

Demographic Response of Mule Deer to Experimental Reduction of Coyotes and Mountain Lions in Southeastern Idaho

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ABSTRACT Manipulating predator populations is often posed as a solution to depressed ungulate populations. However, predator–prey dynamics are complex and the effect on prey populations is often an interaction of predator life history, climate, prey density, and habitat quality. The effect of predator removal on ungulate and, more specifically, mule deer (*Odocoileus hemionus*) populations has not been adequately investigated at a management scale. We tested the efficacy of removing coyotes (*Canis latrans*) and mountain lions (*Puma concolor*) for increasing survival and population growth rate of mule deer in southeastern Idaho, USA, during 1997–2003. We assigned 8 game management units (GMUs) to treatments under a 2 × 2 factorial design (treatments of coyote removal and lion removal) with 2 replicates of each treatment or reference area combination. We used methods typically available to wildlife managers to achieve predator removals and a combination of extensive and intensive monitoring in these 8 GMUs to test the hypothesis that predator removal increased vital rates and population growth rate of mule deer. We determined effects of predator removal on survival and causes of mortality in 2 intensive study sites, one with coyote and mountain lion removal and one without. We also considered the effects of other variables on survival including lagomorph abundance and climatic conditions. In these 2 intensive study areas, we monitored with radiotelemetry 250 neonates, 284 6-month-old fawns, and 521 adult females. At the extensive scale, we monitored mule deer population trend and December fawn ratios with helicopter surveys. Coyote removal decreased neonate mortality only when deer were apparently needed as alternate prey, thus removal was more effective when lagomorph populations were reduced. The best mortality model of mule deer captured at 6 months of age included summer precipitation, winter precipitation, fawn mass, and mountain lion removal. Over-winter mortality of adult female mule deer decreased with removal of mountain lions. Precipitation variables were included in most competing mortality models for all age classes of mule deer. Mountain lion removal increased fawn ratios and our models predicted fawn ratios would increase 6% at average removal rates (3.53/1,000 km²) and 27% at maximum removal rates (14.18/1,000 km²). Across our extensive set of 8 GMUs, coyote removal had no effect on December fawn ratios. We also detected no strong effect of coyote or mountain lion removal alone on mule deer population trend; the best population-growth-rate model included previous year's mountain lion removal and winter severity, yet explained only 27% of the variance in population growth rate. Winter severity in the current and previous winter was the most important influence on mule deer population growth. The lack of response in fawn ratio or mule deer abundance to coyote reduction at this extensive (landscape) scale suggests that decreased neonate mortality due to coyote removal is partially compensatory. Annual removal of coyotes was not an effective method to increase mule deer populations in Idaho because coyote removal increased radiocollared neonate fawn survival only under particular combinations of prey densities and weather conditions, and the increase did not result in population growth. Coyote-removal programs targeted in areas where mortality of mule deer fawns is known to be additive and coyote-removal conditions are successful may influence mule deer population vital rates but likely will not change direction of population trend. Although mountain lion removal increased mule-deer survival and fawn ratios, we were unable to demonstrate significant changes in population trend with mountain lion removal. In conclusion, benefits of predator removal appear to be marginal and short term in southeastern Idaho and likely will not appreciably change long-term dynamics of mule deer populations in the intermountain west. © 2011 The Wildlife Society.

KEY WORDS alternate prey, *Canis latrans*, climate, coyote, mortality, mountain lion, mule deer, *Odocoileus hemionus*, predator control, *Puma concolor*, survival analysis.

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Respuesta Demografica del Ciervo Mula a la Reducción Experimental de Coyotes y Pumas en el Sureste de Idaho

RESUMEN La manipulación de las poblaciones de depredadores se plantea a menudo como una solución para reducir las poblaciones de ungulados. Sin embargo, las dinámicas depredador-presa son complejas y el efecto sobre las poblaciones de presas es a menudo una interacción entre depredador, historia de vida, clima, densidad de presas y calidad del hábitat. El efecto de la eliminación de depredadores en ungulados y, más concretamente, en la población de ciervo mula (*Odocoileus hemionus*) no ha sido adecuadamente investigado con una perspectiva de gestión. Pusimos a prueba la eficacia de la eliminación de coyotes (*Canis latrans*) y pumas (*Puma concolor*) para aumentar la supervivencia y la tasa de crecimiento de la población de venados en el sureste de Idaho, USA, durante el periodo 1997–2003. Se asignaron ocho unidades de gestión de la caza (GMU) a los tratamientos bajo un diseño factorial 2×2 (tratamientos de eliminación de coyote y eliminación de pumas) con dos repeticiones de cada tratamiento o combinación de zona de referencia. Se utilizaron métodos comunmente disponibles a los gestores de la fauna silvestre para el traslado de depredadores y una combinación de vigilancia extensiva e intensiva en estas 8 GMU para probar la hipótesis de que la eliminación de depredadores aumenta las tasas vitales y la tasa de crecimiento de la población del ciervo mula. Se determinaron los efectos de la eliminación de depredadores en la supervivencia y las causas de mortalidad en los dos sitios de estudio intensivo, uno con la eliminación de ambos, pumas y coyotes y el otro sin dicha eliminación. También se consideraron los efectos de otras variables en la supervivencia, como la abundancia de lagomorfos y las condiciones climáticas. En estas dos áreas de estudio intensivo, monitorizamos con radiotelemetría 250 recién nacidos, 284 cervatillos de 6 meses de edad, y 521 hembras adultas. En una escala espacial mas amplia, monitorizamos la tendencia de la población de ciervo mula y la tasa de supervivencia de cervatillos en el mes de Diciembre con censos realizados desde un helicóptero. La eliminación de coyotes redujo la mortalidad neonatal sólo cuando los ciervos se necesitaban como presa alternativa, por lo que la eliminación fue más eficaz cuando las poblaciones de lagomorfos se redujeron. El mejor modelo de mortalidad de venados capturados a los 6 meses de edad fué el que incluía precipitación de verano, precipitación de invierno, masa cervatillo, y eliminación del león de montaña. Durante el invierno la mortalidad de venados hembra adultas disminuyó con la eliminación de pumas. Las variables relativas a precipitación se incluyeron en la mayoría de los modelos de mortalidad para todas las clases de edad de ciervo mula. La eliminación de pumas aumento la tasa de cervatillos y los modelos predijeron el 6% de incremento en la tasa de cervatillo para una tasa de extracción media (3,53/1.000 km²) y 27% para una tasa de extracción máxima (14,18/1.000 km²). La eliminación de coyotes no tuvo ningún efecto sobre los coeficientes de cervatillo de diciembre en ninguno de los 8 GMU. Tampoco se detectó ningún efecto de la eliminación de coyotes o pumas en la tendencia numerica de la población de ciervos mula, el modelo con la tasa de crecimiento más alta era el que incluyó los pumas eliminados el año anterior y la gravedad del invierno, sin embargo, sólo explicó el 27% de la varianza en la tasa de crecimiento de la población. La severidad del invierno en el año actual y anterior fue la influencia más importante en el crecimiento de población de ciervos mula. La falta de respuesta en la tasa de abundancia de cervatillo o de venados a la reducción de coyote en esta extensa escala sugiere que la disminución de la mortalidad neonatal debida a la eliminación de coyote es parcialmente compensatoria. La extracción anual de coyotes no era un método eficaz para aumentar las poblaciones de ciervo mula en Idaho porque la eliminación de coyote aumento la supervivencia de cervatillos con radiocollares sólo bajo determinadas combinaciones de densidades de presas y condiciones meteorológicas, y el aumento no se tradujo en un crecimiento de la población. Los programas específicos de eliminación de coyotes en las áreas donde se sabe que la mortalidad de ciervo mula es aditiva y en las que las condiciones de extracción de los coyotes tienen éxito, pueden influir en las tasas vital de población de ciervo mula, pero probablemente no van a cambiar la tendencia numerica de la población. Aunque la reducción de pumas aumentó la sobrevivencia de ciervos mula y la tasa de cervatillos, no hemos podido demostrar cambios significativos en la tendencia de la población con la eliminación de pumas. En conclusión, los beneficios de la eliminación de depredadores parecen ser marginal y a corto plazo en el sureste de Idaho, y no van a cambiar sensiblemente la dinámica a largo plazo de las poblaciones de ciervo mula en el oeste montañoso de los Estados Unidos.

Réponse Démographique du Cerf Mulet à la Réduction Expérimentale des Populations de Coyotes et de Pumas dans le Sud de l'Idaho

RÉSUMÉ La manipulation des populations de prédateurs est souvent proposée comme une solution pour réduire les populations d'ongulés. Cependant, les dynamiques prédateur-proie sont complexes et l'effet sur les populations

de proies est souvent une interaction entre le cycle de vie du prédateur, le climat, la densité des proies et la qualité de l'habitat. L'effet de la suppression du prédateur sur les populations d'ongulés et, plus spécifiquement, de cerf mulet (*Odocoileus hemionus*) n'a jamais été étudié de façon satisfaisante pour un objectif de gestion. Nous avons testé l'efficacité de la suppression des coyotes (*Canis latrans*) et des pumas (*Puma concolor*) sur l'augmentation de la survie et du taux de croissance de la population de cerf mulet dans le sud-est de l'Idaho, États-Unis, de 1997 à 2003. 8 unités de jeu de gestion (GMUs) ont été soumises aux traitements selon un plan factoriel 2×2 (traitements de suppression du coyote et de suppression du puma) avec 2 répétitions de chaque combinaison de traitement ou de zone de référence. Nous avons utilisé des méthodes que les gestionnaires de la faune ont généralement à disposition pour effectuer les retraits de prédateurs et la combinaison de surveillances extensive et intensive dans ces 8 GMUs afin de tester l'hypothèse selon laquelle le retrait des prédateurs augmente le taux vital et le taux de croissance de la population de cerf mulet. Les effets de la suppression des prédateurs sur la survie et les causes de mortalité ont été déterminés dans les deux sites d'étude intensive, l'un avec le retrait des pumas et des coyotes et l'autre sans. Les effets sur la survie d'autres variables, incluant l'abondance des lagomorphes et les conditions climatiques, ont été examinés. Dans ces deux zones d'étude intensive, nous avons suivi par radio-télémetrie 250 nouveau-nés, 284 faons de 6 mois, et 521 femelles adultes. À plus grande échelle, la tendance démographique de cerf mulet et le ratio de faons en Décembre ont été suivis par hélicoptère. L'élimination des coyotes diminue la mortalité néonatale seulement lorsque les cerfs semblent nécessaires comme proies alternatives, ainsi le retrait des coyotes est plus efficace lorsque les populations de lagomorphes sont réduites. Le meilleur modèle de mortalité des cerfs mulet à 6 mois d'âge obtenu inclut les précipitations estivales et hivernales, la masse des faons, et le retrait du puma. La mortalité hivernale des biches adultes diminue avec la suppression des pumas. Les variables liées aux précipitations sont incluses dans la plus part des modèles de mortalité pour toutes les classes d'âge de cerf mulet. La suppression des pumas augmente le ratio de faons et nos modèles prédisent une augmentation de 6% du ratio de faons pour des taux de retrait moyens ($3,53/1,000 \text{ km}^2$) et de 27% pour des taux de retrait maximum ($14,18/1,000 \text{ km}^2$). La suppression du coyote n'a eu aucun effet sur les ratios de faons de Décembre pour les 8 GMUs extensives. Aucun effet important du retrait du coyote ou du puma seul sur la tendance démographique des cerfs mulet n'a été détecté; le meilleur modèle de taux de croissance de la population inclut le retrait des pumas l'année précédente et la sévérité de l'hiver, qui cependant n'explique que 27% de la variance du taux de croissance de la population. La sévérité de l'hiver de l'année en cours et de la précédente est la variable la plus influente sur la croissance de la population de cerfs muets. L'absence de réponse du ratio de faons et de l'abondance du cerf mulet à la réduction des coyotes pour une large échelle (paysage) suggère que le déclin de la mortalité néonatale due à la suppression du coyote est partiellement compensé. Le retrait annuel des coyotes n'est pas une méthode efficace pour accroître les populations de cerfs muets dans l'Idaho car la suppression du coyote a augmenté la survie des faons suivis par radio-télémetrie seulement sous certaines combinaisons de densité des proies et de conditions météorologiques, et l'augmentation ne se traduit pas par une croissance démographique. Les programmes de retrait du coyote ciblant les zones où la mortalité des faons est connue pour être additive et où les conditions permettent un retrait du coyote avec succès, peuvent influencer les taux vitaux de la population de cerfs mulet, mais ne changera probablement pas le sens de la tendance démographique. Bien que le retrait des pumas augmente la survie des cerfs mulet et le ratio de faons, nous n'avons pas pu démontrer de changement significatif dans les tendances démographiques après élimination des pumas. En conclusion, les avantages de la suppression des prédateurs semblent être marginaux et à court terme dans le sud-est de l'Idaho et ne modifieront pas sensiblement les dynamiques à long terme des populations de cerf mulet dans l'ouest montagneux des États-Unis.

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INTRODUCTION

Predator regulation of ungulates is a complex and controversial issue. Predation is considered regulatory if predation rate decreases with decreasing density (density-dependent) and if predation results in an equilibrium density that is lower than nutritional carrying capacity (K ; Caughley 1979, Sinclair 1989). Peek (1980) restated 2 common competing theories of ungulate regulation: 1) stability results from an interaction between ungulates and the plants they eat; and 2) stability is imposed by predators. Peek (1980) and Caughley (1981) noted that regulation by food and regulation by predators are not mutually exclusive and may be expected to act concomitantly, leading to a third hypothesis that the strength of predation can be mediated by habitat productivity (Nilsen et al. 2009). Predation can affect a prey population only if it is at least partially additive to mortality from other causes, which seems to occur for many ungulates (Keith 1974, 1983; Caughley 1976, 1981; Vucetich et al. 2005). Theberge and Gauthier (1985) noted that 3 conditions must be met to assert that predators are regulating ungulate prey: the ungulate population is depressed well below K , mortality is the primary factor influencing changes in prey numbers, and predation is the major cause of mortality.

