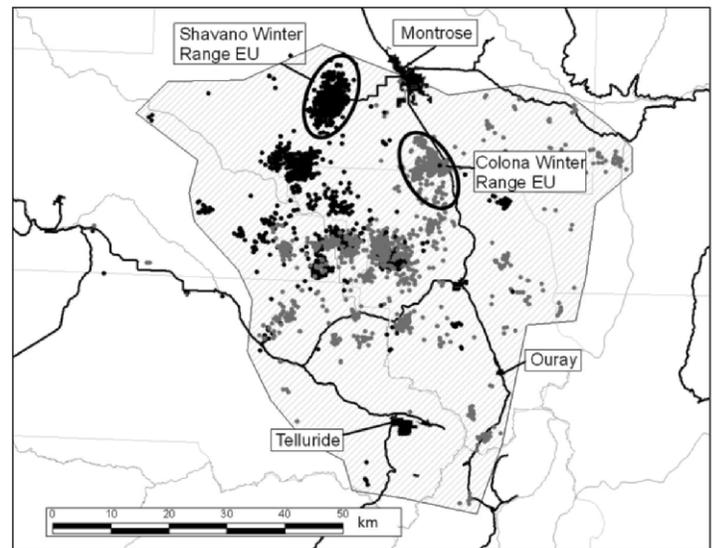


Figure 2. Annual locations of radiocollared mule deer on the Uncompahgre Plateau and adjacent San Juan Mountains in southwest Colorado, USA, 2000–2004. Locations of deer captured in the Shavano experimental unit (EU) are shown in black; locations of deer captured in the Colona EU are shown in gray.

The population estimate was based on a 20-year population model that incorporated periodic estimates of population size from sample-based aerial surveys, annual harvest estimates, and annual measurements of age and sex ratios. Beginning in 1997, the model included annual measurements of overwinter fawn survival and annual survival of adult females. The CDOW issued 2,435–2,760 licenses for adult male deer annually across the 3 GMUs during our study. Hunters harvested 1,200–1,600 adult male deer/year, or roughly 3–4% of the population. There were no hunting seasons for adult female or fawn deer, although ≤ 135 adult females were harvested annually to alleviate game damage across the 3 GMUs. Each winter-range EU comprised mostly public land and received roughly equal hunting pressure on adult male deer during late October and early November.

METHODS

Site Selection

We selected our winter range EUs (Fig. 2) based on several criteria. First, we selected EUs that were separated by ≥ 15 linear km to prevent individual deer from occupying >1 EU. Second, we selected EUs with high deer densities (i.e., >30 deer/km²) so that we could capture adequate samples of deer without making EUs large. We restricted the size of EUs to roughly 15 km² to lessen logistical constraints associated with daily delivery of the nutrition enhancement treatment. We believed 15 km² would be adequate to meet sample-size objectives of deer, given deer densities. Deer densities were estimated across the Uncompahgre Plateau using sample-based helicopter surveys with 0.65-km² sample units (Kufeld et al. 1980; B. E. Watkins, unpublished data). Deer densities generally increased from northwest (<2 deer/km²) to southeast (>30 deer/km²) across the Uncompahgre Plateau; therefore we located our study area on the southern half of the plateau. Finally, we selected EUs that comprised similar habitats with low numbers of wintering elk (i.e., <50 elk in a normal winter). We defined summer range based on migratory movements of radiocollared deer captured in the winter-range EUs.

We studied free-ranging deer and therefore EU size was not static. We defined the core of each EU as the area that received the nutrition treatment and contained roughly 90% of the radiocollared deer captured in that unit. The core of the Colona EU was 7 km² when it received the treatment during 2000–2002. However, during 2002–2004, to achieve sample-size objectives we expanded the core area to 12 km² in response to shifts in deer distribution. The core of the Shavano EU was 22 km² throughout the study. Each EU encompassed approximately 40 km² when considering movements of all radiocollared deer (Fig. 2). Summer range for 95% of the radiocollared deer covered 2,500 km², whereas the total summer range encompassed approximately 4,000 km².

Treatment

We increased NCC by enhancing deer nutrition using a supplemental diet, which was intended to simulate optimum habitat quality from a nutritional standpoint. We opted not to use mechanical treatments or prescribed fire because the treatments could have failed to effectively increase NCC, making it impossible to determine the relative importance of habitat quality and predation. Additionally, we did not want to study the

effectiveness of habitat-treatment strategies until after we determined whether habitat was indeed limiting.

The Colona EU received a nutrition enhancement treatment during winters 2000–2001 and 2001–2002 and the Shavano EU served as a control. We then reversed the treatment–control designations during winters 2002–2003 and 2003–2004 (i.e., crossover experimental design). We only enhanced nutrition of deer on winter range. Multiple studies have found habitat quality on summer range to be a key limiting factor of ungulate body condition, fecundity, and survival (Julander et al. 1961, Gaillard et al. 2000, Cook et al. 2004). In our study area, however, anecdotal evidence strongly suggested that quality of summer-range habitat was high relative to other summer ranges across the western United States, whereas quality of winter-range habitat was poor relative to other winter ranges.

We enhanced nutrition of deer in the treatment EU from early-mid December through April each year by providing a pelleted supplemental feed. The supplement was developed through testing with both captive and wild deer and has been safely used in applied research and management (Baker and Hobbs 1985, Baker et al. 1998). The pelleted ration was commercially produced in the form of $2 \times 1 \times 0.5$ cm wafers (Baker and Hobbs 1985) by Ranch-Way Feed Mills (Fort Collins, CO). The supplement provided 63% *in vivo* dry matter digestibility and 22% crude protein (Baker et al. 1998). Average-sized fawns and adult females in the treatment EU should have met maintenance energy requirements during winter (Thompson et al. 1973, Baker et al. 1979, Holter et al. 1979*b*) by consuming 0.7–0.9 kg and 1.1–1.4 kg of the supplement per day, respectively (Swift 1983, Baker et al. 1998). Based on estimated deer and elk densities in treatment EUs (C. J. Bishop, unpublished data), expected elk consumption rates (i.e., 4.5 kg/elk/day), and daily quantities of the supplement provided, we estimated that consumption was roughly 1.4–2.0 kg/deer/day. Deer consuming the supplement should have exceeded maintenance protein requirements (Ullrey et al. 1967, Smith et al. 1975, Holter et al. 1979*a*).

We distributed pellets daily from 22.7-kg bags using pickup trucks, all-terrain vehicles, and snowmobiles on primitive roads throughout the EU. We distributed each bag of pellets in approximately 20–25 piles in a linear fashion. We spread pellets throughout the entire EU to minimize animal concentrations and to prevent dominant animals from restricting fawn access to the feed. We supplied pellets *ad libitum* such that residual pellets remained throughout the EU when we provided the next day's ration, except during winters 2001–2002 and 2003–2004, when elk often consumed residual pellets. This protocol required distribution of 800–2,000 kg of feed per day, depending on number of elk present, weather, and availability of natural forage. Our approach typically allowed all ages and sexes of deer unlimited access to the supplement. We documented deer use of feed using visual observations and daily monitoring of radiocollared deer. We recorded 1,957 visual observations of radiocollared deer consuming the supplement.

We designed our study such that diet quality of treatment deer should have exceeded diet quality potential of deer on native winter range, even under optimum habitat conditions. Our intent was not to determine the exact level of nutritional enhancement

necessary to effect a change in fecundity or survival, but rather to determine if nutrition was a significant factor limiting fawn recruitment in a declining population where predation and disease were common proximate mortality factors.

Response Variables

Enhanced nutrition of wintering deer could positively impact populations by increasing productivity of adult females and by increasing survival of ≥ 6 -month-old fawns and adult females. We therefore evaluated the effect of treatment on fawn production, neonatal survival, overwinter fawn survival, and annual survival of adult females. We initially planned to use December fawn:adult female ratios as a response variable to reflect fecundity and neonatal survival. However, we struggled to measure fawn:adult female ratios with desired precision and without bias (Bishop et al. 2005b). High deer densities and heavy cover in combination with small EUs contributed to the problem of measuring age ratios adequately. Others have demonstrated that young:adult female ratios can be poor measures of recruitment in ungulates and that pregnancy rates, fetal numbers, and juvenile survival rates should be estimated directly from marked animals (Bonenfant et al. 2005). We therefore measured fecundity and survival rates directly beginning in year 2 of the study. Specifically, we measured pregnancy and fetal rates of adult females (Feb), fetal survival (Feb–Jun), neonatal survival (Jun–Dec), and overwinter survival of fawns (Dec–Jun). We defined pregnancy rate as the proportion of adult females having ≥ 1 fetus in utero during late February, and we defined fetal rate as mean number of fetuses per pregnant adult female during late February. We defined fetal survival as the survival rate of fetuses in utero from February to birth, which we treated as a fecundity parameter. We evaluated the effect of treatment on fawn production and survival exclusively using direct measures of fecundity and survival rates. We also measured annual survival of adult females each year. We then used fecundity parameters (i.e., pregnancy and fetal rates and fetal survival) and survival parameters (i.e., neonatal, overwinter fawn, and adult female survival) in a matrix population model to quantify the population rate of change (λ ; Caswell 2001).

Sample Size Objectives

All fetuses and neonates we used were offspring of radiocollared adult females occupying one of the winter-range EUs. This condition was necessary to appropriately assign treatment status to neonates captured on summer range. Given our dependence on marked adult females to achieve target samples of neonates, we increased our adult female sample throughout the study rather than maintain a specified sample size. We placed vaginal implant transmitters (VITs) in some adult females to facilitate capture of neonates. During 2002, we based sample size of adult females receiving VITs on an evaluation of VIT effectiveness for capturing neonates (Bishop et al. 2002, 2007; Bishop 2007). During 2003–2004, we based sample sizes on number of adult females needed to achieve a target sample of neonates.

We desired to have adequate power to detect a difference in neonatal survival rates of 0.15 between experimental groups (EGs) because this difference reflected the approximate reduction in December fawn:adult female ratios that occurred during the 2 decades in which the Uncompahgre deer population declined

(White et al. 2001; B. E. Watkins, unpublished data). Experimental group refers to deer that directly (ad F and ≥ 6 -month-old fawns) or indirectly (fetuses and neonates) received treatment (treatment EG) or did not receive treatment (control EG). For example, treatment EG included neonatal fawns born from radiocollared adult females that occupied the treatment EU the previous winter. A sample size of 40 neonates per EG per year provided power of 0.81 to detect a difference of 0.15 in survival between treatment and control fawns, assuming survival of control fawns was 0.40. We assumed a control survival rate of 0.40 based on previous neonatal survival rates measured on the Uncompahgre Plateau and December fawn:adult female ratios measured during the late 1980s and 1990s, when the Uncompahgre population declined (White et al. 2001, Pojar and Bowden 2004). We determined that 60 radiocollared adult females (30 treatment and 30 control) equipped with VITs would facilitate capture of ≥ 80 newborn fawns (Bishop et al. 2002, 2007; Bishop 2007). We also assumed that we would capture some fawns from treatment and control adult females that were wearing radiocollars but lacking VITs.

Our target sample size for estimating overwinter survival of fawns was 40 fawns/EG/year. White and Bartmann (1998) measured a 0.15 change in overwinter fawn survival in response to reduced deer density in northwest Colorado. We expected enhanced nutrition to cause a similar effect, and therefore, desired to detect a 0.15 difference for purposes of determining sample size. We assumed a control survival rate of 0.40 based on long-term data from Colorado, Idaho, and Montana, USA (Unsworth et al. 1999). However, data from 4 deer populations across western Colorado indicated that overwinter fawn survival averaged 0.72 during our study (Lukacs et al. 2009).

Capture, Handling, and Radiomarked Samples

We captured and radiomarked 139 adult females during 20 November–14 December 2000–2003, and 241 6-month-old fawns during 20 November–19 December 2001–2003 using baited drop nets (Ramsey 1968) and helicopter net-gunning (Barrett et al. 1982, van Reenen 1982). We captured 165 adult females (including 19 recaptures) during 26 February–2 March 2002–2004, using helicopter net-gunning, and we radiomarked those that were pregnant (2002, $n = 36$; 2003, $n = 58$; 2004, $n = 60$). We hobbled and blindfolded all deer before handling. During drop-net captures, we used stretchers to carry deer away from nets before release. During net-gun captures, we ferried deer ≤ 3.5 km by helicopter to a central handling location.

We fitted deer with vinyl-belted radiocollars equipped with mortality sensors (Lotek, Inc., Newmarket, ON, Canada; Advanced Telemetry Systems, Inc., Isanti, MN), that activated after remaining motionless for 4 hours. We permanently attached radiocollars on all adult females; thus, many adult females were present in samples from multiple years. We temporarily attached radiocollars on 6-month-old fawns by cutting the collar belting in half and reattaching the 2 ends using rubber surgical tubing. Fawns shed collars ≥ 6 months postcapture. We stitched neckband material (Ritchey Mfg. Co., Brighton, CO) to the left side of each radiocollar, which we engraved with a unique marking for visually identifying deer. We measured mass (kg), hind foot length (cm), and chest girth (cm) of each deer and estimated deer age using

tooth replacement and wear (Severinghaus 1949, Robinette et al. 1957, Hamlin et al. 2000).

We measured maximum subcutaneous fat thickness on the rump (cm) and thickness of the longissimus dorsi muscle (cm) of each adult female during captures in February–March using a SonoVet 2000 portable ultrasound unit (Universal Medical Systems, Bedford Hills, NY) with a 5-MHz linear transducer (Stephenson et al. 1998, 2002; Cook et al. 2001). We plucked an area of hair at each measurement point and used lubricant to enhance contact between the transducer and skin. We determined a body condition score for each deer by palpating the rump (Cook et al. 2001, 2007). We combined ultrasound measurements with the body condition score to estimate body fat of each deer (Cook et al. 2007).

We also established pregnancy status and measured fetal rates of each adult female during captures in February–March by performing transabdominal ultrasonography using an Aloka 210 portable ultrasound unit (Aloka, Inc., Wallingford, CT) with a 3-MHz linear transducer (Stephenson et al. 1995). We shaved the left caudal abdomen from the last rib and applied lubricant to facilitate transabdominal scanning. We were unable to obtain accurate fetal counts for 9 adult females, which we excluded from the fetal sample. We also excluded fetuses from 5 adult females that died before giving birth and from 2 adult females that we could not locate following spring migration. Our resulting fetal sample comprised 255 fetuses from 138 adult females in our radiocollared sample (29 ad F with 1 fetus, 101 ad F with 2 fetuses, 8 ad F with 3 fetuses). Nine adult females were present in 2 different years' samples; thus, the 255 fetuses were from 129 unique adult females. Of the 9 adult females 6 had twins each year, 2 females had a singleton one year and twins the other year, and one female had twins and triplets in successive years.

We fitted each pregnant deer with a VIT (Advanced Telemetry Systems, Inc.) and released nonpregnant adult females without a radiocollar or VIT. We performed the ultrasound and VIT-insertion procedures in a 4.3 × 4.9-m wall-frame tent to minimize disturbance from helicopter rotor wash and adverse weather conditions and to create a dim environment to facilitate ultrasonography. Our VITs had temperature-sensitive switches that caused pulse rates to increase from 40 pulses to 80 pulses per minute when the temperature dropped below 32° C. A temperature drop below 32° C was indicative of the VIT being expelled from the deer. We used VITs as an aid to determine timing and location of birth the following June. Bishop et al. (2007) provided a detailed description of VITs and VIT insertion procedures we used.

We located each adult female with a VIT using aerial telemetry every 2–3 weeks during March–May and every morning during June. When we detected a VIT with a fast (i.e., postpartum) pulse rate, we used very high frequency receivers and directional antennae from the ground to simultaneously locate the VIT and radiocollared adult female, which were typically in close proximity. We attempted to account for each adult female's fetus or fetuses as live or stillborn fawns to quantify in utero fetal survival from February to birth. We assumed that no fetuses were resorbed, which is a reasonable assumption for mule deer (Robinette et al. 1955, Medin 1976, Carpenter et al. 1984). We classified each

fawn found dead at a birth site as stillborn unless evidence suggested the fawn was born alive. In most cases, we confirmed that the fawn had died before birth via laboratory necropsy. We located most radiocollared adult females that did not receive VITs approximately every other day from the ground during June, relying on adult female behavior and searches in the vicinity of the adult female to locate neonates. We did the same for any adult female with a VIT that failed because of premature expulsion or battery failure. We usually terminated unsuccessful neonate searches 30–45 minutes following initial location of the radiocollared adult female, although search times occasionally lasted an hour in heavy cover.

We captured and radiocollared 276 neonates born from radiocollared adult females during 4 June–8 July 2002–2004 (2002, $n = 54$; 2003, $n = 103$; 2004, $n = 119$). We removed 6 fawns from the sample because of possible capture-related abandonment or injury, resulting in a sample of 270 radiocollared neonates from 178 adult females in our radiocollared sample (88 ad F with 1 marked fawn, 88 ad F with 2 marked fawns, 2 ad F with 3 marked fawns). We captured neonate(s) from the same adult female as in a previous year on 32 occasions, and we captured the same female's fawns for a third consecutive year on 5 occasions. Thus, we captured 270 neonates from 136 unique adult females. We captured and monitored an average of 2.0 (SE = 0.085), and maximum of 5, neonates per unique adult female during the study.

We wore surgical gloves when securing and handling neonates to minimize transfer of human scent. We captured 75% of neonates in our sample within 2 days of birth. We secured and handled neonates with little or no effort because they rarely attempted to run or resist handling. A short chase was occasionally required to capture older neonates, which often struggled during handling. We placed a drop-off radiocollar with a 2-hour mortality sensor (Advanced Telemetry Systems, Inc.) on each captured neonate. Radiocollars were constructed with elastic neck-band material to allow expansion. Hole-punched, vinyl-belted tabs extended from the end of the elastic and from the transmitter for attachment purposes. We made collars temporary by cutting the vinyl tab extending from the elastic and reattaching the belting with latex tubing, which generally caused the collars to shed from the animal >6 months postcapture. We right-censored 46 neonates that snagged and shed their collars on fences during fall migration, typically 4–5 months postcapture.

We recorded mass (kg), hind foot length (cm), age (days), and sex of each captured neonate. We placed neonates in a cloth bag to measure mass. We estimated neonate age primarily based on radiomonitoring of the adult females and secondarily based on hoof characteristics, condition of the umbilical cord, pelage, and behavior (Haugen and Speake 1958, Robinette et al. 1973, Sams et al. 1996, Pojar and Bowden 2004). Daily monitoring of adult females with functioning VITs allowed us to determine specific dates of birth, and monitoring of other radiocollared adult females often allowed us to identify dates of birth within a 1–2 day period. Handling times approximated 5 minutes per fawn. All deer capture and handling procedures, including VIT techniques, were approved by the CDOW's Animal Care and Use Committee (project protocols 11-2000 and 1-2002).

Monitoring and Cause-Specific Mortality

We radiomonitored deer daily from the ground and approximately biweekly from the air throughout the study to determine fates and mortality causes. We detected signals daily from all radiocollared neonates during the summer and fall and from most radiocollared deer during winter, which typically allowed us to retrieve mortalities within 24 hours of the mortality event. During summer and migration periods, we could not ground-monitor approximately 15–25% of adult and yearling deer on a routine basis. We therefore failed to detect some deer mortalities for several days, or on occasion, for ≥ 1 week.

When we located a dead deer in the field, we conducted a thorough site inspection to record tracks, scat, drag trails, blood, hair, and any other signs that could help determine cause of death. We then collected the carcass or performed a field necropsy on site. We collected and submitted all fresh, intact neonate carcasses to the CDOW's Wildlife Health Laboratory (Fort Collins, CO) or the Colorado State University Diagnostic Laboratory (Fort Collins, CO) for necropsy. We also submitted fresh, intact adult and 6-month-old fawn carcasses to the laboratory for necropsy when logistically feasible. During laboratory necropsies, various tissue samples were extracted for bacteriology, virology, polymerase chain reaction, and virus isolation. We performed field necropsies on all other deer mortalities when at least some portion of the carcass was present. When feasible, we collected and submitted heart, lung, liver, kidney, and spleen samples to the laboratory for analysis. We submitted one fresh sample and one formalin-fixed sample of each tissue. Myers (2001) provided a detailed explanation of necropsy protocols and laboratory diagnostic techniques.

We identified coyote and domestic dog predation based on canine puncture wounds and associated hemorrhaging, torn tissue on the hind legs, tracks, signs indicating a chase or struggle, blood on the ground or vegetation, and buried carcasses (neonates only). Carcasses of deer killed by coyotes were sometimes dismembered and spread across the site, although we did not rely on this observation alone to confirm coyote predation. We identified mountain lion and bobcat (*Lynx rufus*) predation based on cached carcasses, canine puncture wounds and associated hemorrhaging, and tracks. We identified black bear (*Ursus americanus*) predation based on canine punctures and associated hemorrhaging, bruising, peeled hide, and bear sign. We identified malnutrition as a cause of death based on an intact carcass with minimal or no femur marrow fat and the lack of any sign indicating disease, predation, or hemorrhaging. We evaluated femur marrow fat based on appearance and texture (Riney 1955), which was sufficient for identifying deer that had mostly or entirely depleted their fat reserves.

We classified fawn mortalities as canid predation, black bear predation, felid predation, unknown predation (i.e., unidentified predator), disease, starvation or malnutrition, injury or accident, and unknown. Canid predation was caused by coyotes, and to a much lesser extent, domestic dogs. Felid predation was caused by mountain lions and bobcats. Disease mortalities included deaths caused by or associated with hemorrhagic disease, severe diarrhea, pneumonia, infections, and congenital deformities. Injuries and

accidents included fence injuries, blunt trauma, drowning, entanglement in debris, and collisions with vehicles.

We classified adult female mortalities as mountain lion predation, coyote predation, black bear predation, unknown predation, disease, suspected disease, malnutrition, injury, parturition death, and unknown. We did not include harvest as a mortality factor because there were no hunting seasons for adult females during our study. Disease mortalities included deaths caused by hemorrhagic disease, pneumonia, and malignant catarrhal fever (MCF; Schultheiss et al. 2007). Suspected disease mortalities comprised deaths we could not specifically diagnose yet were consistent with disease. We suspected disease because carcasses were intact and field necropsies indicated the deer did not die of predation, malnutrition, or trauma. Injuries primarily included collisions with vehicles, and parturition deaths included any death associated with giving birth.

Statistical Methods

We separately modeled body fat of adult females, pregnancy rates, fetal rates, fetal survival, neonatal survival, overwinter survival of fawns, and annual survival of adult females as a function of the nutrition treatment and other relevant variables. We also modeled cause-specific mortality separately for neonates, wintering fawns, and adult females. For each analysis, we developed a priori model sets based on our expectations of important variable relationships with the ultimate goal of quantifying the effect of nutrition enhancement treatment. We used Akaike's Information Criterion adjusted for sample size (AIC_c) to select among candidate models and we corrected for overdispersion when appropriate using quasi-likelihood ($QAIC_c$). We used model-averaging to reflect model selection uncertainty in estimates of parameters (Burnham and Anderson 2002). In a few instances, however, we based parameter estimates on the model with the lowest AIC_c , generally because that model received all of the Akaike weight.

Body fat and reproductive rates.—We modeled estimated body fat of adult females as a function of treatment and year using PROC MIXED in SAS (SAS Institute, Cary, NC). We modeled pregnancy rates of adult females as a function of treatment and year using PROC LOGISTIC in SAS, and we modeled fetal rates of pregnant adult females as a function of treatment, year, and age class (yearling or ≥ 2 -yr-old F) using PROC MIXED. We did not obtain any data on yearling fetal rates during 2002, and we obtained fetal counts from only 9 yearlings during 2003 and 2004. Thus, we only had power to detect large differences in fetal rates between yearlings and older females.

Fetal survival.—We were unable to determine fate of 96 of the 255 fetuses documented in utero because some VITs were ineffective and newborn fawns were difficult to detect. We therefore developed a joint likelihood that included several nuisance detection parameters to estimate fetal survival in the absence of known fates (Bishop 2007, Bishop et al. 2008). We numerically maximized the natural logarithm of the likelihood function using a quasi-Newton optimization algorithm in PROC NLMIXED in SAS to obtain parameter estimates and the variance-covariance matrix. We modeled fetal survival as a function of treatment and year. There was a potential for overdispersion because our fetus sample comprised a high proportion of siblings. Sibling fetuses may have lacked indepen-

dent fates because they shared the same maternal resources. However, we did not find evidence of overdispersion in our fetal data (Bishop et al. 2008).

Neonatal survival.—We analyzed neonatal survival using the Known Fates option in Program MARK (White and Burnham 1999), which accommodated staggered entry and exit times of marked fawns during the analysis period (Kaplan and Meier 1958, Pollock et al. 1989). We modeled survival as a function of fawn age (i.e., days survived since birth), Julian date of birth, treatment, year, fawn sex, estimated fawn mass at birth (kg), and estimated fawn hind foot length at birth (cm). We incorporated fawn age into our models first by evaluating whether survival varied weekly or biweekly as fawns aged and second by fitting linear and nonlinear trend models. Trend models required fewer parameters and evaluated whether daily survival probabilities of neonates changed as fawns aged. We expressed Julian date of birth as the number of days following the earliest detected birth in a given year. We used 182 daily intervals to construct encounter histories of survival from birth to 6 months of age. We included fawns that were ≤ 1 day old at capture in the first interval, fawns that were > 1 and ≤ 2 days old at capture in the second interval, and so forth. A majority of neonates in our sample (0.748) were ≤ 2 days old at capture and most (0.904) were ≤ 4 days old at capture. We measured fawn mass and hind foot length at capture rather than at birth, so measurements were confounded with fawn age. To make measurements comparable, we estimated fawn mass and hind foot length at birth by regressing capture mass and foot length as a function of age using PROC REG in SAS (Bishop 2007, Bishop et al. 2008).

Similar to fetal survival, our neonatal survival data were potentially overdispersed because our sample included 88 sets of twins and 2 sets of triplets. Sibling neonates shared maternal resources and used the environment similarly in time and space, which could have caused dependence among neonate fates. Bishop et al. (2008) found evidence of modest overdispersion in these data and recommended setting the overdispersion parameter (c) equal to 1.25 in a quasi-likelihood analysis. We therefore used QAIC_c to select among neonatal survival models with $\hat{c} = 1.25$.

Overwinter survival of fawns.—We analyzed overwinter survival of fawns using the Nest Survival option in Program MARK (White and Burnham 1999) because it allowed data with irregular radiomonitoring of collared animals (i.e., ragged telemetry data; Rotella et al. 2004). On winter range, we monitored signals of most radiocollared fawns daily, whereas we monitored a few fawns weekly or biweekly. Once deer left winter range, our monitoring of all fawns became more sporadic because of field logistics. We typically determined exact dates of fawn mortalities, although in some cases, we could only determine an approximate date. The ragged telemetry analysis allowed us to incorporate all available information from these different monitoring scenarios.

We modeled overwinter survival of fawns as a function of time, treatment, year, fawn sex, early winter mass (kg), chest girth (cm), and hind foot length (cm). We estimated survival from 17 December to 16 June, which resulted in 182 daily intervals. We selected 17 December as the start date because 16 December was the mean 6-month birthday of fawns captured as neonates. We

estimated survival over a 6-month period (i.e., through 16 Jun), which is when fawns reached 1 year of age. We constrained time 4 ways in our models: weekly, monthly, seasonally (i.e., winter or spring), and as a trend. We included all fawns captured and radiocollared in the treatment EU in survival analyses with a treatment designation regardless of whether they accessed the pelleted supplement.

Annual survival of adult females.—We analyzed annual survival of adult females using the Nest Survival option in Program MARK (White and Burnham 1999) because our radiomonitoring was irregular among individuals and throughout the year. We modeled annual survival of adult females as a function of time, treatment, year, age, timing of capture, early winter mass (kg), chest girth (cm), and hind foot length (cm). We estimated annual survival from 15 December to 14 December, which resulted in 365 daily intervals. We constrained time 3 ways in our models: biweekly, monthly, and seasonally (i.e., winter–spring or summer–fall). Many adult females were included in multiple years' samples, although we only measured individual covariates when adult females were initially captured and radiocollared. We used these individual covariate values in multiple years' samples because they reflected overall differences in deer body size. We included timing of capture (i.e., Nov–Dec or Feb–Mar) as a variable to evaluate whether individual covariates of adult females varied depending on what time of year we measured them. Similar to 6-month-old fawns, we included all adult females captured and radiocollared in the treatment EU in survival analyses with a treatment designation regardless of whether they accessed the pelleted supplement.