Differing conclusions about the role of predation on ungulates within a specific area are quite likely because of complex interactions of environmental variables that influence potential population growth rate and density, including additive versus compensatory mortality, primary productivity, abundance of alternate prey species, and variability in the predator-species community (Theberge and Gauthier 1985, Messier 1994, Orians et al. 1997). Earlier studies of predator control often failed to use adequate experimental designs and often concluded predator control increased ungulate populations without addressing confounding factors (see reviews by Boutin 1992, Orians et al. 1997, Ballard et al. 2001). Connolly (1978*b*) cited 31 studies that supported the hypothesis of ungulate population regulation by predators, whereas 27 studies suggested no regulation. In a review of more recent work, Ballard et al. (2001) summarized conditions within a mule deer (*Odocoileus hemionus*) population that determine whether predation constitutes additive or compensatory mortality. Evidence in these 2 reviews suggested that predators do not cause declines in mule deer populations in undisturbed environments, but may prevent or delay population recovery after a decline.

Emerging evidence suggests top predators may be capable of regulating ungulates to lower densities in some predator-prey systems. Research has documented the effectiveness of predator removal to increase recruitment and potentially population size in white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and pronghorn (*Antilocapra americana*) populations on a limited scale (Beasom 1974, Guthery and Beasom 1977, Stout 1982, Smith et al. 1986, Hayes et al. 2003, Boertje et al. 2009). Complementary evidence is provided by recent studies on trophic cascades precipitated by the loss of a top predator in terrestrial systems (Hebblewhite et al. 2005, Terborgh et al. 2006, Beyer et al. 2007). In these examples, loss of large predators such as wolves (*Canis lupus*) released herbivores from regulation, and allowed herbivore density to increase to nutritional carrying capacity, altering vegetative characteristics of the landscape. Similarly, removal of coyotes (*Canis latrans*) influenced the faunal community in western Texas by reducing species richness and diversity of small mammals and increasing diversity of mesopredators (Henke and Bryant 1999).

Consistent with the interactive effects of predation and food, ungulates will often minimize predation risk by trading use of quality habitat for security at the expense of optimal nutrition (Pierce et al. 2004, Kauffman et al. 2007, Wirsing et al. 2008, Hebblewhite and Merrill 2009). Thus, under risk of predation, food and predation may interact to drive behavioral decisions to avoid optimal foraging habitats or adopt inefficient foraging strategies, contributing to reduced ungulate density. These decisions at the individual level can translate to population-level interactions between predation and bottom-up primary productivity to mediate the strength of predation, the third hypothesis outlined above. For example, recent meta-analyses of roe deer (*Capreolus capreolus*) populations across Europe show that predators can only regulate or limit roe deer at higher latitudes under low primary productivity (Melis et al. 2009). At lower latitudes with higher primary productivity, the strength of predation is reduced and likely compensatory. These results have been corroborated as well in North America, especially for white-tailed deer (Dumont et al. 2000), but climatic variation still helps explain population fluctuations as in roe deer (Melis et al. 2009).

Mule deer have historically exhibited volatile population fluctuations in the western United States (Unsworth et al. 1999, Gill et al. 2001, Peek et al. 2002). These fluctuations have been especially evident in the intermountain west, which includes Idaho, Nevada, Utah, Colorado, Wyoming, and Montana. Mule deer populations in the western United States

gradually increased beginning in the 1920s, peaked in the late 1940s to early 1960s, then declined during the late 1960s to mid-1970s (Denny 1976). In southern Idaho, populations rebounded through the 1980s and then underwent a widespread decline in the 1990s (Idaho Department of Fish and Game 1999). The complex combinations of factors that drive these population fluctuations are only partially understood but include climate, predation, competition with other herbivores, and interactions among factors. On top of this complex template of interacting variables, the role of human management actions such as predator control, harvest management, and habitat improvement on reversing population declines is difficult to understand.

The role of predation in population regulation of mule deer is difficult to assess because ecological communities in which mule deer occur are complex, with alternate prey species and a rich predator community. A direct positive relationship exists between coyotes and the abundance of lagomorphs, the primary prey of coyotes (Hoffman 1979; Todd and Keith 1983; Knowlton and Gese 1995; O'Donoghue et al. 1997, 1998). Clark (1972) reported that changes in coyote density were correlated with density of black-tailed jackrabbits (*Lepus californicus*) in southeastern Idaho. Contradictory predator/prey dynamics may occur with increased primary prey density; coyote populations may increase, thereby increasing the predation rate and decreasing deer survival (Prugh 2005), or conversely, coyotes may focus predation on increasing primary prey and decrease deer predation rate. For example, Patterson and Messier (2000) documented that coyote kill-rates on white-tailed deer were inversely related to snowshoe hare (*Lepus americanus*) densities. Similarly, Hamlin et al. (1984) observed that fawn mortality in mule deer attributed to coyotes was lowest when microtine rodent populations were high in Montana. Mountain lions (*Puma concolor*) are obligate predators of ungulates, but alternate prey also may impact the predation rate on mule deer, as lagomorphs are often a major prey item (Cunningham et al. 1999). Thus, effects of predator control may be uncertain in ecologically complex communities.

Studies that have tested the effect of coyote removal on mule deer demography have observed varied results (Austin et al. 1977, Robinette et al. 1977, Smith and LeCount 1979, Trainer et al. 1981), although no removals were implemented at large scales (>1,000 km²). Harrington and Conover (2007) evaluated the effect of coyote removal for protection of livestock on mule deer and pronghorn populations at a landscape scale but did not examine confounding effects such as habitat and climate. Bartmann et al. (1992) used an experimental framework to determine that the effect of coyote removal on fawns in winter was compensatory, as fawn survival did not change, although mortality due to predation was reduced. Two studies observed minimal effects of removing mountain lions on mule deer populations (Robinette et al. 1977, Logan and Sweanor 2001). Logan and Sweanor (2001) concluded that mountain lion predation was partially compensatory and mule deer populations were limited by the interaction of predation and climate-induced habitat condition.

Controversial and uncertain as the effect of predation may be on ungulates, wildlife professionals often receive considerable pressure to reduce predator populations in an effort to increase populations of ungulates (Todd 2002), including mule deer,

despite questionable cost:benefit analyses. As reviewed above, however, management applications of predator removal were often ineffective for increasing mule deer populations because: 1) populations were at or near K and mortality was compensatory, 2) predation was not a limiting factor, 3) predator populations were not sufficiently reduced, 4) complexities of multi-species predator-prey communities were not considered, and 5) predator control efforts were diluted because they were dispersed over a large area (>1,000 km²; Ballard et al. 2001). Ballard et al. (2001) critiqued the weak state of evidence for effects of predator control on mule deer, in particular the small scale over which most previous control efforts had occurred (i.e., <1,000 km², sensu Mosnier et al. 2008). Large-scale experimental tests of predator removal are necessary to evaluate the efficiency, logistical practicality, and cost of removals to increase mule deer populations and, ultimately, hunter harvest and harvest opportunities. Furthermore, most mule-deer-predator-control studies were conducted over short time frames (1–3 yr) and often failed to examine confounding or interacting variables (Ballard et al. 2001). To enhance decision-making processes regarding predator removal, Ballard et al. (2001) and others (Orians et al. 1997) recommended a rigorous, large-scale experimental approach over a sufficiently long temporal scale to include favorable and severe weather conditions, as well as measurements of alternate prey, hunter harvest, and habitat condition.

Mule deer numbers in southern Idaho declined significantly during winter 1992–1993, and provided an example of the challenge of understanding the causes of fluctuating mule deer populations. Loss of up to 50% of a population in some areas was attributed to dry conditions during the previous summer, resulting in inadequate fat storage and fawn growth, followed by above-average winter snowfall (Idaho Department of Fish and Game 1999, Bishop et al. 2005). The theory of density-dependence (Caughley and Sinclair 1994, Eberhardt 2002), supported by empirical evidence in ungulates (Robinette et al. 1977, McCullough 1979), predicts that mule deer fawn-to-adult female ratios, recruitment, and population size should have increased following such dramatic declines during subsequent years. However, mule deer populations in southern Idaho were stationary or continued to decline during 1993–1997. In addition, the number of fawns per 100 adult females in late fall–early winter decreased from 89 (SD = 7.21) during 1988–1990 to 68 (SD = 5.97) during 1994–1997 (Hurley and Unsworth 1998). The failure of the populations to increase was puzzling because weather conditions favored survival, harvest of antlerless deer was eliminated in 1994, and populations were apparently below K , as evidenced by minimal mortality from winter malnutrition and vacant peripheral winter range (Idaho Department of Fish and Game 1999).

A possible explanation for the stationary or declining populations may be reduced productivity through nutrition or senescence in adult females (Connolly 1981, Hamlin and Mackie 1989, Bishop et al. 2009). Alternatively, high predator-caused mortality of adults or fawns or both may have driven declines (Ballard et al. 2001). The major causes of mortality in these populations were weather (favoring survival during this period), hunting (lowered during this period), and predation by mountain lions and coyotes (Unsworth et al. 1999, Bishop et al. 2005).

These lines of evidence supported the potential role of predation in preventing the recovery of mule deer populations after the declines of 1992–1993. This situation provided an opportunity to test the role of predators in suppressing the recovery of mule deer populations.

We tested the hypothesis that predator reduction increases mule deer populations at temporal and spatial scales relevant to wildlife managers in mule deer populations. Bishop et al. (2009) designed companion research to investigate the effect of enhanced nutrition, together targeting 2 alternate hypotheses of declining mule deer populations in the western United States. We followed recommendations for study design identified by Ballard et al. (2001), and conducted predator removal at spatial (>1,000 km²) and temporal scales (6 yr) adequate to control for potentially confounding variables on mule deer demography. We used existing management tools by working cooperatively with the U.S. Department of Agriculture's (USDA) Wildlife Services and sport hunters to reduce predator populations. From a wildlife manager's perspective, predator removal must affect the entire target deer population to be of value. We assured the management relevance of our predator removal experiment by conducting predator removals and deer population monitoring at the scale of a game management unit (GMU; range: 923–3,511 km²). We hypothesized that predator removal would increase the growth rate of mule deer populations through increased survival of adult females and fawns (Table 1). Thus, our objectives were: 1) evaluate coyote and mountain lion removal as a means to increase survival and abundance of mule deer and 2) identify the influence of deer population characteristics, alternate prey abundance, and weather conditions on effectiveness of predator removal to enhance mule deer population dynamics (see specific predictions in Table 1).

STUDY AREA

The study area encompassed 14,700 km² and included Idaho Department of Fish and Game (IDFG) GMUs 54, 55, 56, 57, 71, 73A, 73 Elkhorn (73E), and 73 Malad (73M) in southeastern Idaho, 1997–2003 (Fig. 1). Elevation ranged from 1,060 m to 3,150 m. Topography was typified by several north-south mountain ranges separated by wide valleys (Appendix A). Topography

and climate were similar across the study GMUs. Southeast Idaho is characterized by hot, dry summers; cool, dry winters; and warm, wet springs (Fig. 2). Average annual weather was 29.8 cm precipitation and 86 growing-degree days (10° C base; U.S. Bureau of Reclamation 2004). During most winters, snow accumulation on the valley floors was <20 cm.

Vegetation communities were similar across all study GMUs (Table 2). Vegetation at lower elevations was dominated by agricultural fields of dry-land grain and Conservation Reserve Program (CRP) perennial grasses, big sage (*Artemisia tridentata*), and juniper (*Juniperus osteosperma*). At higher elevations, mountain-shrub complexes of antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos* spp.), and serviceberry (*Amelanchier alnifolia*) were found on more xeric sites. Patches of aspen (*Populus tremuloides*) and chokecherry (*Prunus virginiana*) occurred on mesic sites. Douglas fir (*Pseudotsuga menziesii*) forests were common on north slopes above 2,000 m. Valley bottoms were primarily private agricultural lands, and uplands were mostly public land, administered by the United States Forest Service (USFS), Bureau of Land Management (BLM), or Idaho Department of Lands. Livestock grazing and recreation, including deer hunting, were primary public land uses.

Each experimental unit (GMU) encompassed a single mountain range that included both summer and winter ranges for one subpopulation of deer with minimal interchange with other experimental units (Appendix A). Game Management Unit 73 (Fig. 1) contained 2 subpopulations and was split into 73 Elkhorn (73E) and 73 Malad (73M) before treatment assignments. Two subpopulations of mule deer also occurred in GMU 71 and only the southern subpopulation was included in the study due to existing population trend area design. Deer wintered on the western and southern portions of each GMU and migrated 10–40 km to summer on the eastern and northern portions of the mountain ranges. Game Management Units 56, 71, 73A, 73E, and 73M were managed with antlered-only hunting regulations. Hunting season length ranged from 14 to 27 days. Season structure in GMUs 54, 55, and 57 offered 27 days of antlered-only hunting with limitations on hunter numbers. Prior to 2000, adult female and fawn (i.e., antlerless) hunting opportunity was not offered anywhere in the study area. Antlerless deer

Table 1. Predicted influence of predator removal treatments and covariates on mule deer survival and population growth in southeastern Idaho during 1997–2003.