Deer–vehicle collisions (DVCs) were a common cause of mortality of adult females captured in the Colona EU but not the Shavano EU. Deer from the Colona EU were commonly in close proximity to highways during spring and fall whereas most Shavano deer were not. We analyzed survival of adult females in the context of a balanced crossover experimental design, which should have minimized confounding of DVCs with the nutrition treatment. However, to evaluate the potential for confounding, we performed 2 analyses of annual survival of adult females. We included all observed DVCs in the first analysis, whereas we right-censored DVCs in the second analysis.

Cause-specific mortality.—We modeled cause-specific mortality of neonates, wintering fawns, and adult females using a generalized logits model (i.e., multinomial logistic regression) in PROC LOGISTIC in SAS. We modeled mortality causes of neonates during summer and fall as a function of fawn age (i.e., days survived since birth), Julian date of birth, treatment, year, sex, and estimated fawn mass at birth (kg). We modeled mortality causes of fawns during winter and spring as a function of year, treatment, sex, time, and early winter mass (kg). We modeled annual mortality causes of adult females as a function of year, treatment, season, age (yr), and mass (kg). We evaluated 2 season variables; the first comprised 4 levels (winter, spring, summer, and fall), whereas the second had 2 levels (winter–spring and summer–fall). In these analyses we only included mortalities rather than the entire sample of radiocollared deer. Our objective was to evaluate variability in relative contributions of different mortality factors to the total observed mortality.

We performed 2 analyses based on 2 resolutions of the proximate categories of mortality for each deer age group (i.e., neonates, winter fawns, ad F). In the first analysis, the dependent variable comprised a separate level for each individual mortality category except the unknown category. We excluded unknown mortalities because they did not represent a unique mortality cause(s), but rather a combination of the other mortality categories. Thus, unknown mortalities provided no information on the distribution of cause-specific mortality in our study. Unknown mortalities comprised 11% of all neonatal and wintering fawn mortalities and 18% of all adult female mortalities. In the second analysis, we reduced the number of mortality categories to 3: predation, disease–malnutrition–starvation, and injury–accident. The latter analysis considered widely differing mortality factors that were easily discernible from one another.

We computed cause-specific rates of mortality for neonates, winter fawns, and adult females by combining the results of our cause-specific mortality and survival analyses. Specifically, for each EG, we multiplied the estimated probabilities of each mortality cause by the overall mortality rate. We obtained the overall mortality rate simply as $1 - \hat{S}$, where \hat{S} is our estimated survival rate. We used the delta method to estimate variances of cause-specific rates of mortality for each EG and deer age group (Seber 1982).

Continuous survival rates.—We estimated fawn survival from the fetal stage to 6 months old as the product of fetal and neonatal survival rates. Similarly, we estimated fawn survival from the fetal stage to 1 year old as the product of fetal, neonatal, and overwinter fawn survival rates. We estimated a treatment effect as the difference in survival between treatment and control EGs. We estimated variances using the delta method (Seber 1982).

Our estimate of survival from fetus to 1 year of age was structured to represent the treatment effect rather than any specific cohort of deer. This structure was necessary because any given winter's treatment applied to 2 cohorts of fawns. We measured overwinter fawn survival as a function of treatment using the current year's cohort of 6-month-old fawns whereas we measured fetal and neonatal survival using the upcoming year's cohort of fawns. Additionally, the crossover point of the experimental design occurred in December, meaning that the fawn cohort associated with the Colona EU switched from a treatment designation to a control designation in December 2002 and vice versa for the fawn cohort associated with the Shavano EU. In this case, estimating survival from the fetal stage to the yearling age class for a specific cohort of fawns would mix treatment and control assignments. Thus, for each year of the study, we estimated survival from the fetal stage to the yearling age class as a function of treatment by taking the product of fetal and neonatal survival rates measured immediately posttreatment and the overwinter survival rate of fawns measured during administration of treatment. For example, during 2001–2002, we estimated survival of fetuses to the yearling age class as the product of 2002 fetal survival, 2002 neonatal survival, and 2001–2002 overwinter fawn survival.

Population rate of change.—We used our fecundity and survival parameter estimates to construct a matrix population model (Leslie 1945, Caswell 2001) for each combination of

treatment (treatment, control) and year (2001–2002, 2002–2003, 2003–2004) in our study. We estimated the finite rate of population change (λ) by applying the same fecundity and survival rate estimates over time to an artificial population until fawn:adult female ratios reached a steady state. This approach provided a theoretical estimate of λ that was representative of the set of input parameters. We used λ estimates as a means to quantify the effect of nutrition enhancement treatment on mule deer population performance. When estimating year-specific λ , we structured population models to represent the treatment effect rather than any specific cohort of fawns, as explained above. We imputed an expected value of yearling fetal rate in 2002 based on our fetal rate models because we lacked data to directly estimate the rate.

Each population model included estimates of pregnancy rates of adult females (PR), fetal rates of yearling females (FR_{Yr}), fetal rates of ≥ 2 -yr-old females (FR_{Ad}), survival rates of fetuses (S_{Fet}), survival rates of male and female neonates ($S_{MN_{Neo}}$ and $S_{FN_{Neo}}$, respectively), overwinter survival rates of female fawns ($S_{FWntFwn}$), and survival rates of adult females during summer–fall (S_{ASum}), winter–spring (S_{AWnt}), and annually (S_A). Our models included 5 population segments: newborn fawns (Neo), 6-month-old female fawns ($FwnF$), 6-month-old male fawns ($FwnM$), yearling females (YrF), and ≥ 2 -yr-old females (AdF). Our models did not include adult males because we needed only adult females to estimate λ . We used the following equations to project a population of deer from December of year t to December of year $t + 1$ for each combination of treatment and year:

$$N_{Neo}(t + 1) = N_{YrF}(t)PR FR_{Yr}S_{AWnt}S_{Fet} + N_{AdF}(t)PR FR_{Ad}S_{AWnt}S_{Fet}$$

$$N_{FwnF}(t + 1) = (0.5)N_{Neo}(t + 1)S_{FN_{Neo}}$$

$$N_{FwnM}(t + 1) = (0.5)N_{Neo}(t + 1)S_{MN_{Neo}}$$

$$N_{YrF}(t + 1) = N_{FwnF}(t)S_{FWntFwn}S_{ASum}$$

$$N_{AdF}(t + 1) = N_{YrF}(t)S_A + N_{AdF}(t)S_A$$

Population size (N_T) of young and adult female deer in December in year t is thus

$$N_T(t) = N_{FwnF}(t) + N_{FwnM}(t) + N_{YrF}(t) + N_{AdF}(t)$$

and the fawn:adult female ratio (R_{FwnAd}) in December in year t is

$$R_{FwnAd}(t) = [N_{FwnF}(t) + N_{FwnM}(t)]/[N_{YrF}(t) + N_{AdF}(t)]$$

We estimated the variance–covariance matrix of our λ estimates ($\hat{\Sigma}_\lambda$) as follows:

$$\hat{\Sigma}_\lambda = \begin{pmatrix} \frac{\partial \hat{\lambda}_j}{\partial \hat{\theta}_i} \end{pmatrix} \hat{\Sigma}_\theta \begin{pmatrix} \frac{\partial \hat{\lambda}_j}{\partial \hat{\theta}_i} \end{pmatrix}^T$$

where $\hat{\lambda}_j$ are λ estimates for each combination of treatment and year, for averages across years (e.g., $\hat{\lambda}_{Treatment}$), and for treatment effect sizes (e.g., $\hat{\lambda}_{Treatment} - \hat{\lambda}_{Control}$); $\hat{\theta}_i$ are the various fecundity and survival estimates; and $\hat{\Sigma}_\theta$ is the variance-covariance matrix of fecundity and survival estimates. The partial derivatives of $\hat{\lambda}_j$ with respect to $\hat{\theta}_i$ are sensitivities (Caswell 2001). Thus, we evaluated

the sensitivity of $\hat{\lambda}$ to changes in estimated fecundity and survival rates. We also decomposed the treatment effect on $\hat{\lambda}$ into individual contributions from each fecundity and survival rate by taking the product of vital rate differences between treatment and control deer and vital rate sensitivities (Caswell 2001).

RESULTS

Adult Female Body Fat and Fecundity

The model of estimated body fat of adult females with the lowest AIC_c included a treatment \times year interaction (no. parameters = 6, AIC_c wt = 1.000). The model with the next lowest AIC_c , which lacked the treatment \times year interaction, had a ΔAIC_c of 27. Estimated percent body fat of treatment adult females was higher than that of control adult females each year, although magnitude of the effect varied annually (Table 1). We found no evidence of variation in pregnancy rates between treatment and control adult females or among years because the intercept model received the most support (no. parameters = 1, AIC_c wt = 0.631). The pregnancy rate model containing the treatment effect had one additional parameter and a ΔAIC_c of 1.97 (no. parameters = 2, AIC_c wt = 0.235), which indicated treatment had minimal effect on pregnancy. Pregnancy rate of all adult female deer during the study was 0.935 (SE = 0.019). Models explaining variation in fetal rates of adult female deer with the lowest AIC_c included year and female age class in interactive (yr \times age class, no. parameters = 6, ΔAIC_c = 0.00, AIC_c wt = 0.428) and additive (yr + age class, no. parameters = 4, ΔAIC_c = 0.47, AIC_c wt = 0.338) models. We found minimal evidence of a treatment effect (yr + age class + treatment, no. parameters = 5, ΔAIC_c = 2.10, AIC_c wt = 0.150). Thus, fetal rates of adult females varied among years and between age classes but did not vary as a function of the treatment (Table 2).

The fetal survival model with the lowest AIC_c included a treatment \times year interaction (no. parameters = 20, ΔAIC_c = 0.00, AIC_c wt = 0.293; Appendix A). The same model, but without the treatment effect on fetal survival (i.e., year only), received essentially no support (no. parameters = 17, ΔAIC_c = 5.99, AIC_c wt = 0.015). Fetal survival was higher overall in the treatment EG than in the control EG, although we observed considerable annual variation in the magnitude of the effect. We observed virtually no difference in fetal survival between treatment and control EGs in 2003, whereas we observed a large difference between EGs in 2004 (Table 3).

Neonatal Survival

The 4 most parsimonious models of neonatal survival had similar $QAIC_c$ weights (Appendix B). The first of these models included neonatal sex, a third-order polynomial trend in fawn age, Julian date of birth, and estimated birth mass (no. parameters = 7, $\Delta QAIC_c$ = 0.00, $QAIC_c$ wt = 0.129). The second model included the same variables as the first model and a year \times birth mass interaction (no. parameters = 11, $\Delta QAIC_c$ = 0.03, $QAIC_c$ wt = 0.127). Addition of the treatment effect resulted in a slight increase in $QAIC_c$ (no. parameters = 12, $\Delta QAIC_c$ = 0.21, $QAIC_c$ wt = 0.116). The fourth model included only the trend in fawn age, date of birth, and birth mass (no. parameters = 6, $\Delta QAIC_c$ = 0.43, $QAIC_c$ wt = 0.104). We found modest evidence of treatment ($\hat{\beta}_{trt} = 0.276$, 95% CI: -0.123 to 0.675), sex ($\hat{\beta}_{sex} = 0.322$, 95% CI:

Table 1. Estimated body fat (%) of adult female mule deer occupying a pinyon-juniper winter range during late February–early March in southwest Colorado, USA, 2002–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation.

Yr	Experimental group	<i>n</i>	Body fat	SE
2002	Treatment	18	10.21	0.597
	Control	18	7.60	0.597
2003	Treatment	30	13.90	0.463
	Control	28	6.64	0.479
2004	Treatment	30	10.63	0.463
	Control	30	7.28	0.463

-0.083 to 0.728), and year ($\hat{\beta}_{year02} = 0.705$, 95% CI: -0.014 to 1.424; $\hat{\beta}_{year03} = 0.380$, 95% CI: -0.078 to 0.839) effects because addition of these parameters to models caused little change in $QAIC_c$ and confidence intervals on beta estimates slightly overlapped zero. Survival of treatment neonates averaged 0.528 (SE = 0.055) and survival of control neonates averaged 0.482 (SE = 0.057). Survival of female neonates averaged 0.533 (SE = 0.058) and survival of male neonates averaged 0.478 (SE = 0.059). The year effect indicated neonatal survival declined during the study (2002: $\hat{S} = 0.562$, SE = 0.104; 2003: $\hat{S} = 0.520$, SE = 0.059; 2004: $\hat{S} = 0.435$, SE = 0.062).

The polynomial trend in fawn age indicated that daily survival probability of fawns was lowest shortly after birth, increased steadily during the first month postpartum, and then remained high and constant except for a slight decrease during fall migration ($\hat{\beta}_A = 0.101$, 95% CI: 0.068 to 0.134; $\hat{\beta}_{A^2} = -0.0011$, 95% CI: -0.0016 to -0.0006; $\hat{\beta}_{A^3} = 3.6 \times 10^{-6}$, 95% CI: 1.5×10^{-6} to 5.7×10^{-6}). Neonatal survival probability decreased the later fawns were born ($\hat{\beta}_{bdate} = -0.223$, 95% CI: -0.409 to -0.037; Fig. 3) and survival probability increased with greater birth mass ($\hat{\beta}_{bmass} = 0.260$, 95% CI: 0.054 to 0.465; Fig. 4). Birth mass had a greater effect on survival probability during 2002 than either 2003 or 2004 ($\hat{\beta}_{year02 \times bmass} = 0.667$, 95% CI: 0.024 to 1.310; $\hat{\beta}_{year03 \times bmass} = 0.104$, 95% CI: -0.345 to 0.554). The effect of birth mass and birth date on survival was partially related to treatment. Fawns in the treatment EG averaged 3.64 kg (SE = 0.058) at birth whereas fawns in the control EG averaged 3.49 kg (SE = 0.057). Mean birth date, expressed as number of days following the first fawn birth, was earlier for fawns in the treatment EG (13.95, SE = 0.509) than fawns in the control EG (15.76, SE = 0.498).

Table 2. Fetal rates of adult female mule deer during late February–early March in southwest Colorado, USA, 2002–2004.

Yr	Age class	<i>n</i>	Fetal rate ^a	SE
2002	≥ 2 yr old	36	1.79	0.075
	Yearling	0		
2003	≥ 2 yr old	45	1.82	0.066
	Yearling	5	1.07	0.190
2004	≥ 2 yr old	56	2.01	0.061
	Yearling	4	1.41	0.206

^a We used model-averaging to estimate fetal rates (Burnham and Anderson 2002).

Table 3. Estimated in utero survival (\hat{s}) of mule deer fetuses from February until birth on a pinyon-juniper winter range in southwest Colorado, USA, 2002–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation.

Yr	Experimental group	<i>n</i>	\hat{s}^a	SE(\hat{s})
2002	Treatment	24	0.857	0.113
	Control	33	0.779	0.158
2003	Treatment	38	0.966	0.033
	Control	44	0.935	0.059
2004	Treatment	57	0.983	0.028
	Control	59	0.747	0.090

^a We averaged across all models in our model set to estimate survival (Burnham and Anderson 2002).

Distribution of cause-specific mortality of neonates varied as a function of age. The model including an intercept and fawn age received all of the Akaike weight (no. parameters = 12, AIC_c wt = 1.000). Causes of fawn mortality changed as fawns aged and as the summer–fall season progressed (Fig. 5). Disease-related deaths were most commonly associated with hemorrhagic disease or severe diarrhea. Also, we isolated bovine viral diarrhea virus (BVDV) from a neonate, but we could not determine whether BVDV contributed to or interacted with fetal or neonatal mortality. When we pooled mortalities into 3 categories, the intercept-only model (no. parameters = 2, AIC_c wt = 0.205) received slightly more Akaike weight than any other model. Proportions of total mortality comprised of predation (0.667, SE = 0.044), starvation and disease (0.243, SE = 0.040), and injuries and accidents (0.090, SE = 0.027) were similar throughout the study and among EGs. Therefore, predation mortality rates were 0.315 (SE = 0.042) for treatment neonates and 0.345 (SE = 0.044) for control neonates. Starvation and disease mortality rates were 0.115 (SE = 0.023) for treatment neonates and 0.126 (SE = 0.025) for control neonates. Injury and accident mortality rates were 0.043 (SE = 0.014) for treatment neonates and 0.047 (SE = 0.015) for control neonates.

Overwinter Fawn Survival

Overwinter fawn survival varied as a function of nutrition enhancement treatment, year, sex, time (monthly), and early winter mass and chest girth (Appendix C). The model with the lowest AIC_c included treatment, year, sex, time, and mass (no. parameters = 11, ΔAIC_c = 0.00, AIC_c wt = 0.435). The same model without the treatment effect received no support (no. parameters = 10, ΔAIC_c = 19.12, AIC_c wt = 0.000). We found strong evidence of a treatment effect ($\hat{\beta}_{trt}$ = 1.350, 95% CI: 0.723 to 1.978; Table 4). Survival of fawns receiving treatment averaged 0.905 (SE = 0.026) whereas survival of control fawns averaged 0.684 (SE = 0.044). The year effect ($\hat{\beta}_{year0102}$ = -0.523, 95% CI: -1.187 to 0.142; $\hat{\beta}_{year0203}$ = -0.104, 95% CI: -0.826 to 0.617) indicated overwinter fawn survival increased during the study (Table 4). Similar to neonates, we found some evidence that female fawns had higher survival than male fawns ($\hat{\beta}_{sex}$ = 0.362, 95% CI: -0.200 to 0.925; Table 4). Lowest monthly survival occurred between mid-January and mid-February ($\hat{\beta}_{month2}$ = -1.552, 95% CI: -2.520 to -0.584), whereas highest monthly survival occurred between mid-March and mid-April ($\hat{\beta}_{month4}$ =

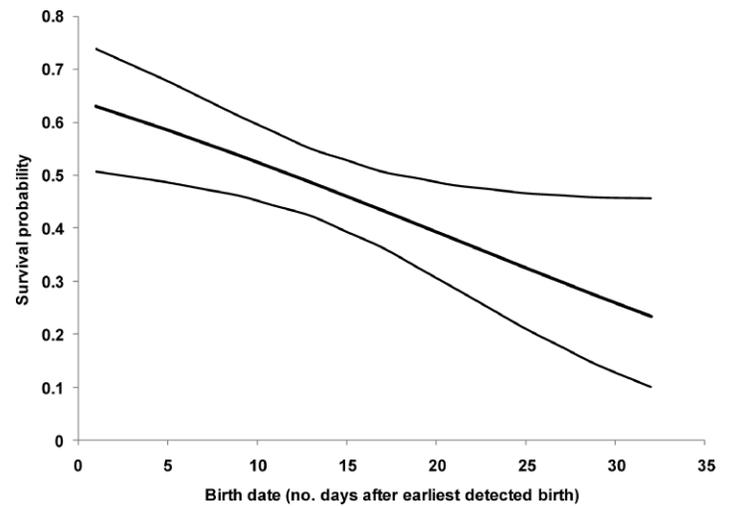


Figure 3. Survival probability (with 95% CI) of mule deer neonates as a function of Julian date of birth of neonates in southwest Colorado, USA, 2002–2004. We expressed Julian date of birth as number of days following the earliest detected birth in a given year.

0.291, 95% CI: -1.139 to 1.720). Probability of fawn survival increased as early winter mass and chest girth increased, although the effect of mass was much greater than that of chest girth ($\hat{\beta}_{mass}$ = 0.145, 95% CI: 0.087 to 0.202; $\hat{\beta}_{chest}$ = 0.043, 95% CI: -0.032 to 0.117; Fig. 6).

Distribution of cause-specific mortality of wintering fawns did not vary over time, among years, or between treatment and control deer. The intercept-only model received virtually all of the Akaike weight (no. parameters = 5, AIC_c wt = 0.911). Coyote predation was the most common proximate cause of overwinter fawn mortality throughout the study (Fig. 7). When we combined mortalities into 3 categories, models with year (no. parameters = 6, ΔAIC_c = 0.00, AIC_c wt = 0.269) and year + sex (no. parameters = 8, ΔAIC_c = 0.45, AIC_c wt = 0.215) received the most support. However, the intercept-only model also received some support (no. parameters = 2, ΔAIC_c = 1.31, AIC_c wt = 0.140), indicating only marginal evidence of annual and sex-specific variation. The

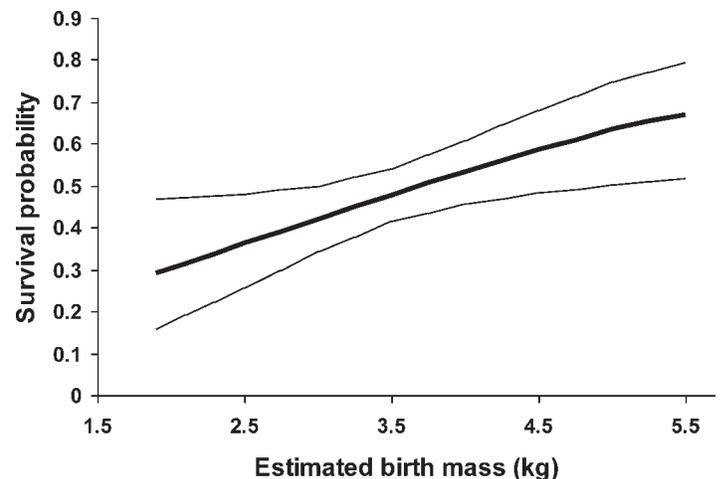


Figure 4. Survival probability (with 95% CI) of mule deer neonates as a function of estimated birth mass of neonates in southwest Colorado, USA, 2002–2004.

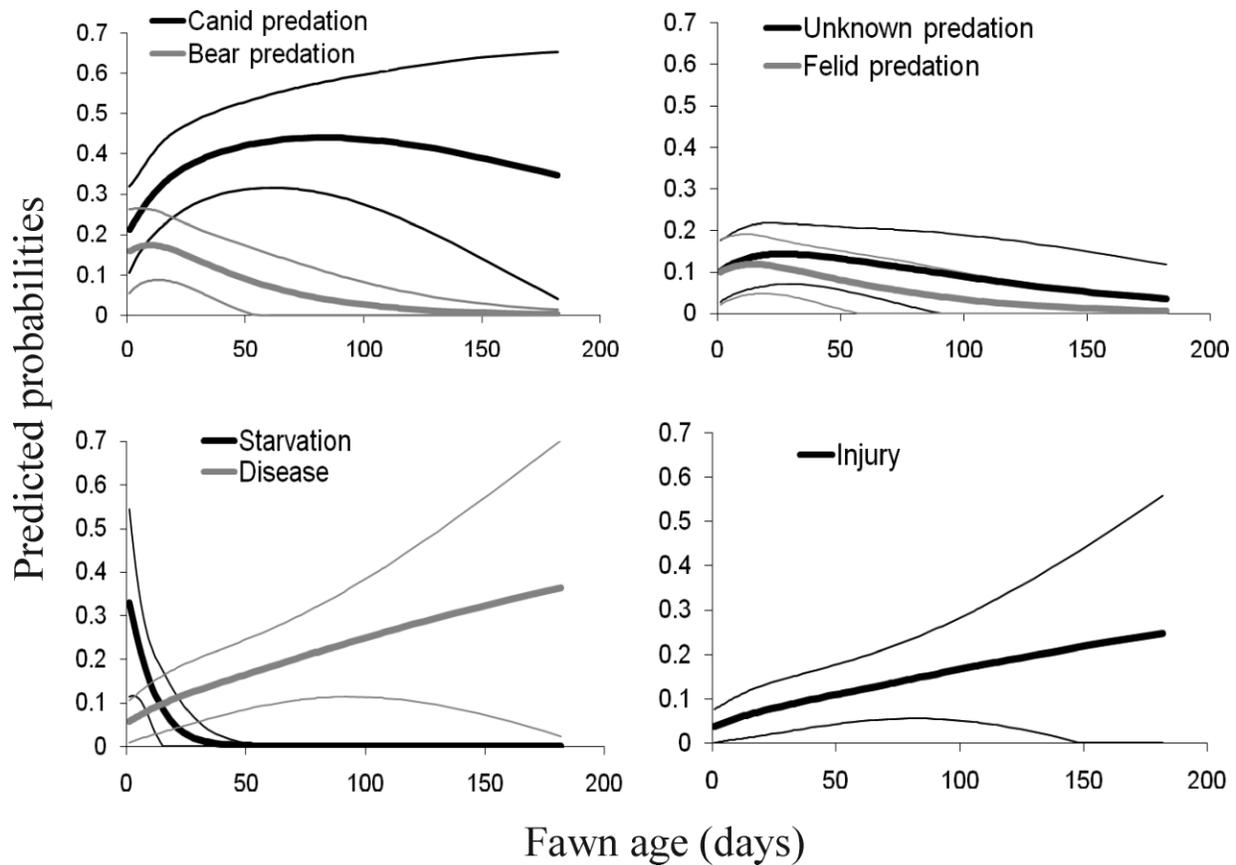


Figure 5. Predicted probabilities (with 95% CIs) of mortality causes of mule deer neonates as a function of fawn age in southwest Colorado, USA, 2002–2004. Cause-specific mortality probabilities are based on total mortality (i.e., \sum probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies.

year effect indicated that the proportion of total mortality attributed to malnutrition or disease declined through the study whereas the proportion of injury and accident mortalities increased (Fig. 8). We lacked evidence to suggest mortality causes varied between EGs, in part because few treatment fawns died during the study ($n = 13$). Increased survival of treatment fawns was therefore explained by roughly a 70% reduction in all cause-specific mortality rates (Table 5).

Predation and malnutrition together accounted for 83% of total fawn mortality (Fig. 7), and most fawns dying from these causes were malnourished. All but 2 fawns killed by coyotes had limited or no femur marrow fat remaining. Four of 6 fawns killed by mountain lions, and both fawns killed by bobcats, were malnourished based on depleted femur marrow fat, and in several cases, evident emaciation. The other 2 fawns killed by mountain lions were in poor condition but had some femur marrow fat remaining.

Annual Survival of Adult Females

Annual survival of adult females varied as a function of treatment, season, age, and hind foot length (Appendix D), regardless of whether DVCs were included in the analysis. For the analysis including DVCs, the model with the lowest AIC_c included a treatment \times season interaction, age, and age² (no. parameters = 6, $\Delta AIC_c = 0.00$, AIC_c wt = 0.130). The same model without the treatment effect received less support (no. parameters = 4, ΔAIC_c

= 1.59, AIC_c wt = 0.055). Including DVCs, model-averaged annual survival estimates were 0.879 (SE = 0.021) for treatment adult females and 0.833 (SE = 0.025) for control adult females. Excluding DVCs, model-averaged annual survival estimates were 0.898 (SE = 0.019) for treatment adult females and 0.867 (SE = 0.023) for control adult females. Also, there was a treatment \times season interaction regardless of whether DVCs were included in

Table 4. Estimated overwinter survival (\hat{s}) of mule deer fawns occupying a pinyon-juniper winter range in southwest Colorado, USA, 2001–2004. Fawns in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation.

Yr	Experimental group	Sex	<i>n</i>	\hat{s}^a	SE(\hat{s})
2001–2002	Treatment	F	18	0.894	0.038
	Treatment	M	21	0.853	0.047
	Control	F	15	0.648	0.081
2002–2003	Control	M	24	0.542	0.087
	Treatment	F	18	0.932	0.027
	Treatment	M	22	0.902	0.035
2003–2004	Control	F	17	0.763	0.069
	Control	M	21	0.671	0.082
	Treatment	F	19	0.938	0.025
	Treatment	M	19	0.912	0.034
	Control	F	25	0.780	0.064
	Control	M	16	0.702	0.082

^a We used model-averaging to estimate survival (Burnham and Anderson 2002).