Model	Prediction
Main effects models	1. Coyote removal will increase deer survival, fawn ratios, and population growth 2. Mountain lion removal will increase deer survival, fawn ratios, and population growth
Group covariates models	1. Increased lagomorph populations will reduce coyote predation on deer. Coyotes are generalist predators and an increase in main prey (lagomorphs or small mammals) will decrease the need for deer as a prey item 2. Increased lagomorph populations will not reduce mountain lion predation on deer. Mountain lions are obligate predators on deer and increased alternate prey will not change selection unless deer numbers decrease 3. Increased precipitation in spring-summer will increase fawn survival and recruitment through increased nutrition of adult females and fawns 4. Increased precipitation in fall-winter will decrease deer survival and recruitment through increased energy expenditure and decreased forage availability 5. Increased winter severity (lower temperature and increased snow depth) will decrease winter survival, recruitment and population growth rates
Individual covariate models	1. Increased fawn mass will increase survival through increased fat reserves and maturity 2. Females fawns generally survive better than males 3. Birth timing near peak fawning will increase survival due to predator swamping near peak fawning, whereas inclement weather will decrease survival of early fawns and delayed maturity will decrease survival of late fawns 4. Neonate siblings will divide available nutrients and predator defense from the dam, decreasing fawn survival

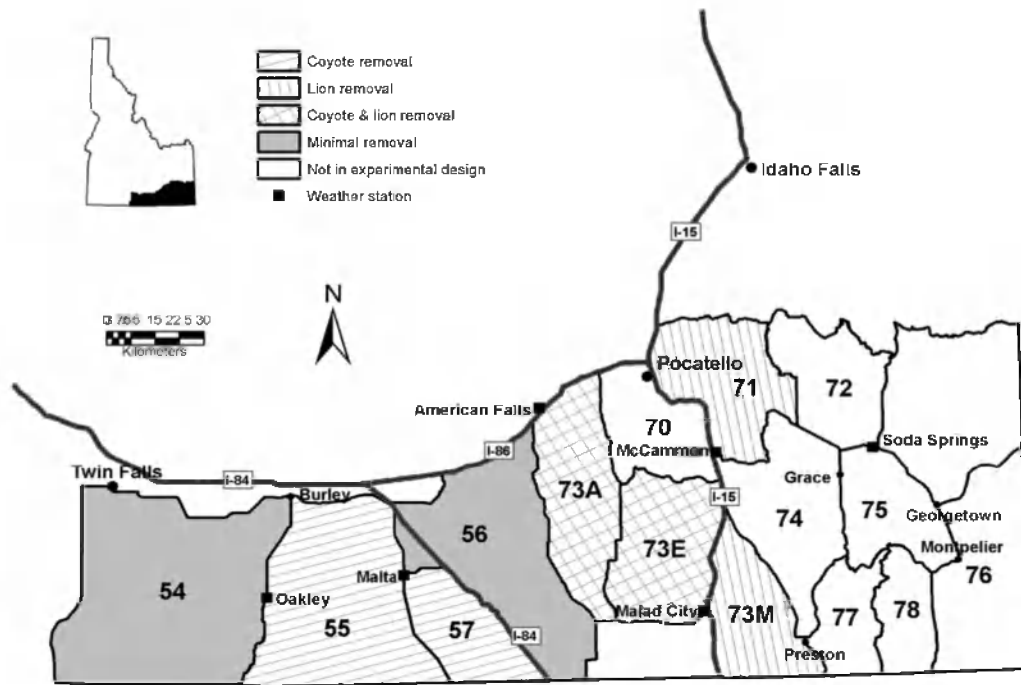


Figure 1. Study areas in southeastern Idaho where we monitored mule deer under different predator removal regimes, 1997–2002. Labels indicate game management units (GMUs). Intensive study units were GMU 56 and GMU 73A where survival was estimated via telemetry.

harvest was limited to general archery or youth-only, any weapon hunts during 2000–2002. Average annual antlerless harvest for 2000–2002 varied between 1.2% and 2.3% of estimated population size for GMUs 54, 56, 71, 73A, 73E, and 73M, whereas antlerless harvest in GMUs 55 and 57 represented <0.5% of the population.

METHODS

Experimental Design

We selected 8 GMUs of similar habitat (Fig. 1, Table 2) to evaluate effects of coyote and mountain lion removal on recruitment and growth of mule deer populations during 1997–2003. We termed these GMUs the extensive study area. Combinations of coyote and mountain lion treatment resulted in a 2×2 factorial treatment design with 2 replicates each (Fig. 1, Table 2). To avoid confusion, we refer to predator-control GMUs as treatment and GMUs without predator control as reference. We randomly assigned 4 GMUs to coyote removal treatment. We then assigned 4 GMUs to increased mountain lion harvest, 2 with coyote removal treatments and 2 without. We grouped GMUs selected for mountain lion removal on the eastern half of the study area to maximize removal effects and minimize the effect of large home ranges of mountain lions. The 2 reference GMUs received no experimental coyote or mountain lion treatment. Although we designed the study to assess efficacy of predator removal on fawn-to-adult female ratios as a factorial approach, predator removal rates varied over time and across replicate sites. Knowledge of true removal density of coyotes and mountain lions from each GMU each year prompted us to modify the factorial design. Instead, we used a regression approach with rate of coyote and mountain lion removal as the key independent variables to analyze the mule deer

recruitment and population response. We used aerial surveys to monitor size of mule deer populations (Unsworth et al. 1994; Table 2) and fawn-to-adult female ratios (fawn ratios) across all study areas. Under the predator-regulation hypothesis, we predicted that predator removal would increase fawn ratios and population rates of increase, as modified by climate covariates (Table 1).

To complement population and recruitment sampling within our extensive study area, we also intensively monitored cause-specific mortality and survival of adult females and fawns with radiotelemetry in GMU 56 (reference area) and GMU 73A (treatment area; Fig. 1). These GMUs were near the center of the overall study area and provided year-long habitat for 2 distinct subpopulations of deer. We predicted predator removal would either decrease mortality if regulated by predators or change the causes of mortality if regulated by nutrition or climate. In this intensive study area, we included the effects of potential confounding factors on the effects of predator removal as influenced by several covariates (Tables 1 and 3), which we describe below.

We organized methods and reporting of results first with main effect and covariate development, followed by deer mortality models from the intensive study area and concluded with population-level analyses from the extensive study area. This organization allowed the progressive examination of how predator removal effects at the individual and group level scaled up to the integrative metric of population growth.

Predator Reduction

Coyote removal and population index.—United States Department of Agriculture Wildlife Services personnel removed coyotes by shooting coyotes from helicopters or fixed-wing aircraft in the 4 treatment GMUs during winter and early spring

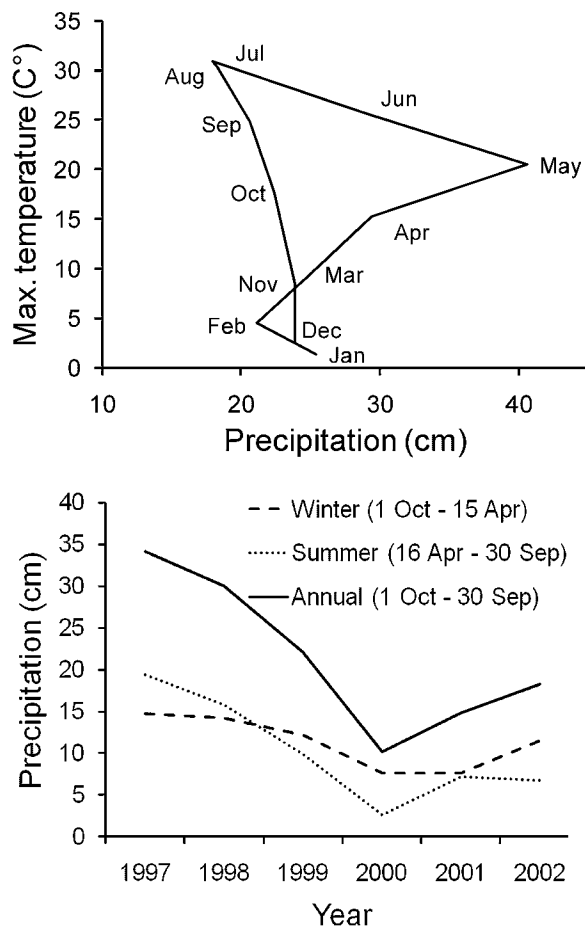


Figure 2. Climograph (top panel) of study area in southeastern Idaho, 1948–2003. Mean values of maximum temperature and total precipitation are plotted by month to depict normal climate patterns throughout the year during seasons. Values are a composite of all weather stations in the study area. Bottom panel depicts the total precipitation in summer growing season (16 Apr–30 Sep) and winter (1 Oct–15 Apr) for each year of the study.

1997–2002 (Fig. 1). Flights were repeated throughout winter while snow cover provided acceptable tracking conditions. Aerial coyote removal began 1 January and continued through mid-April. Beginning in 1999, additional ground efforts including trapping, calling, shooting, and pup removal at den sites were implemented through July. Ground efforts were concurrent with aerial removal and intensified when snow conditions

deteriorated; most of the ground effort was concentrated during the early pup rearing time period (late spring to early summer). Ground-based efforts were also concentrated within fawning areas where neonates were especially vulnerable (Knowlton 1976). Wildlife Services also removed coyotes from reference GMUs in response to specific livestock depredation problems. We converted total number of coyotes removed from a GMU (both reference and treatment) by Wildlife Services to density of coyotes removed based on land area of the GMU (no. removed/1,000 km²). Recreational coyote harvest was open year-round to sportsmen possessing a hunting or furbearer license (required for trapping). All furbearer licensees were mandated to report coyote harvest by county, which did not necessarily align with GMU boundaries; thus, recreational harvest was reported as a check on anomalous recreational harvest but we did not incorporate it into analyses.

Effectiveness of coyote removal was influenced by snow conditions, aircraft availability, effort, methods, and coyote ecology. Aerial coyote removal was most effective during periods with 100% fresh snow cover, but helicopter availability often did not coincide with optimal snow conditions. This variability in conditions resulted in differential removal of coyotes among treatment areas (study GMUs) and years, which we partially mitigated with ground-based efforts. As previously mentioned, different removal rates between treatment GMUs and among years led us to a regression model-based analysis, rather than a strict analysis of variance (ANOVA) design-based analysis of efficacy of predator control.

We conducted annual scat surveys in all study units to estimate coyote density (Knowlton 1984). We randomly selected 50 1.6-km road or trail segments as transects in each of the 8 study GMUs. We surveyed transects from May to July of each year. Observers drove an all-terrain vehicle (ATV) once in each direction along each road at <8 km/hr and removed scats at the beginning of the survey period. We duplicated the process approximately 10 days later to count the number of new scats deposited. The index was expressed as scats/mile per day and we calculated the density as coyotes/km² = ((Index) × 100 – 2.66)/29.58 (Knowlton 1984). In 1998, we surveyed transects in Units 56 and 73A (the intensive study areas) only, and we expanded efforts to all units in 1999. We discontinued transects in GMUs 71 and 54 after 1999 and 2000, respectively, due to logistical constraints. We sampled the remaining 6 GMUs through 2002.

Table 2. Mule deer population estimates from initial aerial surveys (Unsworth et al. 1994) within predefined survey areas, southeastern Idaho, 1995–1998. Percent vegetation type is the land area of these major vegetation types within each game management unit (GMU).

GMU	Treatment	Area (km ²)	Survey year	Estimate		% Vegetation type			
				<i>n</i>	±90% CI	Sagebrush	Deciduous	Coniferous	Agriculture
54	Reference	3,511	1996	2,445	159	49.2	6.2	4.1	26.6
55	Coyote	2,654	1995	785	89	50.0	2.9	12.1	25.2
56	Reference	2,338	1998	2,561	256	44.0	3.7	6.9	41.6
57	Coyote	923	1997	717 ^b		54.3	0.9	14.6	17.9
71 ^a	Lion	941	1996	1,003	120	36.3	16.3	14.2	27.4
73A	Both	1,128	1996	1,324	97	32.3	5.4	10.3	41.5
73 Elkhorn ^a	Both	1,434	1996	908	104	36.7	7.5	10.0	44.1
73 Malad ^a	Lion	1,031	1996	962	270	28.3	10.7	11.4	46.3

^a Portion of GMU based on mule deer herd segment use (Appendix A).

^b No population estimate available, so we applied a correction factor for population estimate in subsequent years (1.35) to raw count of 531.

Table 3. Definitions and variable abbreviations of factors we tested in mortality, fawn ratio, and population-rate-of-change models in southeastern Idaho during 1997–2003. Intensive analysis type refers to mortality models in Game Management Units (GMUs) 56 and 73A; extensive refers to fawn ratio and population rate of change for all GMUs.

Abbreviation	Definition	Analysis type
CRD	Coyotes removed/1,000 km ² annually in GMU	Intensive and extensive
LRD	Mountain lions removed/1,000 km ² annually in GMU	Intensive and extensive
StudyArea	0 = GMU 73A, 1 = GMU 56	Intensive
Lagomorphs	Annual lagomorph population index for the intensive study GMUs 56 and 73A	Intensive
Precip	Total precipitation (cm) for the current season	Intensive and extensive
PreviousPrecip	Total precipitation (cm) for the previous season	Intensive and extensive
Z-Precip	Z-score of current season precipitation minus Z-score of previous season precipitation	Intensive
WSI	Winter Severity Index	Extensive
Mass	Estimated mass (kg) of neonate fawns at age 4 days and mass (kg) of 6-month-old fawns at capture	Intensive
Sex	Used in fawn models only, coded as 0 = female, 1 = male	Intensive
BirthTime	Timing of neonate fawn birth in relation to median birth date for cohort	Intensive
Siblings	Presence of siblings with neonate fawn, coded as 0 = no sibling, 1 = siblings present	Intensive

Mountain lion removal and population index.—We altered hunting-season length or harvest quotas to manipulate mountain lion harvest during 1998–2002. Mountain lion hunting seasons were closed 48 hr after hunter harvest reached a predetermined quota. Structure of mountain lion seasons in liberal-harvest (treatment) GMUs was changed from liberal female quota systems for the 1997–1998 seasons to general seasons (not limited by quota) in 1998–1999, then back to liberal quotas for the 1999–2000 through 2001–2002 seasons. Female quotas in the conservative-harvest (reference) GMUs remained unchanged throughout 1997–2002. Number of mountain lions harvested in each GMU was determined through a mandatory registration of all successful mountain lion hunters in Idaho. Most mountain lion removal occurred from 1 December (start of hound season) to 15 January (approx. 80%) with remaining removal distributed until the season close on 31 March. We converted the total number of mountain lions removed from a GMU to density (no. removed/1,000 km²) of lions removed.

We gauged the magnitude of mountain lion removal using a lion-population index. We indexed mountain lion populations within intensive-study GMUs from 1998 to 2001 by combining dust-track (Smallwood and Fitzhugh 1995) and aerial snow-track survey methods (Van Sickle and Lindzey 1991) to develop a ground-based tracking method. We divided the reference (56) and treatment (73A) GMUs into 46-km² quadrats and then stratified the quadrats into high or low probability of finding a mountain lion track based on habitat type and expert opinion. We drew a random sample of 25% of the quadrats in each stratum from each GMU and we surveyed transects in proportion to strata availability while snow conditions remained acceptable. Two days after a snowfall of ≥ 5 cm, we counted tracks from snowmobiles along up to 32 km of snow-covered roads in each quadrat. Personnel traveled at 10–16 km/hr along routes in both directions. We measured stride length and track dimensions for each mountain lion track observed on transect to identify unique individuals (Smallwood and Fitzhugh 1993). The index was expressed as the number of unique tracks/km for all quadrats within a GMU.

Lagomorph Abundance

We developed estimates of relative lagomorph density using indices within intensive GMUs (56 and 73A) where we also estimated survival rates of mule deer (Fig. 1). Because coyotes are

generalist predators and shift prey selection based on availability (Hamlin et al. 1984, Randa et al. 2009, but see Patterson et al. 1998), we predicted that increased lagomorph density would decrease mortality of fawns (Table 1). We used vehicle headlight surveys to estimate lagomorph abundance from 1998 to 2002 (Trout 1978) in the 2 intensive units. We initiated surveys 1 hr after sunset on clear nights from late August to early October. We established 1 transect in each GMU within the intensive study area to sample all habitats used by mule deer. Length of each transect was proportional to GMU area (i.e., GMU 56 = 104 km, GMU 73A = 56.2 km). Observers traveled secondary roads at 32–48 km/hr and recorded lagomorphs observed in vehicle headlight beams on the roadbed. We recorded species of lagomorphs: black-tailed jackrabbits (*L. californicus*), white-tailed jackrabbits (*L. townsendii*), or mountain cottontail (*Sylvilagus nuttallii*); and distance along transect. The index was expressed as a weighted average (by transect length) of lagomorphs observed per 100 km for both GMU transects to produce an overall area estimate.