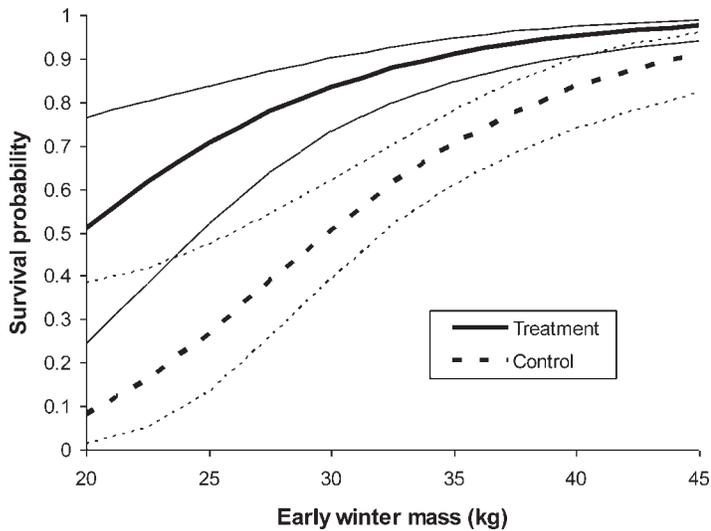


Figure 6. Predicted survival probabilities (with 95% CIs) of mule deer fawns during winter (Dec–Jun) as a function of early winter mass in southwest Colorado, USA, 2001–2004. We present survival probabilities separately for fawns that received enhanced nutrition (treatment) during winter–spring and fawns that did not receive supplementation (control).

the analysis. Treatment deer experienced higher survival during winter–spring than summer–fall, whereas control deer did not (Table 6). Probability of adult female survival increased as hind foot length increased; the effect was most pronounced in the analysis that excluded DVCs ($\hat{\beta}_{foot} = 0.116$, 95% CI: -0.032 to 0.263). Models that evaluated a linear relationship between survival probability of adult females and age of adult females had similar weight to models that tested a quadratic relationship between survival and age. The quadratic effect received most support in the analysis that included DVCs, which indicated that survival probability increased slightly until females were 5 years

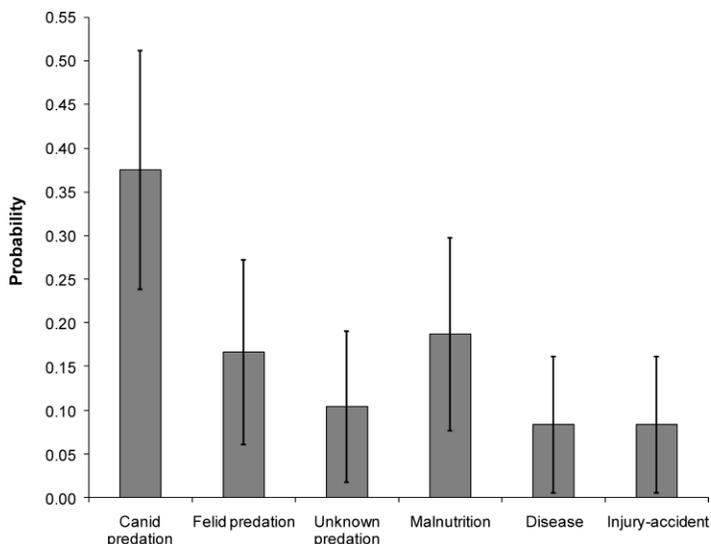


Figure 7. Estimated probabilities (with 95% CIs) of mortality causes of ≥ 6 -month-old mule deer fawns in southwest Colorado, USA, 2001–2004. Cause-specific mortality probabilities are based on total mortality (i.e., Σ probabilities = 1), and therefore represent a deer’s relative likelihood of dying from a particular cause given that the deer dies.

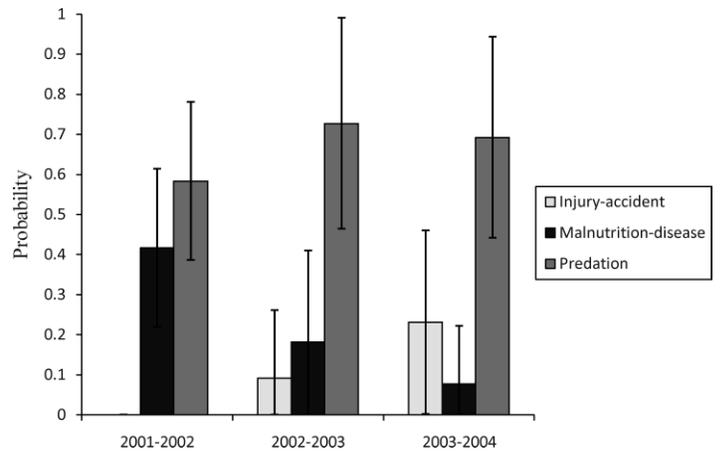


Figure 8. Estimated probabilities (with 95% CIs) of mortality causes of ≥ 6 -month-old mule deer fawns as a function of year in southwest Colorado, USA, 2001–2004. Cause-specific mortality probabilities are based on total mortality (i.e., Σ probabilities = 1), and therefore represent a deer’s relative likelihood of dying from a particular cause given that the deer dies. We lumped mortality causes into 1 of the 3 categories shown.

old, after which survival probability declined with age ($\hat{\beta}_{age} = 0.188$, 95% CI: -0.134 to 0.509 ; $\hat{\beta}_{age^2} = -0.018$, 95% CI: -0.039 to 0.004 ; Fig. 9).

Distribution of cause-specific mortality of adult females varied in response to female age. The model with an intercept and female age received most of the Akaike weight (no. parameters = 16, AIC_c wt = 0.834). Adult females ≤ 8 years old died principally from collisions with vehicles, disease, and mountain lion predation. Older females died principally from malnutrition and coyote predation (Fig. 10). All but 2 adult females killed by coyotes had minimal or no femur marrow fat remaining, indicating they were malnourished. When we pooled mortalities into 3 categories, 2 models received most of the Akaike weight: 1) intercept + season (no. parameters = 8, AIC_c wt = 0.521) and 2)

Table 5. Estimates of cause-specific mortality rates of mule deer fawns during winter on a pinyon–juniper winter range in southwest Colorado, USA, 2001–2004. Fawns in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation. The sum of cause-specific mortality rates across each experimental group equals the overall mortality rates of treatment (0.095) and control (0.316) fawns in our study.

Mortality cause	Experimental group	Mortality rate	SE
Canid predation ^a	Treatment	0.036	0.012
	Control	0.119	0.027
Felid predation	Treatment	0.016	0.007
	Control	0.053	0.018
Unknown predation	Treatment	0.010	0.005
	Control	0.033	0.014
Malnutrition	Treatment	0.018	0.007
	Control	0.059	0.019
Disease	Treatment	0.008	0.004
	Control	0.026	0.013
Injury-accident	Treatment	0.008	0.004
	Control	0.026	0.013

^a Canid predation mostly represents coyote predation. Of 18 canid predation events on wintering fawns, 15 were caused by coyotes, 1 was caused by domestic dog, and 2 others were caused by either coyotes or domestic dogs.

Table 6. Estimated annual survival (\hat{s}) of adult female mule deer ($n = 274$) in southwest Colorado, USA, 2000–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation. We present estimates from 2 analyses. We included mortalities resulting from deer–vehicle collisions (DVCs) in the first analysis, whereas we right-censored DVCs in the second analysis.

Analysis	Experimental group	Season	\hat{s}^a	SE(\hat{s})
DVCs included	Treatment	Winter–spring	0.952	0.016
	Treatment	Summer–fall	0.924	0.017
	Control	Winter–spring	0.911	0.018
	Control	Summer–fall	0.915	0.019
DVCs censored	Treatment	Winter–spring	0.964	0.014
	Treatment	Summer–fall	0.932	0.016
	Control	Winter–spring	0.922	0.018
	Control	Summer–fall	0.941	0.016

^a We used model-averaging to estimate survival (Burnham and Anderson 2002).

intercept + season + age (no. parameters = 10, AIC_c wt = 0.412). During winter and summer, mortalities caused by disease or malnutrition were most common and there were few DVCs. The opposite was true during spring and fall (Fig. 11). Predation was relatively constant throughout all seasons.

We observed modest evidence that cause-specific mortality of adult females varied between experimental groups. The model with an intercept and treatment effect received the third-most Akaike weight (no. parameters = 16, AIC_c wt = 0.034) after age and season models. Survival of adult females receiving treatment was higher than control adult females primarily because malnutrition was eliminated and mountain lion predation declined by 86% (SE = 15) in response to treatment (Table 7). We also observed a 32% (SE = 48) reduction in coyote predation, although the confidence interval on the effect was large and overlapped zero. Rates of mortality caused by DVCs were nearly identical for treatment and control deer, although most DVCs were associated with the Colona EU, which indicates the crossover experimental design minimized any potential confounding between the nutrition enhancement treatment and DVCs (Table 7). Combined rates of disease and suspected disease were similar among treatment and control deer. We found no evidence of novel diseases or chronic wasting disease, the latter of which has not been documented in southwest Colorado. We observed several cases each of hemorrhagic disease, MCF (Schultheiss et al. 2007), and pneumonia, and we failed to identify the exact cause of death in a number of other disease-related cases. During 2000–2002, >50% of adult females were seropositive (i.e., titers $\geq 1:32$) for BVDV, although seroprevalence unexpectedly dropped to <25% in 2002–2003. We are uncertain if or how BVDV interacted with fecundity or mortality.

Recruitment and Population Rate of Change

We estimated fawn survival from the fetal stage to 6 months of age separately for each treatment, year, and sex combination, consistent with model selection results from our fetal and neonatal survival analyses (Table 8). We likewise estimated fawn survival from the fetal stage to 1 year of age separately for each treatment, year, and sex combination (Table 9). Fetal to yearling survival rates increased by 0.14–0.20 in response to the treatment, although 95% confidence intervals slightly overlapped zero (Table

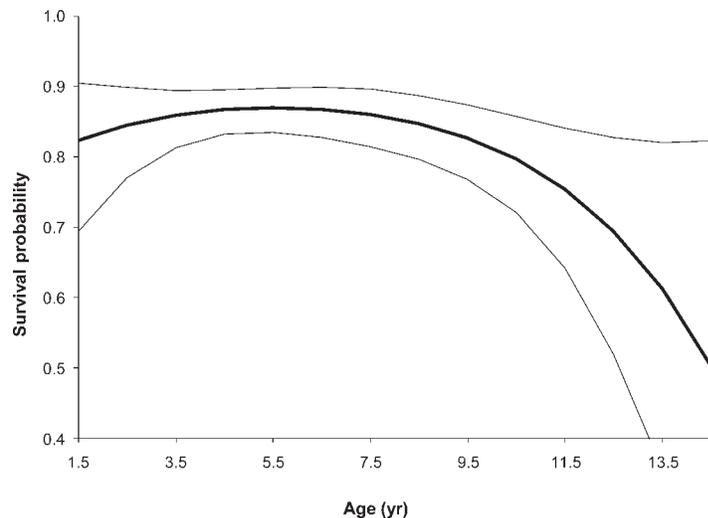


Figure 9. Predicted probability (with 95% CI) of annual survival of adult female mule deer as a function of age, southwest Colorado, USA, 2000–2004.

10). Across years, survival from the fetal stage to the yearling age class averaged 0.478 (SE = 0.061) for treatment females and 0.417 (SE = 0.062) for treatment males, and survival averaged 0.306 (SE = 0.053) for control females and 0.238 (SE = 0.046) for control males. Across sexes and years, survival of treatment fetuses to the yearling age class averaged 0.447 (SE = 0.052), whereas survival of control fetuses to the yearling age class averaged 0.271 (SE = 0.042). Thus, treatment caused the rate of fetal to yearling survival to increase by 0.177 (SE = 0.082, 95% CI: 0.016 to 0.337).

We used survival estimates of adult females that included DVCs when estimating population rate of change (λ) because we did not find evidence that DVCs were confounded with the nutrition treatment. Our estimates of λ were 1.15–1.17 for treatment deer and 1.02–1.06 for control deer, with some overlap in 95% confidence intervals (Fig. 12). Average $\hat{\lambda}$ was 1.165 (SE = 0.036) for treatment deer and 1.033 (SE = 0.038) for control deer. Treatment caused $\hat{\lambda}$ to increase by 0.139 (95% CI: 0.020 to 0.259) during 2001–2002, 0.113 (95% CI: 0.023 to 0.204) during 2002 to 2003, and 0.145 (95% CI: 0.048 to 0.242) during 2003–2004. When averaged across years, treatment caused $\hat{\lambda}$ to increase by 0.133 (95% CI: 0.049–0.217). Population rate of change was more sensitive to changes in annual survival of adult females than to changes in any other demographic rate (Table 11). However, treatment effects on overwinter fawn survival and adult female survival caused similar increases in $\hat{\lambda}$ (Table 11). The treatment effect on production and survival of young (i.e., fetal, neonatal, and overwinter fawn survival) caused $\hat{\lambda}$ to increase by 0.084 whereas the treatment effect on adult female survival caused $\hat{\lambda}$ to increase by 0.048.

DISCUSSION

Diet Quality

Deer receiving the supplemental pellet were in better condition than deer consuming natural vegetation only (Table 1). We provided a supplemental pellet that would allow deer to meet or exceed maintenance nutrient requirements. Maintenance energy requirements reported for wintering deer include estimates

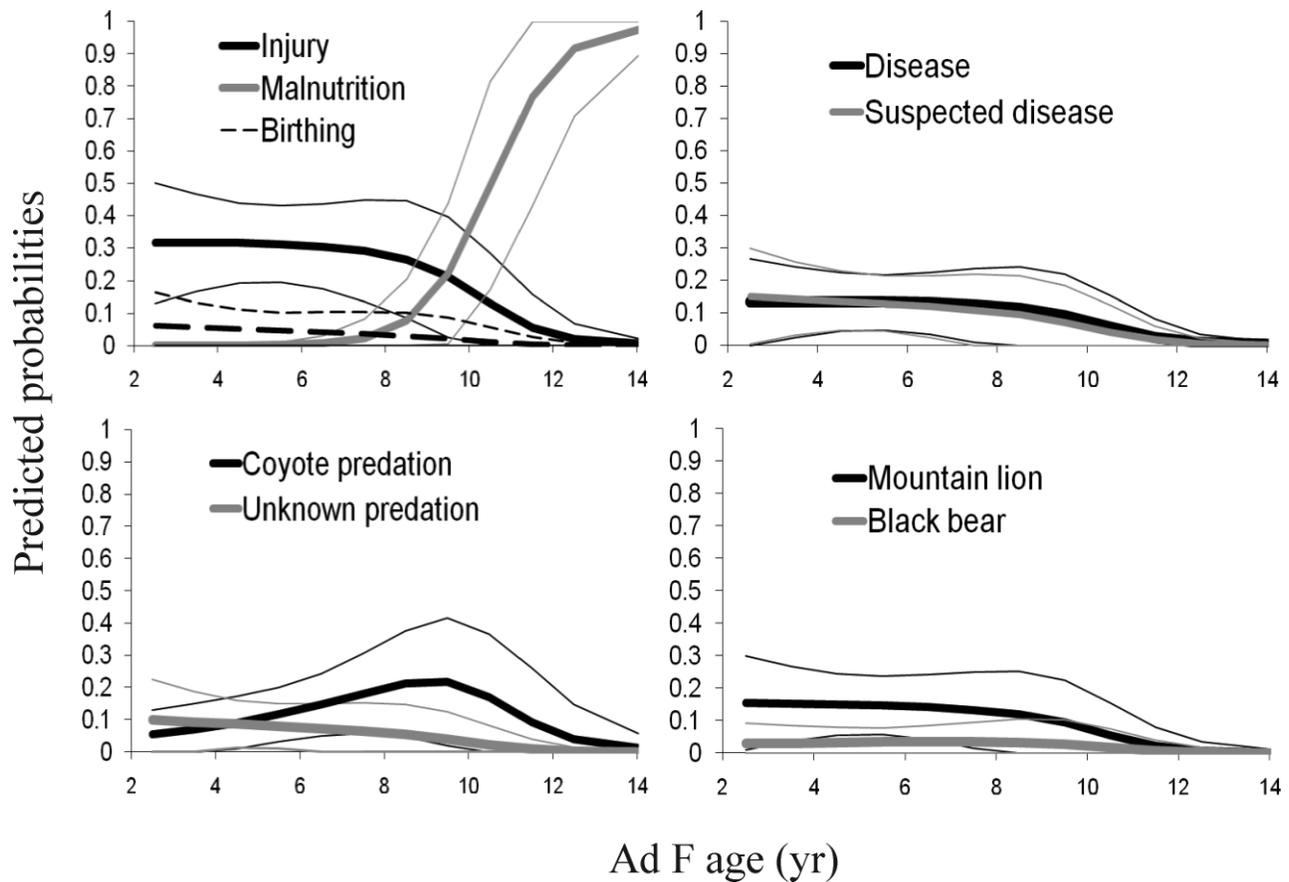


Figure 10. Predicted probabilities (with 95% CIs) of mortality causes of adult female mule deer as a function of female age in southwest Colorado, USA, 2000–2004. Cause-specific mortality probabilities are based on total mortality (i.e., \sum probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies.

ranging from 109 to 158 kilocalories (kcal) of metabolizable energy (ME) per kilogram body weight^{0.75} ($W_{\text{kg}}^{0.75}$) per day (Thompson et al. 1973, Baker et al. 1979, Holter et al. 1979b). Assuming a requirement of 135 kcal ME/ $W_{\text{kg}}^{0.75}$ /day, a 36-kg fawn consuming 900 g dry matter/day, or a 65-kg adult female consuming 1,400 g dry matter/day, would require a diet having approximately 60% digestible energy (DE) to achieve maintenance (Swift 1983). Ammann et al. (1973) found that deer must consume diets containing $\geq 50\%$ DE to adjust intake to meet maintenance energy requirements. Deer must consume diets containing roughly 6–7% crude protein (CP) to meet maintenance nitrogen requirements (Dietz 1965, Holter et al. 1979a). As described in the Methods, deer consuming the supplement should have exceeded maintenance protein and energy requirements.

In contrast, deer consuming only natural forage likely failed to meet maintenance nutrient requirements from dietary intake during much of the winter. Principal forage species of deer on the winter range EUs were Utah juniper, big sagebrush, black sagebrush (*Artemisia nova*), cheatgrass (*Bromus tectorum*), crested wheatgrass (*Agropyron cristatum*), and alfalfa (*Medicago* spp.) residual. Sagebrush and juniper were the main forage species available from late December through early March. Winter estimates of in vitro dry matter digestibility (IVDMD) are 40–48% for Utah juniper (Bunderson et al. 1986, Welch 1989), 45–65% for big sagebrush (Ward 1971, Kufeld et al. 1981, Welch

and Pederson 1981, Welch 1989), and 53% for black sagebrush (Welch et al. 1983, Welch 1989). Winter estimates of CP range from 6–12% for these same species (Welch 1989, Wambolt 2004). Diet quality of wintering deer in the control EU may have been

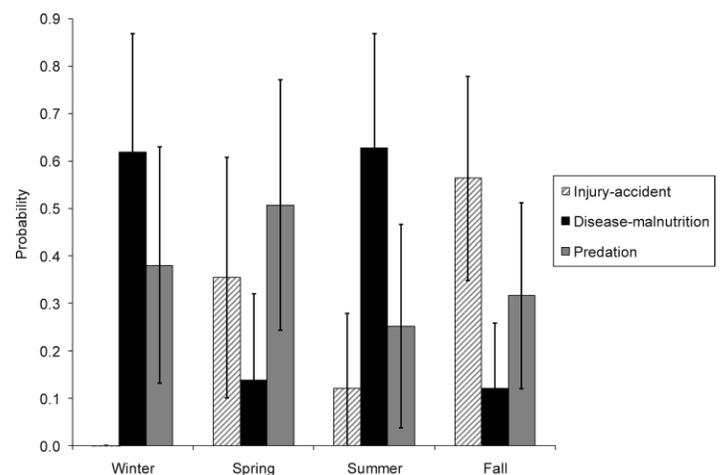


Figure 11. Estimated probabilities (with 95% CIs) of mortality causes of adult female mule deer as a function of season in southwest Colorado, USA, 2000–2004. Cause-specific mortality probabilities are based on total mortality (i.e., \sum probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies. We lumped mortality causes into 1 of the 3 categories shown.

Table 7. Annual estimates of cause-specific mortality rates of adult female mule deer in southwest Colorado, USA, 2001–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation. The sum of cause-specific mortality rates across each experimental group equals the overall mortality rates of treatment (0.121) and control (0.167) adult females in our study.

Mortality cause	Experimental group	Mortality rate	SE
Vehicle collision-injury	Treatment	0.040	0.013
	Control	0.040	0.012
Mountain lion predation	Treatment	0.005	0.004
	Control	0.032	0.011
Coyote predation	Treatment	0.013	0.008
	Control	0.020	0.009
Unknown predation	Treatment	0.013	0.008
	Control	0.008	0.006
Bear predation	Treatment	0.000	0.000
	Control	0.008	0.006
Malnutrition	Treatment	0.000	0.000
	Control	0.028	0.010
Disease	Treatment	0.027	0.011
	Control	0.008	0.006
Suspected disease	Treatment	0.009	0.006
	Control	0.024	0.010
Birthing	Treatment	0.013	0.008
	Control	0.000	0.000

lower than the above values indicate because sagebrush and juniper species contain terpenoids, which may inhibit microbial digestion (Nagy et al. 1964, Carpenter et al. 1979, Schwartz et al. 1980). On a similar pinyon–juniper–sagebrush winter range in northwest Colorado, deer diets during January–March ranged from 24% to 38% IVDMD and 5% to 7% crude protein (Bartmann 1983). Spring IVDMD and CP estimates of immature, green cheatgrass (IVDMD, 65–72%; CP, 17–21%) and crested wheatgrass (IVDMD, 71–73%; CP, 27–28%) are high (Austin et al. 1994, Bishop et al. 2001), although these species offer minimal forage value during winter. In vitro dry matter digestibility of alfalfa generally ranges from 50% to 70% (Weir et al. 1960, Robles et al. 1981, Lenssen et al. 1988, Belyea et al. 1989) and CP of alfalfa is roughly 17–25% (Weir et al. 1960, Lenssen et al. 1988). Alfalfa was clearly a valuable forage item for deer, but it was limited in quantity and only available through mid-December.

Table 8. Estimated survival (\hat{S}) of mule deer fawns from the fetal stage to 6 months old as a function of a nutrition enhancement treatment, year, and fawn sex in southwest Colorado, USA, 2001–2004.

Yr	Experimental group	Sex	\hat{S}	SE(\hat{S})
2001–2002	Treatment	F	0.527	0.122
	Treatment	M	0.485	0.124
	Control	F	0.436	0.129
	Control	M	0.395	0.122
2002–2003	Treatment	F	0.553	0.076
	Treatment	M	0.501	0.087
	Control	F	0.488	0.079
	Control	M	0.435	0.081
2003–2004	Treatment	F	0.470	0.083
	Treatment	M	0.413	0.078
	Control	F	0.336	0.075
	Control	M	0.292	0.075

Table 9. Estimated survival (\hat{S}) of mule deer fawns from the fetal stage to 1 year old as a function of a nutrition enhancement treatment, year of treatment delivery, and fawn sex in southwest Colorado, USA, 2001–2004.

Treatment yr	Experimental group	Sex	\hat{S}	SE(\hat{S})
2001–2002	Treatment	F	0.471	0.111
	Treatment	M	0.414	0.109
	Control	F	0.282	0.091
	Control	M	0.214	0.075
2002–2003	Treatment	F	0.516	0.072
	Treatment	M	0.452	0.080
	Control	F	0.372	0.069
	Control	M	0.292	0.065
2003–2004	Treatment	F	0.441	0.079
	Treatment	M	0.377	0.073
	Control	F	0.262	0.062
	Control	M	0.205	0.058

Fecundity and Survival

We found no differences in pregnancy and fetal rates between EGs. Any treatment effects likely would have been carried over from the previous year's treatment because most adult females were bred before the start of treatment delivery each year. Both pregnancy and fetal rates were high for each EG, equaling or exceeding previous estimates measured on the Uncompahgre Plateau and elsewhere across Colorado (Andelt et al. 2004). Pregnancy and fetal rates were not a limiting factor to the mule deer population during our study.

We observed strong support for a treatment effect in fetal survival, primarily because the effect was large during 2004. We found marginal evidence of a treatment effect in neonatal survival. Our sample sizes were insufficient to detect small to moderate effects (i.e., survival increase of 0.05–0.10) with desired power, especially during 2002. Overdispersion in our neonatal survival data further reduced power to detect a treatment effect (Bishop 2007, Bishop et al. 2008). Principal drivers of neonatal survival included birth mass and birth date, which were only partly related to the treatment. Survival increased with earlier birth dates and increased birth mass, which has been observed previously in mule deer (Lomas and Bender 2007) and other ungulates (Singer et al. 1997, Keech et al. 2000, Cook et al. 2004).

We found strong evidence of a treatment effect on overwinter fawn survival, even when survival of control fawns was high. Overwinter survival of treatment fawns ($\hat{S} = 0.905$, SE = 0.026) was exceptionally high when compared to overwinter fawn survival across Colorado during 1997–2008 ($\hat{S} = 0.721$, SD = 0.024;

Table 10. Estimated effect of a nutrition enhancement treatment, delivered during winter and spring, on survival of mule deer fawns from the fetal stage to 1 year old in southwest Colorado, USA, 2001–2004. The treatment effect represents the increase in survival attributable to the treatment.

Treatment yr	Sex	Effect	95% lower CL	95% upper CL
2001–2002	F	0.189	–0.108	0.486
	M	0.199	–0.082	0.478
2002–2003	F	0.144	–0.020	0.308
	M	0.160	–0.004	0.323
2003–2004	F	0.179	–0.009	0.367
	M	0.172	–0.012	0.356

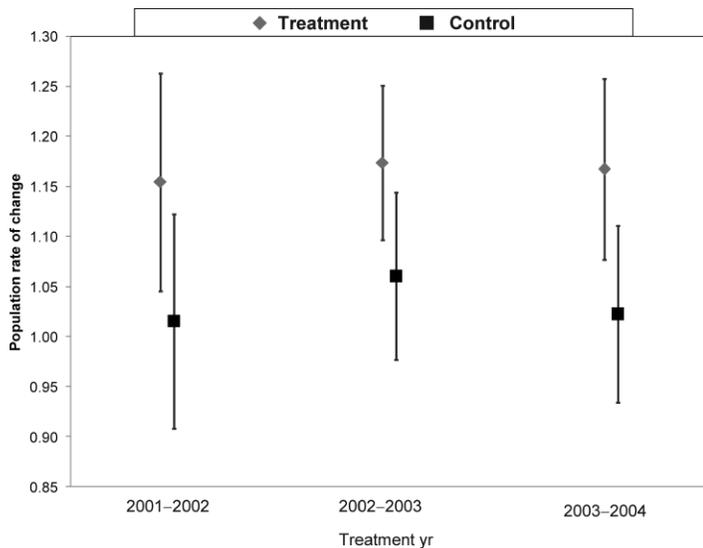


Figure 12. Estimates and 95% confidence intervals of the population rate of change, λ , for mule deer that received enhanced nutrition via supplementation during winter and early spring (treatment) and mule deer that received no supplementation (control) in southwest Colorado, USA, 2001–2004.

Lukacs et al. 2009) and overwinter fawn survival in Colorado, Idaho, and Montana during 1981–1996 ($\hat{\delta} = 0.444$, $SE = 0.033$; Unsworth et al. 1999). Early winter mass explained additional variation in the data. Probability of survival increased as early winter mass increased, which has been documented previously (White et al. 1987, Unsworth et al. 1999, Bishop et al. 2005a, Taillon et al. 2006). Effects of nutrition treatment and early winter mass on survival probability provide strong evidence that fawn body condition dictated overwinter survival.

We observed higher survival of female fawns than male fawns during both the neonatal and overwinter survival periods. Higher survival of female neonates has been documented in deer previously (Jackson et al. 1972), but most studies have found little or no evidence for sex differences in neonatal survival (Gaillard et al. 1997, Ricca et al. 2002, Pojar and Bowden 2004, Lomas and Bender 2007). Sex differences in overwinter fawn survival have been documented more commonly, with females having higher survival (Bartmann et al. 1992, White and Bartmann 1998, Unsworth et al. 1999, Bishop et al. 2005a). Higher survival of female fawns, and hence higher recruitment of female yearlings, creates a reduced adult male:adult female ratio prior to any harvest effects.

The nutrition treatment had a positive effect on adult female survival during winter and spring, when deer received treatment. During summer and fall, however, survival was similar among treatment and control adult females and lower than expected. A priori, we expected survival of control adult females to be lower during winter and spring than summer and fall because of harsher weather and limited nutrient availability, which is consistent with past research (Bartmann et al. 1992, Ricca et al. 2002, Bender et al. 2007). However, survival of control adult females was similar during winter–spring and summer–fall periods. Natural survival rates of adult females (i.e., hunting mortality excluded) across the whole Uncompahgre Plateau during the past 10 years were lower during summer and fall than winter and spring (Lukacs et al.

Table 11. Sensitivity of estimated population rate of change ($\hat{\lambda}$) to changes in estimated fecundity and survival rates of mule deer; contributions of each vital rate parameter to the overall effect of enhanced nutrition (treatment) of deer on $\hat{\lambda}$; and percent of the treatment effect on $\hat{\lambda}$ accounted for by each parameter; in southwest Colorado, USA, 2001–2004.