Weather Covariates

Annual variation in mule deer survival in Idaho is large (Unsworth et al. 1999, Bishop et al. 2005) and likely tied to climate; therefore, we developed 2 synthetic climatic variables to minimize the number of parameters in mortality models. Previous studies indicated that below-average summer precipitation, which reduced forage quality (Marshal et al. 2005), accompanied by above-average winter precipitation resulted in low over-winter survival and reduced population growth (Hamlin and Mackie 1989, Peek et al. 2002, Bishop et al. 2005). We also hypothesized that high previous winter precipitation accompanied by low summer precipitation would result in decreased fawn survival during summer mediated by reduced nutritional condition of adult females (Table 1).

We used data from the AgriMet weather station (U.S. Bureau of Reclamation 2004) in Malta, Idaho, to quantify seasonal precipitation and temperature during 1998–2003 for survival modeling and fawn-to-adult female ratio analysis. This weather station was located in the geographic center of the study area and the only station that provided complete data during this study period. The summer period (16 Apr–30 Sep) corresponded to the growing season (min. temp $> -2^{\circ}$ C), with most precipitation falling as rain. We considered 1 October to 15 April as winter,

when most precipitation fell as snow. We included total seasonal precipitation in survival and fawn-to-adult female ratio modeling.

Our first synthetic climate covariate, termed Z-precipitation, captured winter and summer climate by subtracting the Z-score or standard score (Zar 1984) of previous-season total precipitation from the Z-score of current-season total precipitation. By standardizing seasonal precipitation across the mean precipitation for the study period (1998–2002), the magnitude of deviation from mean was comparable across seasons. During winter, a larger value of this variable indicates below-average summer precipitation and above-average winter precipitation. The opposite is true during summer when a larger value indicates below-average winter precipitation and above-average summer precipitation.

Previous studies also showed that winter severity decreased mule deer vital rates and density (Mackie et al. 1998, Peek et al. 2002). To account for differential effects of snow depth and temperature on population growth rate of mule deer populations, we used data (Western Regional Climate Center 2004) within or near each GMU (Fig. 1) to generate a second synthetic climate variable, winter-severity index (WSI), for each study area. We estimated missing values for individual weather stations by regressing monthly means of the chosen weather station with monthly means of the nearest weather station (Fig. 1). We used total snowfall during December and January and monthly mean maximum temperature during November through March as indicators of winter severity. To create a standardized index of winter severity, we also calculated Z-scores (Glover and Mitchell 2002, Peek et al. 2002) from these monthly values. These scores were expressed as number of standard deviations of that monthly value above or below the 50-yr mean. We estimated a snow severity index (SSI) from mean Z-scores for total snowfall in December and January. A winter temperature severity index (TSI) consisted of the average Z-score of mean monthly maximum temperature for November through March. We then calculated the WSI as: $WSI = (SSI - TSI)/2$.

Mule Deer Survival and Productivity

We used radiotelemetry to evaluate the effect of predator removal and other factors on survival of individual deer within intensive study areas. Minimal coyote removal and conservative lion harvest occurred in the reference area (GMU 56), whereas both liberal mountain lion harvest and active coyote removal was focused in the treatment area (GMU 73A).

Capture methods.—We used methods described by White et al. (1972), Smith (1983), and Riley and Dood (1984) to capture neonate fawns from 1998 to 2002. We observed adult females exhibiting fawning behavior until they fed their newborn fawns or otherwise identified fawn locations through behavior (White et al. 1972). We searched the identified area and captured fawns by hand after the female moved away. To minimize capture influences or predator attraction, we used latex gloves to handle the fawn and did not collect blood or insert an ear tag. To sample the entire reproductive unit and reduce capture bias, we attempted to capture all fawns in a litter. We measured fawn mass, chest girth (directly behind shoulders on the exhale), hind foot length (tip of hoof to calcaneus), and growth ring of front

hoof (Robinette et al. 1973) to estimate age and condition. We fitted fawns with brown or black expandable radiocollars designed to break away 6–8 months after capture. Transmitters were equipped with mortality sensors (4-hr delay) and weighed 89–98 g.

We captured adult deer and 6-month-old fawns during winter using drive nets (87% of captures), net-guns (11%), and clover traps (2%) from 1998 to 2002. In the first year, we captured deer during December–March. Thereafter, captures began in December and were completed by 22 January. We fitted adult females and 6-month-old fawns with ear tags and 320-g radiocollars with mortality sensors. We measured hind foot length and chest girth of all animals. Transmitters deployed on female fawns were permanently affixed and pleated to expand as the animal grew. All 6-month-old male collars were designed to break away within 1 yr. We measured fawn mass to the nearest 0.4 kg with a calibrated spring scale and estimated age of adult females from tooth eruption and wear patterns (Robinette et al. 1957).

We tested for the possibility of disease-related compensatory mortality, which could confound predator removals, by comparing disease profiles of study animals to regional estimates of disease prevalence across Idaho. We collected a blood sample from each adult female during 1998–2000, allowed it to clot, centrifuged it, and harvested sera. We tested sera for pregnancy and exposure to disease agents to ensure we were not missing important non-predation mortality. Sera were analyzed for pregnancy-specific Protein-B (PSPB) by Bio-Tracking, Inc., Moscow, Idaho, USA (Sasser et al. 1986) and tested for respiratory and other infectious pathogens common to the western United States at Bureau of Animal Health Labs, Boise, Idaho, USA. Sera were tested for anaplasmosis, bluetongue, bovine respiratory syncytial virus (BRSV), brucellosis, bovine virus diarrhea (BVD), epizootic hemorrhagic disease (EHD), infectious bovine rhinotracheitis (IBR), parainfluenza-3 (PI3), *Lepto swaziac*, *L. australis*, *L. autumnalis*, *L. ballum*, *L. bratislava*, *L. canicola*, *L. gryppo*, *L. harjo*, *L. ictero*, and *L. pomono Idaho*. We defined disease prevalence as: $P_i = x_i/n_i$, where x_i = number of deer positive for exposure, and n_i = number of deer sampled. An Idaho Department of Fish and Game veterinarian or laboratory biologist was on site during most captures to assist with sampling and assure animal welfare. The animal handling protocol was approved by the Animal Care and Use Committee, Idaho Department of Fish and Game Wildlife Health Laboratory, Caldwell, Idaho, USA.

Survival and cause-specific mortality of mule deer.—We monitored telemetry signals for mortality of adult and 6-month-old deer via aerial or ground telemetry every 2 days during winter and spring (1 Dec–15 May) and approximately twice weekly during summer and autumn (16 May–30 Nov). These dates coincided with winter use through spring migration and summer use through fall migration of mule deer. We monitored neonates at 1- to 2-day intervals during summer and twice weekly throughout autumn until collars were shed. When we received a mortality signal, we investigated the site within 24 hr. We identified the cause of death using criteria developed by Wade and Bowns (1985) and categorized mortalities as coyote, mountain lion, bobcat, unknown predator, malnutrition, natural, other, and unknown. We retrieved whole carcasses of fawns and

delivered them to the IDFG Wildlife Health Lab, Caldwell, Idaho, USA, for necropsies and disease sampling when possible. We considered adults and 6-month-old deer that died ≤ 5 days after capture to be possibly capture-related and removed them from analysis.

We estimated survival rates (Kaplan and Meier 1958, Pollock et al. 1989) and variances for neonates (birth to 6 months), 6-month-old fawns (6–12 months), and adult females (>12 months) in each GMU by year and pooled across years. We tested differences in pooled survival rates by age group and season between reference and treatment GMUs using log-rank tests (Pollock et al. 1989, Hosmer and Lemeshow 1999). We tested for differences in mean age of adult females between treatments by mortality cause with *t*-tests in STATA ver. 10.1 (StataCorp, College Station, TX). We used competing-risk analysis to assess differences in mortality cause between age classes in reference and treatment areas by calculating a cumulative incidence function (CIF) for each age class and mortality cause (Heisey and Patterson 2006). We tested for differences in CIFs between predator removal treatments using the PepeMori test (Pintilie 2006). We conducted analyses using STATA ver. 11.1 (Coviello and Boggess 2004, StataCorp).

We modeled relationships between instantaneous mortality rates and predator removal, alternate prey abundance, weather, and body mass using Cox proportional hazards models (Cox and Oakes 1984, Murray 2006). This semi-parametric method allowed for left-truncation (i.e., staggered entry where animals continually enter the analysis) and right-censoring. We right-censored an animal when the transmitter failed, the collar was shed, or the animal left the study area. We calculated hazard ratios, often called risk ratios, for each predictor (Hosmer and Lemeshow 1999, Harrell 2001), where a hazard ratio >1 represents increasing risk of mortality and <1 represents decreasing risk as the predictor increases (Cantor 1997). We considered the hazard ratio significant if the 95% confidence interval did not overlap 1.0. We initiated the study period after the first capture in each GMU. We considered neonates at risk at birth and under observation at estimated age of capture. Failure time for 6-month-old fawns and adults was the number of days between marking and death or censoring. The primary assumption for Cox models is that predictors are proportional with respect to time, or the relationship between log of the hazard rate and the variable does not change with time (no time-by-predictor interactions; Harrell 2001). We tested this assumption graphically and using Schoenfeld's test to assess violations of the time-by-predictor interaction assumption (Hosmer and Lemeshow 1999).

We tested the primary treatment of predator control using coyote and mountain lion removal rate (no. removed/1,000 km²) as a covariate in Cox models. We separated mortality analyses by age of fawns (neonate, 6-month-old) for summer-autumn (16 May–30 Nov) and winter-spring (16 Dec–15 May) as these samples were independent (i.e., different animals). The beginning dates are slightly modified from previously defined seasonal periods based on initial capture of fawns for that season. The time period for winter mortality time period of adults was 1 December to 15 May. We modeled mortality for both 6-month-old fawn and adult mule deer with predator-removal efforts beginning in December (the start of that winter). For example,

we modeled winter mortality 1998 (1 Dec 1997 to 15 May 1998) for adults with coyote and mountain lion removal of the same period (1 Dec 1997 to early summer 1998). We modeled summer mortality (16 May–30 Nov) in 1998 with the same removal. We modeled adult female mule deer with season as a covariate.

Individual animal predictors used in fawn mortality models included sex, mass, and number of siblings for neonates and sex and mass for 6-month-old fawns. Because we captured fawns on different dates during the capture period, we were concerned that growth or weight loss could have confounded the value of mass as a predictor. For 6-month-old fawns, we examined differences in weight over time (during the capture period) by sex between GMUs 56 and 73A and among years with analysis of covariance (ANCOVA). For neonates, we examined mass differences over time between sexes and among years. If we detected a significant change in mass in the group of captured fawns, we adjusted individual mass to the predicted mass at median age of capture (4 days) to make individual body size comparable across years. We included age as a continuous linear predictor by individual years for adult females and we imputed missing values for individual measurements by using average values by year and study area. We incrementally aged surviving individuals as we included them in the next-year analysis.

We used Akaike Information Criteria with small sample size correction (AIC_c) for model selection (Burnham and Anderson 2002). Because sample size of proportional hazards models is a function of the number of deaths (Harrell 2001), we limited the number of predictor variables considered using a forward-type selection process (Klein and Moeschberger 2003). We limited the predictors examined to main effects (coyote and mountain lion removal), main and alternate prey, precipitation, and individual animal predictors (Table 3). We included study area as a covariate to explain inherent site differences in survival not related to the removal treatment. We reasoned this inclusion would strengthen the test of main effects by removing variance not explained by included covariates. We screened predictors for collinearity by season and retained the predictor most closely related to mortality (Murray and Conner 2009). We began by comparing AIC_c for all 1-predictor models. We added predictors to the 1-predictor model with the lowest AIC_c until a new 2-predictor model was selected. We used variable inflation factors >2 (VIF; STATA ver. 10.1) to identify possible confounding predictors. Model building continued in this fashion until the AIC_c did not decrease with addition of new variables (Klein and Moeschberger 2003). We added and retained interactions of covariates included in the top model only if the additional terms decreased AIC_c . We designated a competing model set for each age class if models were <4 ΔAIC_c of the top model (Appendix B). We conducted statistical analyses for survival and mortality models using STATA ver. 10.1 and considered parameters significant at $\alpha \leq 0.05$. We generated estimates of survival from the top models for the range of covariate values to evaluate goodness-of-fit and effect size of individual parameters.

Changes in Deer Fawn Ratios and Population Growth Rate

Neonatal fawn-at-heel ratios.—We used fawn-at-heel ratios during the fawning season to index parturition rates of mule deer in the reference and treatment GMUs within the intensive

study area and predicted that with predator control, fawn-at-heel ratio would increase (Table 2). To estimate fawn-at-heel ratios, we observed deer in fawning areas every 3–4 days during 25 May–25 June, 1998–2002. Distinct adult females with fawns were observed from a distant vantage point until the observer was confident all fawns with an individual adult female were identified. Observation usually included a feeding and bedding cycle with fawns in plain view. We verified observations with capture attempts of neonates and repeated observations of the adult female using the same habitat patch. We calculated fawn-at-heel ratio, which included only adult females with fawns, as:

$$\hat{R} = \frac{\sum_{i=1}^G f_i}{\sum_{i=1}^G d_i} \quad (1)$$

where f_i is the number of fawns in the i th animal group observed ($i = 1, \dots, G$), d_i the number of adult females in the i th animal group observed ($i = 1, \dots, G$), and G the number of animal groups observed during the time period.

We calculated variance for fawn-at-heel ratios by cluster sampling where we treated each group of deer as a cluster (Cochran 1977:249, Samuel and Garton 1994):

$$\hat{V}(\hat{R}) = \frac{(1-(G/N)) \sum_{i=1}^G (f_i - \hat{R}d_i)^2}{G\bar{d}^2 (G-1)} \quad (2)$$

where \hat{R} is the ratio of fawns to adult females, f_i the number of fawns in group, d_i the number of adult females per group, \bar{d} the mean number of adult females per group, G the number of groups observed, and N the number of groups in the population.