Parameter	Sensitivity of $\hat{\lambda}^a$	Treatment effect on $\hat{\lambda}^b$	
		$\Delta\hat{\lambda}$	%
Pregnancy rate	0.201	0.000	0.0
Ad fetal rate	0.085	0.000	0.0
Yearling fetal rate	0.025	0.000	0.0
Fetal survival	0.213	0.025	18.7
Neonatal survival	0.354	0.016	11.8
Overwinter fawn survival	0.227	0.044	33.1
Ad F survival	1.049	0.048	36.4

^a We averaged sensitivities of each parameter across treatment classes and yr.

^b We averaged contributions of each vital rate parameter to the treatment effect on $\hat{\lambda}$ across yr.

2009). Most summer mortalities of adult females appeared to be disease related and were apparently independent of nutrition. Adult female mortality during summer–fall equaled or exceeded winter–spring mortality in 3 other deer populations in western Colorado as well (Lukacs et al. 2009). Thus, although summer mortality was higher than expected, our results are consistent with other recent findings in Colorado.

Dependence Among Fecundity and Survival Rates

Fetal rates and fetal, neonatal, and overwinter fawn survival varied annually, as did the magnitude of treatment effects, but not in synchrony. The highest measured fetal rates occurred during 2004, when fetal and neonatal survival rates (i.e., survival from fetus to 6 months old) were lowest. The largest treatment effect in fetal survival occurred during 2004, when treatment had the least effect on neonatal survival. Neonatal survival rates declined during the study, whereas overwinter survival rates increased each year of the study. We observed annual variation in each fecundity and survival parameter, yet recruitment of yearlings as a function of treatment was relatively constant. Likewise, we observed minimal temporal variability in the estimated population rate of change ($\hat{\lambda}$) for each EG, particularly treatment deer (Fig. 12). These results suggest a compensatory relationship among stage or season-specific survival rates, and therefore, emphasize the need to consider overall yearling recruitment when assessing population dynamics. For example, many state wildlife agencies measure December fawn recruitment annually to evaluate population status and to help determine numbers of deer licenses to issue to hunters. December fawn recruitment alone, without accompanying data on overwinter fawn survival, could be misleading.

A possible explanation for this compensatory relationship is the timing of death of lightweight or otherwise unthrifty fawns, which have a lower probability of surviving to the yearling age class. In some years, conditions may facilitate high survival of these fawns to winter, at which point their survival probability declines significantly. In other years, these fawns may have low survival probabilities during summer and fall, which reduces December fawn recruitment but increases overwinter fawn survival because the poorest condition fawns have already been removed from the population. The same relationship could apply to fetuses and

neonates, as we saw among control deer in 2004. Stillborn fetuses in 2004 were mostly small, lightweight, and seemingly undernourished. If these fetuses had been born alive, they likely would have suffered high mortality rates as neonates. The effect would have been to increase fetal survival and decrease neonatal survival. Population monitoring programs should evaluate overall recruitment of young to the yearling age class.

Proximate Mortality Factors

We found minimal evidence of differences in mortality causes of fawns between EGs. Increased survival rates of fawns associated with the treatment effect were explained by the reductions in rates of all mortality causes rather than any specific mortality cause. Incidence of predation, malnutrition, starvation, disease, and injuries and accidents all declined as a result of enhanced nutrition. The magnitude of the decline was far more pronounced for ≥ 6 -month-old fawns because that cohort is where we observed the greatest treatment effect. We found some evidence of differences in mortality causes of adult females between experimental groups. Increased survival rates of adult females associated with the treatment were explained by reductions in malnutrition and predation rates.

We expected rates of malnutrition and starvation to decline in response to treatment because enhanced nutrition should directly counteract these factors. Malnutrition was substantially reduced among wintering fawns and eliminated among adult females as a result of the treatment. However, we observed only a small reduction in starvation rates of neonates in response to the treatment, which could have several explanations. First, neonates received the treatment indirectly through their dams, whereas wintering fawns and adult females consumed treatment directly. Second, treatment allowed adult females in poor condition to survive winter and reproduce; these adult females may have been poorly prepared to meet lactation demands. In contrast, control adult females in the poorest condition died overwinter, prior to fawning. Third, adult females occupying the periphery of the treatment EU likely did not receive ad libitum portions of treatment throughout winter. Partial utilization of treatment may have improved survival of these adult females without improving their reproductive performance. We did not censor individuals on the periphery of EUs because we lacked detailed location data to make objective determinations and we wanted to avoid biased detection of a treatment effect.

The effect of the treatment on factors other than malnutrition and starvation is less straightforward. Several explanations exist to explain why predation on neonates might decline in response to enhanced nutrition of adult females. First, adult females may better detect predators and defend their fawns. Second, enhanced nutrition might reduce rates of diarrhea that increase fawn scent, making fawns less vulnerable to detection by predators. Third, as fawns become older, those in better condition may be better able to escape predators. We observed only modest evidence that enhanced nutrition of adult females lowered rates of predation on neonates. Our results are consistent with past research suggesting that some amount of predation on newborn fawns is expected independent of adult female or fawn nutrition (Hamlin et al. 1984, Ballard et al. 2001).

Predation rates of older fawns and adults would be expected to

decline in response to enhanced nutrition if improved body condition enhanced the ability of deer to escape or avoid predators. We found strong evidence that enhanced nutrition of deer reduced coyote predation of ≥ 6 -month-old fawns. Studies have found that coyotes primarily killed malnourished fawns during winter (Bartmann et al. 1992, Bishop et al. 2005a). We found that most fawns killed by coyotes in the control EU were malnourished based on degree of emaciation and visual inspection of femur marrow fat. Our results suggest that coyote predation of ≥ 6 -month-old fawns was compensatory with respect to nutrition. That is, coyotes selected fawns in poor condition, which would be expected to have the lowest survival probabilities regardless of proximate mortality cause. Our results are consistent with other field experiments that directly demonstrated compensatory mortality by manipulating coyote numbers instead of deer nutrition (Bartmann et al. 1992, Hurley and Zager 2006). Our results further support the notion that observed coyote predation of wintering fawns in the intermountain West, albeit common, should not be viewed as sufficient evidence that coyotes are having a negative impact on deer populations. Our results also suggest that coyote predation on adult females was largely compensatory with respect to nutrition because coyotes selected for older females in poor condition, which is consistent with Hurley and Zager (2006).

Felid predation accounted for roughly 15% of total mortality of ≥ 6 -month-old fawns and adult females, most of which was caused by mountain lions. We expected mountain lion predation to account for a greater proportion of total mortality of treatment deer, because mountain lions are capable of killing healthy animals and of potentially having a negative impact on ungulate populations (Bleich and Taylor 1998, Ballard et al. 2001, Robinson et al. 2002, Festa-Bianchet et al. 2006). Instead, mountain lion predation was substantially reduced among adult females and ≥ 6 -month-old fawns as a result of treatment, indicating that mountain lions selected for animals in poorer condition. Our winter-range EUs were characterized by pinyon-juniper-sagebrush mosaics with high deer densities and limited canyon habitat. Perhaps predation strategies of mountain lions in our EUs favored selection of deer in poorer condition, whereas under different circumstances, predation strategies may be weakly related, or even unrelated, to prey body condition. We encourage cautious interpretation of our finding because EUs were small relative to home range sizes of mountain lions, indicating a few mountain lions may have accounted for most of the predation we observed. Therefore, our results may reflect individual behavior of only a few lions, which may or may not typify the species in this type of environment. Similar to our findings, in a recent study in north-central Colorado near Boulder, chronic wasting disease infection increased predation rates of mountain lions on mule deer nearly 4-fold, suggesting lions selected deer that were in a compromised state of health (Miller et al. 2008).

Our daily activity in the treatment EU (i.e., delivering pellets) could have deterred predation; however, we spent similar time in each EU each winter monitoring radiocollared deer and collecting fawn:adult female ratio data from the ground. Treatment was delivered by ≤ 3 individuals during morning hours, when deer were typically bedded. Our largest winter field crew comprised 4 individuals, who divided tasks among treatment and control EUs.

Additionally, our winter-range EUs were situated in a rapidly developing area where human activity was common. Presence of our field crew likely had little influence on predator activities.

The large effect of enhanced nutrition on $\hat{\lambda}$ in the presence of ongoing predation suggests habitat was ultimately the critical limiting factor of the Uncompahgre deer population. Predation should have minimal impact on populations that are at or near NCC (Ballard et al. 2001). Hurley and Zager (2006) observed no increase in $\hat{\lambda}$ in response to coyote reductions and only a slight increase in $\hat{\lambda}$ in response to mountain lion reductions. Our findings regarding relative effects of habitat versus predation should not be extrapolated to more complex predator-prey systems that include additional predator species such as wolves (*Canis lupus*).

Disease was a common mortality factor among neonatal fawns and adult females, but not ≥ 6 month old fawns. We found no evidence that enhanced nutrition reduced rates of disease in adult females. Deer intermixed with domestic sheep and cattle on summer range and were occasionally in close proximity to livestock on winter range, which likely explains the prevalence of BVDV and MCF. Bovine viral diarrhea has been linked to stillbirths and neonatal mortality in livestock (Sprecher et al. 1991, Baker 1995, Grooms 2004); however, we lacked means to evaluate any possible link between BVDV and deer fetal or neonatal mortality. The degree to which disease may be negatively impacting the deer population remains unclear; however, our findings indicate disease would not restrict population growth if deer obtained adequate nutrition.

Population Rate of Change

Our estimates of λ were most sensitive to changes in adult female survival, which was expected based on past research (Gaillard et al. 1998, 2000). Pfister (1998) found that sensitivities of demographic parameters were inversely related to process variance for a host of diverse plant and animal species. This pattern is also found in ungulates, in which process variance is low for adult females and comparatively high for juveniles (Gaillard et al. 1998, 2000; Unsworth et al. 1999). Parameter sensitivity and parameter variability are each important considerations when evaluating ungulate population dynamics. Although $\hat{\lambda}$ was most sensitive to changes in adult female survival, overwinter fawn survival was as important as adult survival in explaining the effect of treatment on λ . Furthermore, the treatment effect on production and survival of young (i.e., fetal, neonatal, and overwinter fawn survival) accounted for nearly twice the increase in $\hat{\lambda}$ as did adult female survival.

Treatment caused λ to increase by an average of 0.133 (SE = 0.043) during our study. The 95% confidence intervals on our estimates of the treatment effect on λ did not overlap zero, providing strong evidence for the effect. The mean estimate of λ for the treatment EG (1.165) would cause a population to double in size in approximately 5 years. For perspective, the Uncompahgre Plateau deer population is currently estimated at roughly 31,000 deer based on a 20-year population model that incorporated periodic estimates of population size from sample-based aerial surveys, annual harvest estimates, annual measurements of age and sex ratios, and beginning in 1997, annual measurements of overwinter fawn survival and annual survival of adult females (Kufeld et al. 1980; B. E. Watkins and B. A.

Banulis, CDOW, unpublished data). Treatment conditions in our study would cause the Uncompahgre Plateau population to increase by $>6,000$ deer per year. This level of response supports the hypothesis that the deer population was food limited, and therefore, limited by NCC. Our results demonstrate that deer nutrition, and therefore forage quality and quantity, is ultimately a critical limiting factor of the population. Our finding is particularly noteworthy considering predation and disease were overall the most common proximate causes of deer mortality prior to and during our study (Gill et al. 2001, Pojar and Bowden 2004). Furthermore, our study took place during 4 mild to average winters, when nutrition might be expected to have a lesser impact on population growth than during more severe winters.

Our research provides additional insights into the role of nutrition in ungulate population limitation. Our results are consistent with research linking nutrition to fecundity and survival in mule and white-tailed deer (Verme 1969, Robinette et al. 1973, Ozoga and Verme 1982, Baker and Hobbs 1985, Mech et al. 1991) and other ungulates (Thorne et al. 1976, Cameron et al. 1993, Keech et al. 2000, Cook et al. 2004). These studies directly link fecundity and survival to 1) body condition of adult females throughout the year, 2) rates of growth and fat accretion in young animals during late summer and fall, and 3) rates at which fat and protein are depleted during winter.

Our results are also consistent with studies that documented density-dependent effects on fecundity or survival of ungulates by manipulating density (Clutton-Brock et al. 1987, Bartmann et al. 1992, White and Bartmann 1998, Stewart et al. 2005). If a population is food limited (i.e., limited by NCC), density reductions should reduce animal competition for the limited supply of higher quality forage and improve fecundity or survival. In our study, enhanced nutrition increased the supply of high-quality forage (i.e., pellets) available for the given number of animals occupying the EUs. Whether reducing density or enhancing nutrition, the amount of higher quality forage items available per animal increases, which should result in increased fecundity or survival if a population is limited by NCC. We emphasize higher quality forage because much of the plant material available to ungulates is of insufficient quality for meeting nutrient needs, particularly during winter. Therefore, ungulate access to forage items that exceed some quality threshold (i.e., higher quality forage) is critical when considering NCC and population limitation (Hobbs and Swift 1985).

MANAGEMENT IMPLICATIONS

The ultimate question is whether habitat treatments can improve deer population performance, or conversely, minimize population declines as other habitat is lost. Our findings provide a scientific basis for pursuing and evaluating vegetative manipulation techniques in late-seral pinyon-juniper winter range as a means to set back succession and increase habitat productivity. However, our measured rates of population increase, in response to artificial nutrition enhancement, would likely not be feasible or sustainable in response to habitat improvements via vegetative manipulations. The objective of such habitat management might be to achieve smaller, yet sustainable, deer population increases over time. Availability of quality habitat is likely to become even more

limiting because productive winter- and summer-range habitats on the Uncompahgre Plateau and adjacent San Juan Mountains are being lost to human development. A coordinated effort to manage habitat at a landscape scale is underway on the Uncompahgre Plateau, referred to as the Uncompahgre Plateau Project (UPP 2007). To evaluate effectiveness of the Project from a deer perspective, an ongoing study is quantifying effects of habitat treatments in pinyon-juniper on deer population parameters (Bergman et al. 2007).

Habitat treatments in the pinyon-juniper woodlands could improve habitat productivity by increasing the quantity and diversity of higher quality forage. Treatments would likely cause the greatest increase in diet quality during winter, although late fall and spring diets might also improve because of increased forage availability. During the past decade, roller-chop and hydro-axe treatments have been performed in pinyon-juniper woodlands on the Uncompahgre Plateau and reseeded with mostly native species, with the intent to increase the quantity and diversity of forbs, grasses, and certain browse species (UPP 2007).