We calculated confidence intervals (95%) for fawn-at-heel ratios as:

$$\hat{R} \pm t_{n-1} \sqrt{V(\hat{R})} \quad (3)$$

Fawn-to-adult female ratios.—We estimated sex and age-class structure of mule deer populations in all 8 GMUs during December and early January 1998–2003 (Table 1). We surveyed a representative sample of 6- to 10-km² quadrats using a Bell 47G3B helicopter (Bell Helicopter, Hurst, TX), including all elevations and habitats in which deer were present. We sampled quadrats without replacement until we obtained a sample of 500 deer or 50% of the estimated population (Unsworth et al. 1994). We classified deer as adult female (≥ 1 yr old), fawn, yearling male (1–2 antler points/side), 3-point male, or ≥ 4 -point male. We computed fawn-to-adult female ratios (FDR) for each GMU each year as previously for fawn-at-heel ratios. We estimated variance of fawn-to-adult female ratio according to Cochran (1977) by:

$$\hat{V}(\hat{R}) = \frac{\sum_{i=1}^G (f_i - \hat{R}d_i)^2}{\bar{d}^2 G(G-1)} \quad (4)$$

We calculated an asymptotic confidence interval as:

$$\hat{R} \pm Z_{1-(\alpha/2)} \sqrt{\hat{V}(\hat{R})} \quad (5)$$

Fawn-to-adult female ratio is an expression of net fecundity; in other words, a function of both reproductive rate and fawn survival. If predation by coyotes and mountain lions is heavily focused on young, predator removal might be manifested in higher fawn survival, and consequently, higher \hat{R} . Productivity (P) also was expected to differ between years and locations due to natural variability. Hence, fawn-to-adult female ratios can be modeled as a function of survival processes (S_j):

$$E\left(\frac{f}{d}\right) = PS_f \quad (6)$$

We employed a hierarchical analysis of deviance (ANODEV) modeling approach, first adjusting fawn ratios for year and site effects prior to examining effects of predator removal. We could account for year effects by using either an indicator variable or precipitation data considered important to fawn survival and adult fecundity. Although year indicators explained 43% of the overall variability in fawn ratios, summer precipitation, previous winter precipitation, and their interaction explained 41%. Hence, to incorporate site effects, we can write equation 1 as:

$$E\left(\frac{f}{d}\right) = \mu Y_i A_j \quad (7)$$

where μ is the mean productivity, A_j the effect of the j th area ($j = 1, \dots, 8$), and Y_i the effect of the i th year ($i = 1, \dots, 9$).

In turn, survival can be written as a function of non-predator and predator effects:

$$S_{f_{ij}} = S_{N_{ij}} S_{Coyote_{ij}} S_{Lion_{ij}} \quad (8)$$

where $S_{N_{ij}}$ is the survival probability for fawns in the i th year at the j th site from non-predator effects, $S_{Coyote_{ij}}$ the probability of surviving coyote predation in the i th year at the j th site, and $S_{Lion_{ij}}$ the probability of surviving mountain lion predation in the i th year at the j th site.

Equation 8 assumes sources of mortality act independently. In turn, we can re-parameterize predator survival parameters as:

$$S_{ij} = e^{-C(\text{PredatorDensity}_{ij} - \text{RemovalDensity}_{ij})} \quad (9)$$

where C is the vulnerability coefficient.

Equation 9 is equivalent to catch-effort models used to characterize fishery and hunting exploitation (Seber 1982:296). Combining equations 4–9 and absorbing site- and time-specific predation densities into the location (A_j) and year (Y_i) effects leads to the multiplicative response model:

$$E\left(\frac{f}{d}\right)_{ij} = \mu Y_i A_j e^{C_L(\text{LionRemovalDensity}_{ij})} e^{C_C(\text{CoyoteRemovalDensity}_{ij})} \quad (10)$$

The log of the expected value leads to the log-linear model:

$$\ln E\left(\frac{f}{d}\right)_{ij} = \ln \mu + \ln Y_i + \ln A_j + C_L(\text{LRD})_{ij} + C_C(\text{CRD})_{ij} \quad (11)$$

Equation 11 attempts to first describe any inherent differences in fawn-to-adult female ratios that may be attributable to annual or location differences in productivity and baseline predator densities. Additional variation in fawn-to-adult female ratios is then described by reductions in mountain lion and coyote

densities. In equation 11, vulnerability coefficients should be positive if predator removal increases fawn-to-adult female ratios. We parameterized both an unweighted and weighted (equation 12) ANODEV model. Fawn-to-adult female ratios were weighted (W) for analyses with:

$$W = \frac{1}{\hat{V}(\ln \hat{R})} \frac{1}{\frac{\hat{R}}{SE(\hat{R})}} = \frac{1}{CV^2} \quad (12)$$

where CV is the coefficient of variation in FDR.

Analysis was based on general linear models using a log-link and normal error structure. A residual analysis indicated a lack-of-fit of the unweighted model ($\chi^2 = 8.42$, $P = 0.004$) to the data. No lack-of-fit was indicated for the weighted model (only 1 of 40 observations had residuals $>\pm 2$) so we used it for interpretation. We used a 1-tailed test of significance for treatment effects in this analysis because we hypothesized predator removal to increase fawn ratios.

Population growth rate.—We used aerial surveys to estimate mule deer population size in all 8 study GMUs during 1997–2003. We conducted surveys in a Bell 47G3B helicopter from late March to mid-April each year to coincide with early spring vegetation growth, when deer occurred in large groups and visibility bias was reduced. We included winter ranges and major migration routes in search areas to account for differences in timing of migration. We sampled all subunits within search areas according to previous protocols (Samuel et al. 1987, Ackerman 1988, Unsworth et al. 1994).

We used population estimates derived from aerial surveys to estimate rates of population change. We calculated annual rate of population change, expressed as r_t (instantaneous rate of change at time t), for each GMU as:

$$r_t = \ln\left(\frac{N_{t+1}}{N_t}\right) \quad (13)$$

where N_t is the population at time t .

We used generalized linear regression models (GLM) to test the effect of varying rates of predator removal on population growth rate. We tested the effect of predator removal ending in the current year's rate of increase estimate (i.e., r_{1999} is the change between 1998 and 1999 surveys and is matched with predator removal from December 1997 to July 1998). We included a GMU-specific WSI in models to control for varying effects of snow depth on winter survival and recruitment. We lagged mountain lion-removal density (lionlag), coyote-removal density

(coyotelag), and winter severity (wsilag) 1 yr to account for the effect of increased survival on total population productivity. However, coyote removal and 1-yr-lagged coyote removal were correlated ($r = 0.73$, $P < 0.001$), as were mountain lion removal and 1-yr-lagged mountain lion removal ($r = 0.58$, $P < 0.001$). As a result, we did not enter lagged effects of a treatment effect into the same model as one with the treatment effect, limiting the maximum number of variables for model selection to 4. Because of this correlation and the repeated-measures nature of population rate of increase, we tested for autocorrelation in the rate of increase and main effects of coyote or mountain lion removal treatments over the 6 1-yr intervals of the study (Hebblewhite 2005). The limited number of variables allowed us to develop a candidate set of models of population growth rate including all combinations of the removal treatments and winter severity.

We ranked the candidate set of models using the Akaike Information Criteria adjusted for small sample sizes (AIC_c; Burnham and Anderson 1998). We determined the top model set by including the ranked models in order until the sum of evidence weights was >0.95 (Burnham and Anderson 1998). We added interaction terms to the top models to identify significant influences on the variable coefficients and the new models ($n = 2$) were included in the top model set (Hosmer and Lemeshow 1999). We estimated relative variable importance (ω) from this model set by summing the model weights across all models where the variable of interest occurred (Burnham and Anderson 1998). We considered statistical tests for fawn-to-adult female ratio and population rate of change analyses significant at $\alpha \leq 0.10$ because of the increased sampling variance related to population surveys.

RESULTS

Predator Reduction

Coyotes were removed from 4 treatment areas (GMUs 55, 57, 73A, and 73E) from winter to summer during 1997–2002 (Fig. 1, Table 4). Coyote-removal density (CRD) increased throughout the study period in response to increased effort and expenditures and averaged 53.3 coyotes/1,000 km² for the study period (Table 4). Mean CRD for livestock conflicts in reference GMUs (54, 56, 71, 73M) was 8.52 coyotes/1,000 km² (SD = 9.71). We increased ground-based efforts in 2000 and 2001 to maintain coyote removal rates, when snow-tracking conditions and helicopter availability hampered efforts. Recreational coyote harvest was low ($\bar{x} \pm SD = 2.7 \pm 1.8/$

Table 4. Coyotes removed (n) and density of coyotes removed per 1,000 km² (CRD) from treatment Game Management Units (GMUs) 55, 57, 73E, and 73A in southeastern Idaho during 1997–2002. Cost includes contract aircraft, ground operating expense, and personnel time for experimental removal of coyotes. Cost does not include coyotes removed for livestock protection.

Year	GMU 55		GMU 57		GMU 73A		GMU 73E		Summary			
	n	CRD	n	CRD	n	CRD	n	CRD	Total coyotes	Mean CRD	Total cost (\$)	Cost/coyote (\$)
1997	81	30.52	27	29.25	60	53.19	50	34.87	218	36.96	34,106	156.45
1998	51	19.22	16	17.34	106	93.97	95	66.25	268	31.15	40,269	150.26
1999	46	17.33	41	44.42	106	93.97	32	22.32	225	55.49	27,211	120.94
2000	52	19.59	44	47.67	127	112.59	151	105.30	374	45.89	47,252	126.34
2001	41	15.45	77	83.42	116	102.84	110	76.71	344	79.19	51,009	148.28
2002	64	24.12	74	80.17	185	164.01	110	76.71	433	70.96	49,119	113.44
Mean	56	21.04	47	50.38	117	103.43	91	63.69	310	53.27	41,494	135.95

1,000 km²) and similar across all experimental units. Mean recreational removal rates by county ranged from 0.45/1,000 km² in Oneida County (GMUs 73E and 73M) to 4.78/1,000 km² in Power County (GMUs 56 and 73A). Most of the harvest in Power County was likely outside of the study area on the Snake River plain, a higher-density coyote habitat than the isolated mountain ranges of the study area.

We completed 1,126 coyote scat transects during the study period. Our coyote density indices were extremely variable, especially in removal units, making interpretation difficult. From the perspective of evaluating effect size of our coyote removal, the initial density estimate for coyotes in the intensive-study GMUs was 0.22/km² adult or 0.15/km² breeding adults obtained from the 1998 GMU 56 transects. We used this reference GMU for an initial estimate because active removal began in 1997 in the removal GMU. Applying this density estimate to GMU 73A, an initial estimate of the absolute numbers of the potential breeding population was 248 adult coyotes in the 1,128-km² study unit. Therefore, regardless of variation in our coyote population index, these densities equate to percentage coyote removal for our experimental treatments ranging from 24% in 1997 to 75% in 2002 for GMU 73A.

Removal rates for mountain lions varied across years and GMUs. In the intensive study area, mountain lion removal

was 2–6 times greater in GMU 73A (treatment) than in GMU 56 (reference) areas during 1998–2002. In the extensive study areas, mountain lion removal was greater in treatment GMUs versus reference GMUs during 1998–2001 but returned to previous levels by 2002 (Table 5) although harvest was unrestricted. Conservative female quotas were met in reference GMUs, resulting in season closure before 31 March. Snow conditions were favorable for developing a lion population index to test effects of lion harvest in 3 (1998, 1999, and 2001) of 5 intensive-removal years (Table 6). Declines in indices reflected increased mountain lion harvest during 1999–2001 in the treatment GMU (Table 6), confirming our ability to reduce lion populations through harvest in the treatment areas. We observed peak lagomorph index values in 1999 followed by the lowest levels in 2000 (Table 7). The index varied 7- and 3.5-fold across years in reference and treatment GMUs, respectively (Table 7).

Mule Deer Survival and Productivity

We captured mule deer neonates ($n = 250$), 6-month-old fawns ($n = 301$), and adult females ($n = 254$) at sites uniformly distributed across seasonal use areas in GMUs 56 and 73A during 1998–2002. Mean annual sample of radiocollared mule deer included 50 neonates, 60 6-month-old fawns, and 104 adult

Table 5. Mountain lions removed per 1,000 km² in conservative harvest units (Game Management Units [GMUs] 54, 56, 55, 57^a; 8,650 km^{2b} total area) and liberal harvest units (GMUs 70, 71, 73 Elkhorn, 73 Malad, 73A; 7,115 km² total area), southeastern Idaho, 1997–2002.

Year	Conservative harvest GMUs					Liberal harvest GMUs				
	54	56	55	57	Mean	71	73 Malad	73A	73 Elkhorn ^c	Mean
1997	6.8	3.5	4.0	3.4	4.4	0	1.6	3.5	1.6	1.7
1998	6.4	1.8	2.2	1.1	2.9	0	2.5	8.9	2.5	3.5
1999	2.8	2.6	4.5	3.4	3.5	2.1	6.9	14.2	6.9	7.5
2000	6.0	1.8	3.1	0	2.7	4.3	2.5	8.9	2.5	4.6
2001	3.2	2.2	3.1	0	2.1	4.3	2.8	4.4	2.8	3.5
2002	4.4	1.3	5.4	2.3	3.4	0	2.2	2.7	2.2	1.8

^a Identified as conservative mountain lion harvest starting in 1998.

^b Excludes 900 km² of non-mountain lion habitat.

^c Excludes 5 kittens removed from GMU 73.

Table 6. Mountain lion track indices, Game Management Units (GMUs) 56 (reference) and 73A (treatment), southeastern Idaho, 1998–2001.

Year	GMU 56 ^a				GMU 73A			
	Quadrats surveyed	Total km	Tracks counted	Tracks/100 km	Quadrats surveyed	Total km	Tracks counted	Tracks/100 km
1998	6	131.2	2	1.53	6	119.9	5	4.17
1999	13	180.5	7	3.88	6	134.0	1	0.75
2001	5	138.9	3	2.16	5	131.4	2	1.52

^a Identified as conservative mountain lion harvest starting in 1998.

Table 7. Lagomorphs observed (n) in headlight surveys, Game Management Units (GMUs) 56 (reference) and 73A (treatment), southeastern Idaho, 1998–2002.

Year	GMU 56			GMU 73A			Combined index
	km surveyed	n	No./100 km	km surveyed	n	No./100 km	Weighted mean
1998	92.8	4	4.31	46.5	1	2.15	3.60
1999	92.8	13	14.00	54.4	4	7.35	11.55
2000	102.4	2	1.95	47.2	1	2.12	2.01
2001	104.0	8	7.69	46.3	2	4.32	6.65
2002	95.6	3	3.14	56.2	3	5.34	3.95

females. Four 6-month-old fawns and 2 adult females died of capture-related injuries.

We collected blood from 95 adult females, 12 yearling females, and 4 female fawns within GMUs 56 and 73A in 1998. During 1998, pregnancy rates were 98%, 83%, and 0% for females ≥ 2 yrs old, females 1.5 yrs old, and fawns, respectively. In 1999, we collected blood from 57 adults and 11 yearling females in 4 study areas (GMUs 54, 56, 71, and 73A); pregnancy rates were 91% for females ≥ 2 yr old and 100% for yearlings. We compared serologic profiles for 135 adult females within the study area with profiles for 58 adult females in 4 other mule deer populations in central and southern Idaho (M. Hurley, Idaho Department of Fish and Game, unpublished data). We reported disease prevalence (P_i) for GMUs within the study as disease name = P_i for the study area (range of P_i for 4 other populations). Diseases documented in the study area and other areas in Idaho included anaplasmosis with a prevalence $P_i = 0$ (range 0–0.76), blue-tongue = 0.03 (range 0–0.13), BRSV = 0.06 (range 0–0), BVD = 0.41 (range 0–0.92), EHD = 0 (range 0–0.13), IBR = 0 (range 0–0.38), and PI3 = 0.27 (range 0.33–0.88).

Neonatal fawns.—Mass gain of neonates differed among years ($F_{4, 225} = 3.67, P = 0.007$) but not among areas. Therefore, we calculated a regression equation for each year to predict mass at age 4 days and remove annual variation in growth rates (Fig. 3). During summer, estimated survival (S) of neonates in the reference area ($S = 0.459, SE = 0.048$) was lower ($\chi^2_1 = 3.41, P = 0.069$) than survival in the treatment area ($S = 0.556, SE = 0.047$) when we combined all years (Fig. 4). Neonatal fawn survival varied by year and was higher in the treatment GMU in 1999 ($\chi^2_1 = 5.47, P = 0.019$), 2002 ($\chi^2_1 = 3.81, P = 0.051$), and apparently lower in 2000 ($\chi^2_1 = 1.93, P = 0.16$; Fig. 5).

Probability of mortality (hazard) increased from birth until July, then declined rapidly in August in the treatment area, but not in the reference area until October (Fig. 6). The hazard function (pooled across years) was apparently higher in the reference area until October; however, 95% confidence intervals overlapped, attesting to variability of survival and removal treatments among years. In our model without the interaction term (second model in Table 8), increased density of coyotes removed, higher lagomorph index, and larger body mass all decreased mortality of neonatal fawns. Coyote removal was the strongest predictor in all models tested without an interaction. The study area term was negative, indicating that mortality was initially higher in the treatment area in the absence of predator removal, suggesting a greater effect than observed in survival estimates without covariates (Fig. 5). Study area indicated lower mortality in the treatment area when modeled univariately, verifying the treatment effect. Addition of a significant interaction of CRD and lagomorph index decreased ΔAIC_c by 1.87, received 0.398 of AIC_c weight, and represented the best model (Appendix B, Table 8). A model with mountain lion removal was competing ($\Delta AIC_c = 3.68$) when included with coyote removal and mass (Appendix B). Low and high survival rates were predicted well by the best model: GMU 56, $S = 0.38$ versus predicted $S (S_{pred}) = 0.43$, GMU 73A, $S = 0.69$ versus $S_{pred} = 0.66$ in 1999; and GMU 56, $S = 0.48$ versus $S_{pred} = 0.47$, GMU 73A, $S = 0.74$ versus $S_{pred} = 0.75$ in 2002.

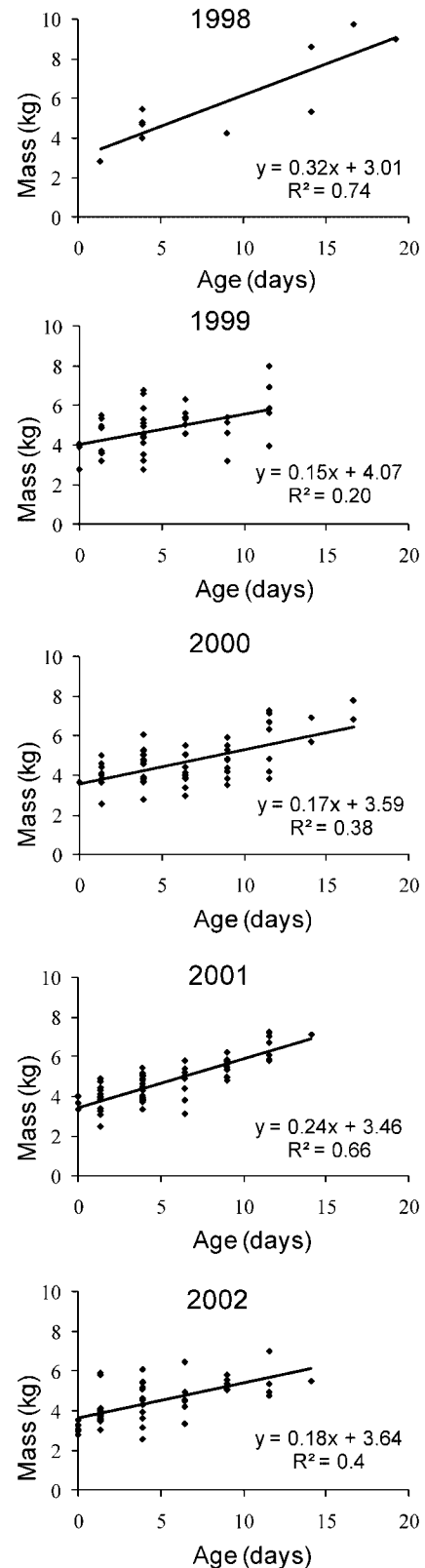


Figure 3. Linear regressions of mass of neonatal mule deer fawns versus age at capture that we used to predict mass at 4 days of age, southeastern Idaho during 1998–2002. Predicted mass was used as a covariate in the neonatal fawn mortality models.

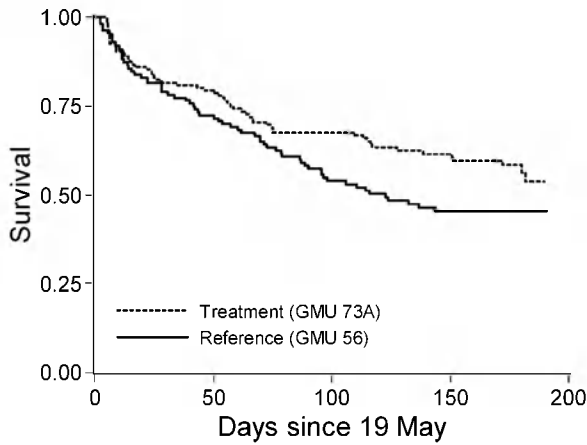


Figure 4. Kaplan–Meier survival curves for neonatal mule deer fawns in summer-fall (19 May–30 Nov) in Game Management Unit (GMU) 56 (reference, $n = 118$) and GMU 73A (treatment, $n = 132$), southeastern Idaho, 1998–2002. We pooled data across years. Minimal numbers of coyotes and mountain lions were removed from the reference area, whereas intensive removal of coyotes and mountain lions occurred in the treatment area.

Six-month-old fawns.—Mass of 6-month-old fawns was greater for males than females ($F_{1, 269} = 32.80, P < 0.001$), declined from 1998 to 2002 ($F_{4, 266} = 5.26, P < 0.001$), and did not vary between study areas ($F_{1, 269} = 1.20, P = 0.263$; Table 9). A significant interaction of year and study area ($F_{4, 266} = 3.46,$

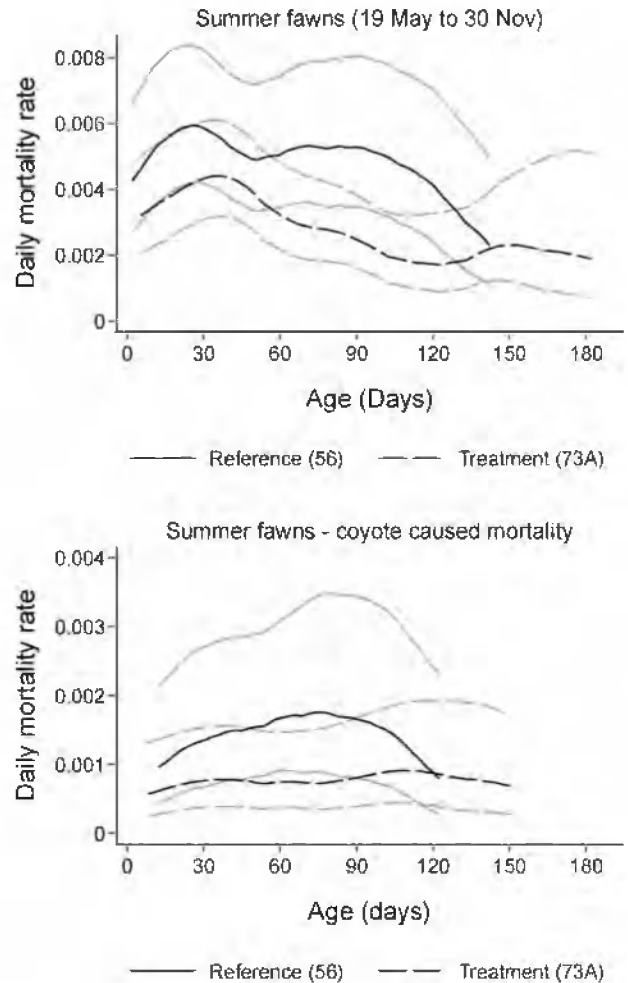


Figure 6. Baseline hazard function for neonatal mule deer fawns in summer (top) and hazard function attributable to coyote-caused mortality (bottom) in southeastern Idaho, 1998–2002. Gray lines indicate 95% confidence intervals. Minimal coyotes and mountain lions were removed from the reference area, whereas intensive removal of coyotes and mountain lions occurred in the treatment area.

$P = 0.009$) suggested the pattern of mass difference varied among years and between study areas. Mass did not change over the capture period ($\beta = 0$) for any of the 5 yr (16 Dec–22 Jan; ANCOVA, $F_{4, 266} = 0.50, P = 0.735$). Therefore, we used measured mass at capture as an individual covariate in survival models.

During winter, fawn survival in the reference area ($S = 0.561, SE = 0.050$) was not different ($\chi^2_1 = 0.947, P = 0.36$) from survival in the treatment area ($S = 0.627, SE = 0.044$) when we combined all years (Fig. 7). Six-month-old (winter) fawn survival varied by year, with treatment GMU higher in 2000 ($\chi^2_1 = 6.81, P = 0.009$) and reference higher in 2002 ($\chi^2_1 = 4.23, P = 0.04$; Fig. 5). Probability of mortality (hazard) increased from December to a peak at approximately 15 March and then declined until May (Fig. 8). The lagomorph index and Z-precipitation were highly correlated ($r = 0.76$); we retained Z-precipitation because it was related to mortality ($\chi^2_1 = 23.1, P < 0.001$) and the lagomorph index was not ($\chi^2_1 = 1.37, P = 0.24$). Three competing models explained mortality of 6-month-old fawns during winter (Appendix B), and the 2 highest contained mountain lion removal as a predictor. In the top model,

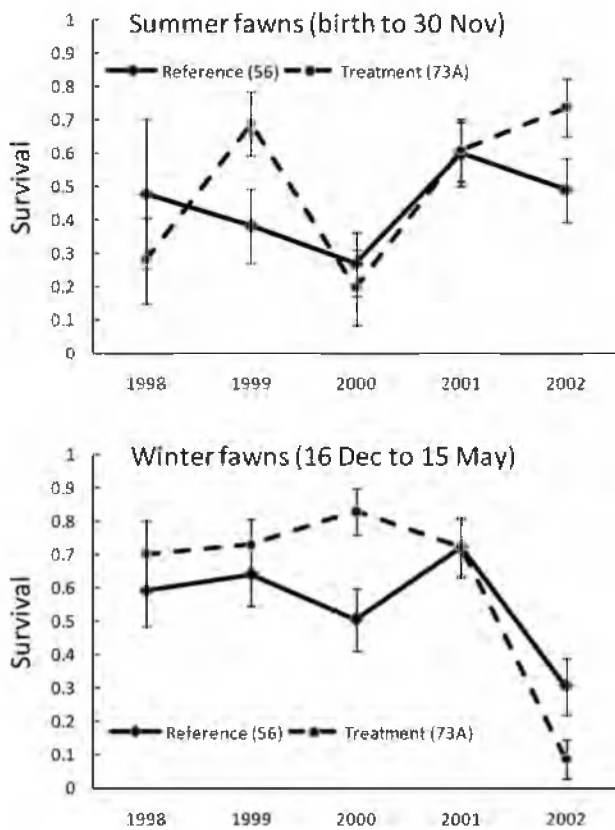


Figure 5. Kaplan–Meier survival estimates and standard errors by year for mule deer fawns in summer and winter in southeastern Idaho, 1998–2002. Minimal numbers of coyotes and mountain lions were removed from the reference area whereas intensive removal of coyotes and mountain lions occurred in the treatment area.

Table 8. Best-competing-mortality models in order of ranking as identified by Akaike Information Criteria (AIC_c; Appendix B) for fawns in summer-fall (16 May–15 Dec), Game Management Unit (GMU) 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998–2002. We evaluated strength of association with mortality time for each model with partial likelihood-ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	AIC _c	Model χ^2	df	Model <i>P</i>	Parameter estimate	Parameter <i>P</i> -value	Hazard ratio	95% Hazard ratio CI
Coyote removal	1,116.92	18.92	5	0.002	-0.011	0.074	0.99	0.99–1.00
Lagomorphs					0.044	0.430	1.04	0.94–1.16
Mass					-0.194	0.092	0.82	0.66–1.03
Study area					-1.359	0.015	0.26	0.09–0.77
Coyote × Lagomorphs					-0.002	0.045	0.99	0.99–1.00
Coyote removal	1,118.79	14.97	4	0.005	-0.015	0.011	0.98	0.97–0.99
Lagomorphs					-0.051	0.111	0.95	0.89–1.01
Mass					-0.203	0.077	0.82	0.65–1.02
Study area					-0.998	0.065	0.37	0.13–1.07
Coyote removal	1119.34	10.31	2	0.006	-0.005	0.008	0.99	0.99–1.00
Mass					-0.231	0.043	0.79	0.63–0.99

Table 9. Mean mass (kg) by sex of 6-month-old mule deer fawns, Game Management Unit (GMU) 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998–2002.