We specifically chose the Uncompahgre Plateau as a study site because the deer population had declined and there were competing hypotheses with respect to habitat versus predation as limiting factors. Our results should not be extrapolated beyond the Uncompahgre Plateau for these reasons. However, given resource limitations that prevent similar studies from being conducted across numerous mule deer populations, it seems warranted to make cautious inference to other pinyon-juniper winter ranges across the Colorado Plateau, which are uniquely dominated by pinyon and Utah juniper (West 1999). The current late-seral status of pinyon-juniper on the Uncompahgre Plateau, which was the basis for our hypothesis of why deer declined, is not unique. Many pinyon-juniper communities are considered degraded primarily because of altered fire patterns and excessive grazing, and therefore, warrant proactive management (Gruell 1999, West 1999). Proposed strategies to restore pinyon-juniper communities could likewise improve deer habitat productivity, and therefore, may be advisable anywhere in the Colorado Plateau ecoregion where deer populations have declined (Watkins et al. 2007). However, there is a need to evaluate the effectiveness of various habitat treatments for mule deer (Bergman et al. 2007).

We caution against the use of our findings to justify winter feeding as a management tool because our objective was to simulate optimum habitat conditions for deer. We provided pellets ad libitum and distributed pellets widely to avoid creation of feed grounds. We expended, on average, \$40,000 and roughly 1,000 person hours per winter to purchase and deliver the supplemental feed to <1,000 deer and ≤ 300 elk across 7–22 km². As a rough extrapolation, >40,000 person hours and approximately \$1.75 million in feed costs would be required to provide supplement in this manner to most of the Uncompahgre deer population for a winter. Others have evaluated the utility of winter feeding as a management strategy to mitigate deer mortality (Baker and Hobbs 1985, Peterson and Messmer 2007).

SUMMARY

- We enhanced nutrition of free-ranging mule deer during winter and spring to simulate an instantaneous increase in nutritional

quality of winter range habitat on the Uncompahgre Plateau in southwest Colorado.

- We evaluated the effect of enhanced nutrition on deer fecundity and survival rates using a life table response experiment.
- Pregnancy rates (i.e., proportion of ad F with ≥ 1 fetus) and fetal rates (i.e., mean no. of fetuses/pregnant ad F) were high among all deer and did not vary in response to the nutrition treatment.
- We observed an overall increase in survival of fetuses from February to birth in response to the treatment, although the magnitude of the effect varied annually.
- We observed marginal evidence of increased neonatal survival in response to the nutrition treatment.
- We observed a large treatment effect in overwinter fawn survival. Overwinter survival of fawns receiving the treatment averaged 0.905 (SE = 0.026) whereas overwinter survival of control fawns averaged 0.684 (SE = 0.044).
- Nutrition treatment had a positive effect on yearling recruitment, expressed as the product of fetal, neonatal, and overwinter survival rates. Survival of treatment fetuses to the yearling age class was 0.447 (SE = 0.052), whereas survival of control fetuses to the yearling age class was 0.271 (SE = 0.042).
- Nutrition treatment had a positive effect on annual survival of adult females (treatment: $\hat{S} = 0.879$, SE = 0.021; control: $\hat{S} = 0.833$, SE = 0.025).
- Combining all fecundity and survival rates into a matrix population model, we observed an increase in $\hat{\lambda}$ in response to enhanced nutrition. Average $\hat{\lambda}$ was 1.165 (SE = 0.036) for treatment deer and 1.033 (SE = 0.038) for control deer. Treatment caused $\hat{\lambda}$ to increase by 0.139 (95% CI: 0.020–0.259) during 2001–2002, 0.113 (95% CI: 0.023–0.204) during 2002–2003, and 0.145 (95% CI: 0.048–0.242) during 2003–2004. Averaged across years, treatment caused $\hat{\lambda}$ to increase by 0.133 (95% CI: 0.049–0.217).
- Increased production and survival of young (i.e., fetal, neonatal, and overwinter survival) accounted for 0.084 of the overall increase in $\hat{\lambda}$ and increased survival of adult females accounted for the remaining 0.048 increase in $\hat{\lambda}$. The treatment effect on overwinter fawn survival alone accounted for 0.044 of the increase in $\hat{\lambda}$.
- Enhanced deer nutrition caused a reduction in coyote and mountain lion predation of ≥ 6 -month-old fawns and adult females.
- The large increase in $\hat{\lambda}$ in response to enhanced nutrition indicates the deer population was food limited, and therefore, limited by habitat in terms of forage quality.
- Our study provides support for evaluating effectiveness of habitat treatments for deer in pinyon-juniper winter range. Specifically, future research is needed to determine whether habitat improvements, as opposed to artificial nutritional supplementation, are capable of causing an increase in $\hat{\lambda}$.

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Appendix A. Model selection results, based on Akaike's Information Criterion with small sample size correction (AIC_c), from an analysis of mule deer fetal survival as a function of year and a nutritional enhancement treatment (trt) in southwest Colorado, USA, 2002–2004.

Model ^a	No. parameters	AIC_c	ΔAIC_c	Akaike wt
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	20	1,137.79	0.00	0.293
$S_1(\text{trt} \times \text{yr}) S_2(\text{trt}) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	21	1,138.27	0.48	0.231
$S_1(\text{trt} + \text{yr}) S_2(.) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	18	1,139.20	1.41	0.145
$S_1(\text{trt}) S_2(.) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	16	1,139.39	1.60	0.132
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(.) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	18	1,140.30	2.51	0.084
$S_1(\text{trt} \times \text{yr}) S_2(\text{yr}) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	22	1,141.06	3.27	0.057
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{trt} \times \text{yr}) b(\text{trt} \times \text{yr})$	26	1,142.06	4.27	0.035
$S_1(\text{yr}) S_2(.) p_1(\text{yr}) p_2(\text{yr}) r(.) a(\text{yr}) b(\text{yr})$	17	1,143.78	5.99	0.015
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(\text{yr}) p_2(.) r(.) a(\text{yr}) b(\text{yr})$	18	1,146.00	8.21	0.005
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(\text{yr}) p_2(\text{trt} \times \text{yr}) r(.) a(\text{trt} \times \text{yr}) b(\text{trt} \times \text{yr})$	29	1,146.93	9.14	0.003
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(\text{trt} \times \text{yr}) p_2(\text{trt} \times \text{yr}) r(.) a(\text{trt} \times \text{yr}) b(\text{trt} \times \text{yr})$	32	1,153.51	15.72	0.000
$S_1(\text{trt} \times \text{yr}) S_2(\text{trt}) p_1(\text{trt} \times \text{yr}) p_2(\text{trt} \times \text{yr}) r(.) a(\text{trt} \times \text{yr}) b(\text{trt} \times \text{yr})$	33	1,155.15	17.36	0.000
$S_1(\text{trt} \times \text{yr}) S_2(\text{trt} \times \text{yr}) p_1(\text{trt} \times \text{yr}) p_2(\text{trt} \times \text{yr}) r(.) a(\text{trt} \times \text{yr}) b(\text{trt} \times \text{yr})$	37	1,163.96	26.17	0.000
$S_1(\text{trt} \times \text{yr}) S_2(.) p_1(.) p_2(.) r(.) a(.) b(.)$	12	1,167.19	29.40	0.000
$S_1(.) S_2(.) p_1(.) p_2(.) r(.) a(.) b(.)$	7	1,174.95	37.16	0.000

^a Fetal survival probability is represented by parameter S_1 . All other model parameters are nuisance parameters: S_2 = neonatal survival probability from birth to 5 days old, p_1 = probability of detecting a neonatal fawn ≤ 1 day old given that we conducted a search ≤ 1 day postpartum, p_2 = probability of detecting a neonatal fawn > 1 day old given that we conducted a search > 1 day postpartum, r = probability of detecting a stillborn fetus when a vaginal implant transmitter (VIT) was not shed at a birth site, a = probability of radiolocating an ad F and searching for her fawn(s) ≤ 1 day postpartum, and b = probability a VIT was shed at a birth site.

Appendix B. Model selection results, based on quasi-likelihood using Akaike's Information Criterion with small sample size correction ($QAIC_c$), from an analysis of mule deer neonatal survival as a function of sex, year, a nutritional enhancement treatment (trt), fawn age trend (A), Julian date of birth (bdate), estimated birth mass (bmass, kg), and estimated birth hind foot length (bhft, cm), in southwest Colorado, USA, 2002–2004.

Model ^a	No. parameters	$QAIC_c^b$	$\Delta QAIC_c$	$QAIC_c$ wt
Sex, bmass, A, A ² , A ³ , bdate	7	1,212.49	0.00	0.129
Sex, bmass \times yr, A, A ² , A ³ , bdate	11	1,212.52	0.03	0.127
Sex, trt, bmass \times yr, A, A ² , A ³ , bdate	12	1,212.70	0.21	0.116
Bmass, A, A ² , A ³ , bdate	6	1,212.92	0.43	0.104
Sex, trt, bmass, A, A ² , A ³ , bdate	8	1,213.33	0.84	0.085
Bmass \times yr, A, A ² , A ³ , bdate	10	1,213.53	1.04	0.077
Trt, bmass, A, A ² , A ³ , bdate	7	1,214.07	1.58	0.059
Trt, bmass \times yr, A, A ² , A ³ , bdate	11	1,214.14	1.66	0.056
Trt, bmass, yr, A, A ² , A ³ , bdate	9	1,214.70	2.21	0.043
Trt, bmass, yr, A, A ² , A ³	8	1,215.18	2.69	0.034
Trt \times yr, bmass \times yr, A, A ² , A ³ , bdate	13	1,215.60	3.11	0.027
Trt, bmass \times yr, A, A ² , A ³ , bdate, bhft	12	1,215.61	3.12	0.027
Trt \times yr, A, A ² , A ³ , bdate \times bmass	12	1,216.39	3.90	0.018
Trt \times yr, bmass \times yr, A, A ² , A ³ , bdate \times bmass	14	1,216.50	4.01	0.017
Trt \times yr, bmass \times yr, A, A ² , A ³ , bdate, bhft	14	1,216.82	4.33	0.015
Trt \times yr, bmass, A, A ² , A ³ , bdate	11	1,217.02	4.53	0.013
Trt \times yr, bmass, A, A ² , A ³	10	1,217.48	4.99	0.011
Trt \times yr, bmass, A, A ² , A ³ , bdate, bhft	12	1,217.63	5.14	0.010

^a We considered 40 models. We listed in the table only those models that received ≥ 0.01 $QAIC_c$ wt. All models that included daily, weekly, or biweekly variation in fawn age received 0 $QAIC_c$ wt.

^b Model selection results were based on $\hat{c} = 1.25$ (Bishop 2007, Bishop et al. 2008).

Appendix C. Model selection results, based on Akaike's Information Criterion with small sample size correction (AIC_c), from an analysis of overwinter survival of mule deer fawns as a function of a nutritional enhancement treatment (trt), year, sex, time (t), early winter mass (mass, kg), early winter chest girth (chest, cm), and hind foot length (cm), in southwest Colorado, USA, 2001–2004. We constrained time 4 ways: weekly, monthly, seasonally (i.e., winter, spring), and as a trend (T).

Model ^a	No. parameters	AIC_c	ΔAIC_c	AIC_c wt
Trt, yr, sex, t(month), mass	11	650.42	0.00	0.435
Trt, yr, sex, t(month), mass, chest	12	651.12	0.70	0.307
Trt \times t(month), yr, sex, mass	16	653.03	2.61	0.118
Trt, yr \times sex, t(month), mass	13	653.76	3.34	0.082
Trt, yr, sex, t(T), mass	7	655.71	5.29	0.031
Trt, yr \times t(month), sex, mass	21	657.82	7.40	0.011
Trt, yr, sex, t(season), mass	7	658.52	8.11	0.008
Trt, yr, sex, t(week), mass	31	660.52	10.10	0.003
Trt, sex, mass	4	661.99	11.57	0.001
Trt, mass	3	662.04	11.62	0.001
Trt, yr, mass	5	662.08	11.66	0.001
Trt, yr, sex, mass	6	662.25	11.83	0.001

^a We considered 23 models. We listed in the table only those models that received ≥ 0.001 AIC_c wt.

Appendix D. Model selection results, based on Akaike's Information Criterion with small sample size correction (AIC_c), from an analysis of annual survival of adult female mule deer as a function of a nutritional enhancement treatment (trt), year, time (t), age, mass (mass, kg), chest girth (chest, cm), and hind foot length (foot, cm), in southwest Colorado, USA, 2000–2004. We constrained time 3 ways: biweekly, monthly, and seasonally (i.e., winter–spring, summer–fall).

Model ^a	No. parameters	AIC_c	ΔAIC_c	AIC_c wt
Trt \times t(season), age, age ²	6	1,275.18	0.00	0.130
Trt \times t(season), age	5	1,275.58	0.40	0.106
Trt \times t(season), age, age ² , foot	7	1,275.77	0.59	0.096
Trt \times t(season)	4	1,276.06	0.89	0.083
Trt, age	3	1,276.16	0.98	0.079
Trt	2	1,276.62	1.44	0.063
Trt, age, foot	4	1,276.62	1.45	0.063
t(season), age, age ²	4	1,276.77	1.59	0.055
Trt \times t(season), age, age ² , age ³	7	1,276.79	1.61	0.055
Trt \times t(season), foot	5	1,276.91	1.74	0.051
Trt, t(season), age	4	1,277.14	1.96	0.046
Trt \times t(season), age \times foot	7	1,277.69	2.51	0.035
Trt, t(season)	3	1,277.73	2.55	0.034
Trt \times t(month)	24	1,277.84	2.66	0.032
Trt, t(season), foot	4	1,278.60	3.43	0.022
Trt, t(biweekly)	27	1,279.40	4.22	0.015
Trt, t(season), chest	4	1,279.66	4.49	0.013
Trt, t(season), mass	4	1,279.69	4.51	0.013

^a We considered 32 models. We listed in the table only those models that received ≥ 0.01 AIC_c wt.



Twin mule deer (*Odocoileus hemionus*) fawns newly born of a radiocollared adult female deer on the southern end of the Uncompahgre Plateau, Colorado, USA. Photo by Michael L. Del Tonto.



Mule deer (*Odocoileus hemionus*) fawn recently captured and radiocollared on the southern end of the Uncompahgre Plateau, Colorado, USA. Photo by Chad J. Bishop.



Adult female and fawn mule deer (*Odocoileus hemionus*) consuming apple pulp and alfalfa hay under a dropnet on the Uncompahgre Plateau, Colorado, USA. Photo by Chad J. Bishop.