Year	GMU 56						GMU 73A					
	Females			Males			Females			Males		
	<i>n</i>	Mass	SE	<i>n</i>	Mass	SE	<i>n</i>	Mass	SE	<i>n</i>	Mass	SE
1998	12	36.57	0.908	12	39.96	1.012	11	34.92	0.959	10	37.67	1.423
1999	9	35.40	2.331	20	40.29	0.986	17	35.45	0.793	17	39.58	1.251
2000	14	34.19	1.168	16	36.85	0.649	11	34.42	0.773	18	38.58	1.166
2001	16	33.39	0.802	14	35.16	0.669	12	35.42	1.346	13	36.57	1.466
2002	13	36.08	0.876	17	37.49	1.228	16	32.94	0.916	14	34.32	1.015

Z-precipitation, mass, and mountain lion removal were important predictors of mortality (Table 10). Inclusion of sex decreased AIC but was not a significant parameter. Below-average summer precipitation and above-average winter precipitation (Z-precipitation) increased mortality, higher mountain lion removal and greater mass decreased mortality, and female mortality was lower than males. Coyote removal was not related to fawn mortality in the winter ($\chi^2_1 = 0.23$, $P = 0.62$).

Our models predicted mortality could decrease up to 37% with maximum mountain lion removal during an average winter.

Mortality decreased $\leq 28\%$ with a wet summer (maximum precipitation observed) and dry winter (minimum precipitation) or increased $\leq 52\%$ with a dry summer and wet winter. Models predicted a 19% decrease in mortality with each 4.55-kg increase in mass, which was the maximum average difference between years.

Adult females.—Hazard functions were not proportional in our adult female mortality models when season was included as a covariate (proportional hazards global test $\chi^2_3 = 9.31$,

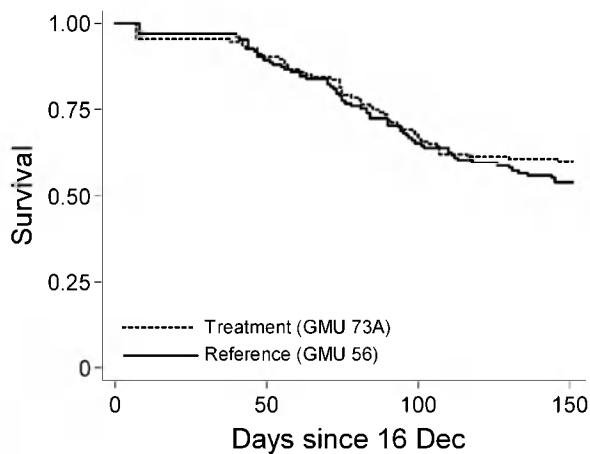


Figure 7. Kaplan-Meier survival curves for 6-month-old mule deer fawns in winter-spring (16 Dec–15 May) in Game Management Unit (GMU) 56 (reference, $n = 143$) and GMU 73A (treatment, $n = 139$), southeastern Idaho, 1997–2002. Data are pooled across years.

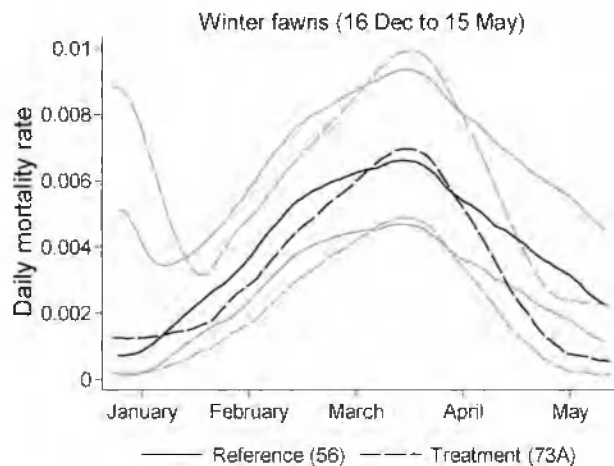


Figure 8. Baseline hazard function for neonate mule deer fawns in winter, southeastern Idaho, 1998–2002. Gray lines indicate 95% confidence intervals. Minimal numbers of coyotes and mountain lions were removed from the reference area, whereas intensive removal of coyotes and mountain lions occurred in the treatment area.

Table 10. Best-competing-mortality models in order of ranking as identified by Akaike Information Criteria (AIC_c; Appendix B) for fawns in winter-spring (16 Dec–15 May), Game Management Unit (GMU) 56 (reference) and GMU 73A (treatment), southeastern Idaho during 1998–2002. We evaluated strength of association with mortality time for each model with partial likelihood ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	AIC	Model χ^2	df	Model <i>P</i>	Parameter estimate	Parameter <i>P</i> -value	Hazard ratio	95% Hazard ratio CI
Z-precipitation	1,121.86	42.97	4	<0.001	0.625	<0.001	1.87	1.32–2.65
Mass					−0.090	<0.001	0.91	0.87–0.96
Lion removal					−0.058	0.045	0.94	0.89–0.99
Sex					0.370	0.69	1.45	0.97–2.14
Z-precipitation	1,123.12	39.65	3	<0.001	0.630	<0.001	1.87	1.32–2.66
Mass					−0.076	<0.001	0.93	0.87–0.97
Lion removal					−0.060	0.037	0.94	0.89–0.99
Z-precipitation	1,124.25	38.52	3	<0.001	0.766	<0.001	2.15	1.52–3.02
Mass					−0.092	<0.001	0.91	0.87–0.96
Sex					0.389	0.055	1.48	0.89–2.20

$P = 0.025$, season $\chi^2_1 = 8.08$, $P = 0.005$). Stratification by season was an option but required the assumption of equal coefficients across strata with different baseline hazards. Given differing life-history traits between seasons, this assumption was biologically unlikely, prompting us to separate mortality models by season.

Survival of adult female mule deer during summer was ≥ 0.93 in all years and both intensive-study GMUs. During summer, adult female survival in the reference GMU ($S = 0.950$, $SE = 0.015$) did not differ ($\chi^2_1 = 1.33$, $P = 0.242$) from the treatment GMU ($S = 0.970$, $SE = 0.009$) when we combined all years, but it

varied among years with the only difference observed between reference and treatment in 1999 ($\chi^2_1 = 6.71$, $P = 0.0096$, Fig. 9). The baseline hazard was lowest in summer for adult females and increased through the winter (Fig. 10). Summer precipitation and the previous winter precipitation were highly

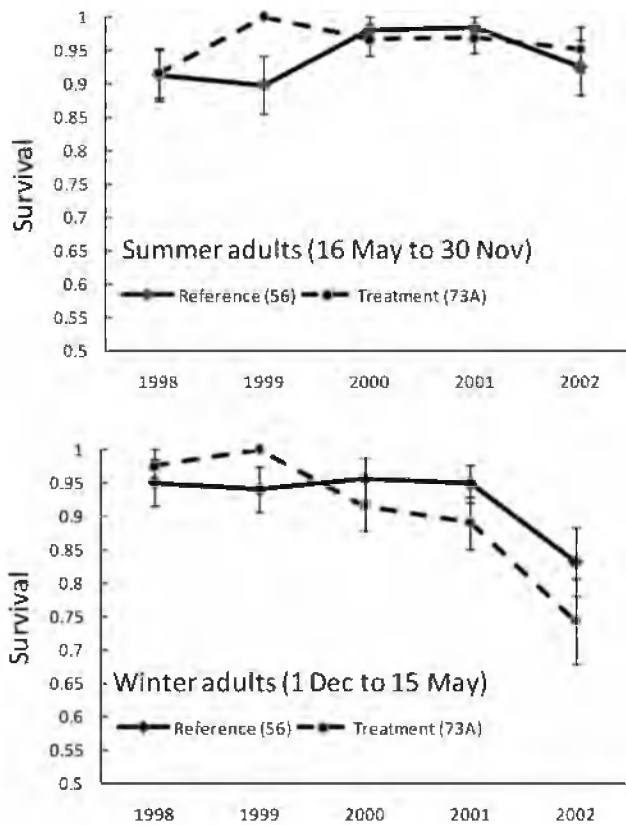


Figure 9. Kaplan–Meier survival estimates and standard errors by year for mule deer adult females in summer and winter in southeastern Idaho, 1998–2002. Minimal coyotes and mountain lions were removed from the reference area, whereas while intensive removal of coyotes and mountain lions occurred in the treatment area.

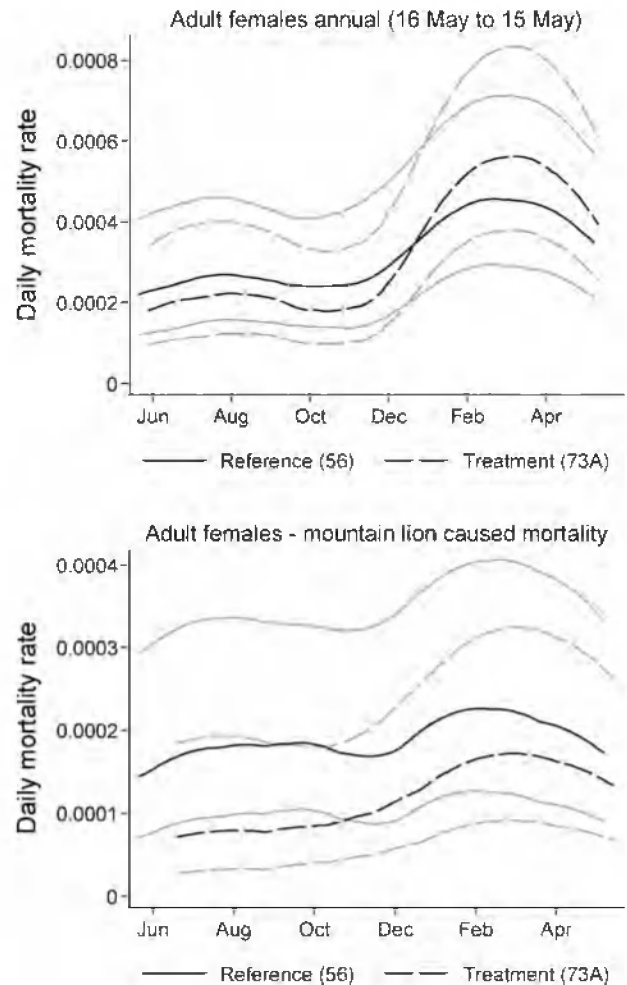


Figure 10. Annual baseline hazard function for adult female mule deer (top) and hazard function attributable to mountain lion-caused mortality (bottom) in southeastern Idaho, 1998–2002. Gray lines indicate 95% confidence intervals. Minimal number of coyotes and mountain lions were removed from the reference area, whereas intensive removal of coyotes and mountain lions occurred in the treatment area.

correlated ($r = 0.87$), therefore we did not enter these covariates into the same model. Correlations of all other covariates were <0.28 . The 2 top models had similar weight (0.28 and 0.29), and the top model included an age-by-lion-removal interaction term (Appendix B). The competing model with the fewest covariates (previous winter precipitation and age) was the third-ranked model ($w = 0.188$). Precipitation in the previous winter was the best predictor of adult female mortality; higher precipitation increased mortality (Table 11). Mortality increased with age and decreased with higher mountain lion removal. The positive interaction indicated the effect of mountain lion removal decreased with increasing age, suggesting compensatory mortality as individuals aged.

Adult female survival during winter in the reference area ($S = 0.932$, $SE = 0.017$) did not differ ($\chi^2_1 = 0.583$, $P = 0.463$) from the treatment area ($S = 0.945$, $SE = 0.026$) across years. The top model for winter ($w = 0.372$) included age, mountain lion removal, and study area, which were all significant ($P < 0.001$, Appendix B, Table 11). Inclusion of additional predictors, although competing models, did not improve the AIC_c score (Appendix B). Mortality of adult females decreased with mountain lion removal, increased with age, and was initially lower in the reference area (Table 11). Annual survival of adult females was apparently higher ($\chi^2_1 = 3.27$, $P = 0.071$; Fig. 9) in the treatment GMU during 1999, coinciding with high mountain lion removal (Table 5). By winter 2001, adult female survival was lower in the treatment area than the reference area during winter (Fig. 9). This pattern is evident in the baseline and lion-caused mortality hazard functions, as both functions were lower in summer in the treatment area than the reference area. However, in winter, the baseline hazard was higher on the treatment area, likely driven by the increased mortality during the severe winter of 2002 (Fig. 2), whereas the lion-caused mortality hazard remained higher on the reference area (Fig. 10). As with neonatal fawns, these patterns suggest mortality without predator removal would have been higher in the treatment area. Coyote removal was not related to adult mortality (hazard ratio = 1.002, $P = 0.395$).

Summer models predicted that maximum recorded precipitation during the previous winter would increase mortality 16%. Our models predicted that mortality would increase 3% during summer and 2.8% during winter with each 2-yr increase in age. Our models predicted a 5.5% decrease in adult female winter mortality following maximum mountain lion removal of 14/1,000 km².

Causes of Mule Deer Mortality

Cumulative-incidence-function mortality rates during 1998–2002 varied between treatments and among age classes (Table 12). Mortality rates of neonatal fawns from coyote, mountain lion, and undetermined predators were apparently lower in the treatment GMU, but not significantly, whereas we observed no differences in winter (Table 12). These multi-year mortality rates exhibited the expected pattern but not the certainty of the mortality models (Tables 8 and 10) likely due to the variation introduced by dissimilar annual predator-removal treatments and sample-size requirements of the PepeMori test (Pintilie 2006).

Annual mountain lion-caused mortality of adult females was lower and natural mortality was higher in the treatment GMU during both seasons (Table 12, Fig. 10). Mountain lions killed older adult females (7.1 yr, $SE = 0.73$) than occurred in the treatment GMU population (5.2 yr, $SE = 0.12$, $t_{12} = 2.48$, $P = 0.015$). The pattern was similar, but not as pronounced in the reference GMU (mountain lion kills, 5.7 yr, $SE = 0.60$; population, 5.2 yr, $SE = 0.11$, $t_{20} = 0.78$, $P = 0.22$). Females killed by lions were older in the treatment area than reference area ($t_{32} = 1.49$, $P = 0.073$). Adult females that died of natural causes (malnutrition or entire carcass with non-predator but unconfirmed cause of death) were older in the treatment GMU (8.1 yr, $SE = 1.11$, $n = 7$, $t_5 = 2.36$, $P = 0.038$) and reference GMU (8.5 yr, $SE = 0$, $n = 2$, $t_2 = 29.51$, $P \leq 0.001$) than were present in the populations, but age of females that died of natural causes was not different between areas ($t_7 = 0.22$, $P = 0.41$). Of the 9 total natural cause deaths, 6 died in winter to early summer of 2002. Contrary to expectations, coyote-caused

Table 11. Best-competing-mortality models in order of ranking as identified by Akaike Information Criteria (AIC_c ; Appendix B) for adult female mule deer by season, Game Management Unit (GMU) 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998–2002. We evaluated strength of association with mortality time for each model with partial likelihood-ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	AIC_c	Model χ^2	Df	Model P	Parameter estimate	Parameter P -value	Hazard ratio	95% Hazard ratio CI
Summer–fall (16 May–15 Dec)								
Previous winter precipitation	317.10	16.98	4	0.0019	0.23	0.007	1.25	1.06–1.47
Age					0.06	0.550	1.07	0.86–1.32
Lion removal					–0.28	0.076	0.76	0.56–1.03
Age \times lion removal					0.03	0.152	1.03	0.99–1.07
Previous winter precipitation	317.17	14.88	3	0.0019	0.23	0.006	1.26	1.07–1.49
Age					0.18	0.014	1.20	1.04–1.38
Lion removal					–0.08	0.119	0.92	0.83–1.02
Previous winter precipitation	317.96	12.07	2	0.0024	0.22	0.009	1.24	1.05–1.46
Age					0.19	0.010	1.20	1.05–1.39
Winter–spring (16 Dec–15 May)								
Age	514.95	31.67	3	<0.0001	0.19	<0.001	1.21	1.08–1.36
Lion removal					–0.25	<0.001	0.78	0.67–0.90
Study area					–1.21	<0.001	0.30	0.14–0.61

Table 12. Fates of radiocollared mule deer by age class and treatment, southeastern Idaho, 1998–2002. We calculated mortality rates with cumulative incidence function (CIF) in the presence of competing causes for all years combined. We tested differences between CIFs with predator removal treatment or reference areas with PepeMori χ^2 tests.

Age class (fate)	Treatment Game Management Unit (GMU) 73A				Reference GMU 56				PepeMori χ^2	
	<i>n</i>	CIF	95% CI lower	95% CI upper	<i>n</i>	CIF	95% CI lower	95% CI upper	χ^2	<i>P</i>
Neonatal fawns (birth to 30 Nov)										
Bobcat	4	0.029	0.010	0.068	4	0.037	0.012	0.086	0.08	0.78
Coyote	13	0.107	0.059	0.170	15	0.128	0.075	0.195	0.94	0.33
Lion	6	0.072	0.027	0.148	13	0.109	0.061	0.173	0.93	0.34
Predation ^a	6	0.052	0.021	0.104	9	0.079	0.039	0.138	0.08	0.78
Natural ^b	13	0.118	0.064	0.189	11	0.118	0.060	0.196	0.15	0.70
Other ^c	3	0.026	0.007	0.069	4	0.036	0.012	0.083	1.33	0.25
Unknown	5	0.057	0.017	0.131	4	0.041	0.013	0.093	0.39	0.53
6-month-old fawns (16 Dec–15 May)										
Bobcat	3	0.022	0.006	0.058	1	0.007	0.001	0.035	0.95	0.33
Coyote	15	0.148	0.070	0.252	23	0.173	0.114	0.242	0.00	0.97
Lion	18	0.135	0.083	0.201	16	0.130	0.070	0.209	0.00	0.95
Malnutrition	9	0.067	0.033	0.118	10	0.074	0.038	0.126	0.16	0.69
Other	2	0.014	0.003	0.047	2	0.014	0.003	0.047	1.21	0.27
Unknown	2	0.014	0.003	0.046	9	0.065	0.032	0.114	4.04	0.04
Adult females (annual)										
Coyote	4	0.013	0.0003	0.026	1	0.004	0	0.011	2.98	0.08
Lion	14	0.049	0.024	0.073	20	0.082	0.047	0.116	2.96	0.09
Predation	3	0.012	−0.001	0.025	3	0.013	0	0.028	0.52	0.47
Natural	7	0.024	0.006	0.041	2	0.008	0	0.019	3.21	0.07
Other	1	0.003	−0.003	0.010	2	0.008	0	0.019	1.12	0.29
Unknown	8	0.027	0.009	0.046	5	0.020	0.003	0.038	1.26	0.26

^a Predation = confirmed predation, but species of predator not identified.

^b Natural = malnutrition, disease, or other non-predatory natural cause (generally whole carcass).

^c Other = human-caused, fence, vehicle accident, etc.

mortality of adult females was higher in the treatment area; four were killed by coyotes in the treatment area and one was killed in the reference area (Table 12).

Changes in Mule Deer Fawn Ratios and Population Growth Rate

Neonate fawn-at-heel ratios.—Based on June fawn-at-heel ratios, twinning rates were high in GMUs 56 and 73A (Fig. 11). A post hoc analysis confirmed that fawn-at-heel ratios

were similar between reference (56) and treatment (73A) GMUs during 1998 and 1999 ($t_{78} = -0.26, P = 0.79$). Observed ratios were lower ($t_{146} = 2.18, P = 0.031$) during 2000–2002 in the treatment area and exhibited a declining trend through 2002.

Fawn-to-adult female ratios.—We calculated early winter fawn-to-adult female ratios (fawn ratios) for each study area and year (Table 13). Overall mean fawn ratio was 0.588 (SE = 0.013) and ranged from 0.322 (SE = 0.029) to 0.839 (SE = 0.048).

Coyote removal ($P = 0.314$) had no effect on fawn ratios, but mountain lion removal had a weak positive effect ($P = 0.109$; Table 14). Vulnerability coefficients that we estimated to test our hypothesis of increased fawn ratios with predator removal were not significant for coyote removal ($-0.0015, SE = 0.0015, t_{28} = -1.016, P = 0.318, 2$ -tailed), but were positive for mountain lion removal ($0.0161, SE = 0.00952, t_{28} = 1.688, P = 0.051, 1$ -tailed). There was no interaction between coyote and mountain lion removals ($P > 0.72$) in either analysis. Individually, summer precipitation ($F_{1, 38} = 4.97, P = 0.032$) and previous winter precipitation ($F_{1, 38} = 3.56, P = 0.067$) had negative effects on fawn ratios, but we found a positive interaction between those terms ($F_{1, 38} = 9.95, P = 0.003$). This interaction suggests a positive influence on neonatal survival with increased late-summer precipitation, whereas early-summer precipitation had a negative effect. Because they were biologically meaningful, we subsequently used precipitation variables in lieu of year effects for modeling changes in fawn ratios.

As removal of mountain lions increased, fawn ratios increased weakly but significantly, regardless of whether coyotes were removed ($P = 0.089, 1$ -tailed; Fig. 12d) or not ($P = 0.063, 1$ -tailed; Fig. 12c). Conversely, as removal density of coyotes

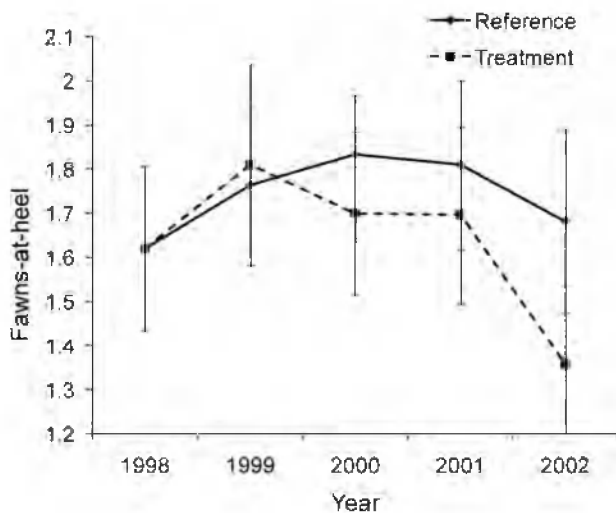


Figure 11. Neonatal mule deer fawn-at-heel ratios and 90% confidence intervals for 2 deer populations within the intensive study area in southeastern Idaho, 1998–2002. Both coyotes and lions were intensively removed from the treatment game management unit (GMU) but not the reference GMU.

Table 13. Fawn-to-adult female ratios (FDR) and SE for mule deer within each of the predator removal treatments during December–January in southeastern Idaho, 1997–2003. We used fawn-to-adult female ratios in years 1999 through 2003 to test the effects of coyote and mountain lion removal.

Winter	Reference 1, Game Management Unit (GMU) 54		Reference 2, GMU 56		Coyote 1, GMU 55		Coyote 2, GMU 57		Lion 1, GMU 71		Lion 2, GMU 73 Malad		Coyote and lion 1, GMU 73 Elkhorn		Coyote and lion 2, GMU 73A	
	FDR	SE	FDR	SE	FDR	SE	FDR	SE	FDR	SE	FDR	SE	FDR	SE	FDR	SE
1997									0.74	NA	0.74	NA	0.68	NA	0.84	0.048
1998			0.64	0.039	0.56	0.047	0.54	0.071			0.50	0.088	0.77	0.072	0.58	0.037
1999	0.60	0.054	0.65	0.034	0.58	0.048	0.51	0.056	0.55	0.051	0.63	0.059	0.57	0.097	0.52	0.033
2000	0.60	0.041	0.47	0.026	0.46	0.041	0.56	0.045	0.62	0.044	0.63	0.060	0.58	0.066	0.71	0.051
2001	0.59	0.044	0.68	0.031	0.60	0.055	0.67	0.052	0.62	0.037	0.64	0.046	0.73	0.052	0.78	0.032
2002	0.54	0.037	0.58	0.025	0.47	0.035	0.57	0.054	0.65	0.033	0.66	0.042	0.61	0.034	0.72	0.037
2003	0.55	0.043	0.55	0.036	0.49	0.034	0.54	0.090	0.32	0.029	0.42	0.039	0.53	0.032	0.51	0.030

increased, fawn ratios did not increase significantly, regardless of whether mountain lions were removed ($P = 0.161$, 1-tailed; Fig. 12b) or not ($P = 0.54$, 1-tailed; Fig. 12a).

The weighted ANODEV estimated a vulnerability coefficient of $C_L = 0.0161$ for mountain lion predation. Hence, we expected fawn ratios to be modified by mountain lion removal (LRD) by the quotient, $e^{0.0161(LRD)}$. Using this equation, we predicted that under the average removal density ($3.53/1,000 \text{ km}^2$) of mountain lions observed across the study GMUs, the fawn ratio would increase by 6% over no removal. We would expect fawn ratios to increase by 27% at the maximum removal rate we observed ($14.84/1,000 \text{ km}^2$) over that of no mountain lion removal.

Population growth rate.—Mule deer population rate of change varied across the study area independent of coyote- or mountain lion-removal treatments (Fig. 13). We tested for autocorrelation in our population data to assess violation of assumptions in linear regression. The dependent variable in regression models, mule deer population rate of increase, was not autocorrelated ($P > 0.22$) within study GMUs for any of the 6 time lags across the study period. As might be expected with assigned experimental treatments, some evidence of autocorrelation existed within individual GMUs for coyote- and lion-removal density, although none for the first time lag (CRD $P > 0.116$, lion-removal density $P > 0.18$), which is biologically most important. Given the lack of autocorrelation, standard GLM regression procedures were appropriate for evaluating the effects of predator removal on mule deer population growth.

Table 14. Weighted analysis of deviance (ANODEV) for fawn-to-adult female ratios based on covariates for coyote or mountain lion removal densities, southeastern Idaho, 1999–2003. We separately tested the main effects of removal for each species after adjusting for year and site effects. df = degrees of freedom, dev = deviance, MDev = mean deviance.

Source	df	Dev	MDev	F	P
Total _{Cor}	39	73.770			
Year effects					
Summer precipitation	1	8.556			
Winter precipitation	1	6.283			
Summer × winter precip.	1	15.284			
Site	7	12.179			
Total after adjusting for year and site effects	29	31.464			
Coyote removal	1	1.136	1.136	1.050	0.314
Error	28	30.293	1.082		
Mountain lion removal	1	2.799	2.799	2.738	0.109
Error	28	28.629	1.022		

The rate of increase of mule deer populations was best explained by severity of the winter preceding the interval of interest. Both winter severity index and the 1-yr lagged winter severity index were included in competing ($<2\Delta \text{AIC}_c$) models (Table 15). There were no significant interactions within the top models, however, when we included the positive lionlag × WSI interaction ($t_{51} = 1.6$, $P = 0.12$) in model 3, this model replaced model 2 as the best model (Tables 15 and 16). This interaction was the only addition that decreased the AIC_c value (-17.59) of the parent model. Although predator removal in the preceding year (lagged predator removal) was included in the top 3 models, little additional information was contributed over the model including only winter severity and lagged winter severity ($\Delta \text{AIC}_c = 0.75$, Table 15). Models with lagged predator-removal-only factor explained little variation in rate of population increase (R^2 lionlag = 0.015, adjusted R^2 coyotelag = 0.016). Nevertheless, model coefficients were positive (Table 16), indicating that increases in lion or CRD, lagged 1 yr, was associated with increased population growth rate.

Relative variable importance, based on the confidence set of models (Table 15; models 1–9, $\Delta \text{AIC}_c = 2.92$, sum of weights = 0.954; Burnham and Anderson 1998:168–169), indicated that winter severity in the preceding winter and winter severity were approximately 2.5 times as important as lagged removal treatments. Populations in several study GMUs were reduced in 2002 due to forage limitations caused by the dry summer in 2001 followed by above-average winter snowfall (Figs. 2 and 13). Populations in the southernmost GMUs (56, 73E, and 73M) declined 43–53% in 2002 (Fig. 13). Lagged removal treatments were 3 times (coyote removal) to 9 times (lion removal) as important as current removal treatments.

DISCUSSION

Our experimental efforts to change mule deer demography through removal of their 2 top predators had minimal effects, providing no support for the hypothesis that predator removal would increase mule deer populations. In contrast to our predictions (Table 1), we found inconsistent effects of predator removal on life-history and population metrics. Population growth rates did not increase following predator reduction as predicted. December fawn ratios increased with mountain lion removal but not coyote removal. We observed decreased mortality of neonate fawns with increased coyote removal and decreased mortality of 6-month-old fawns and adult females with increased

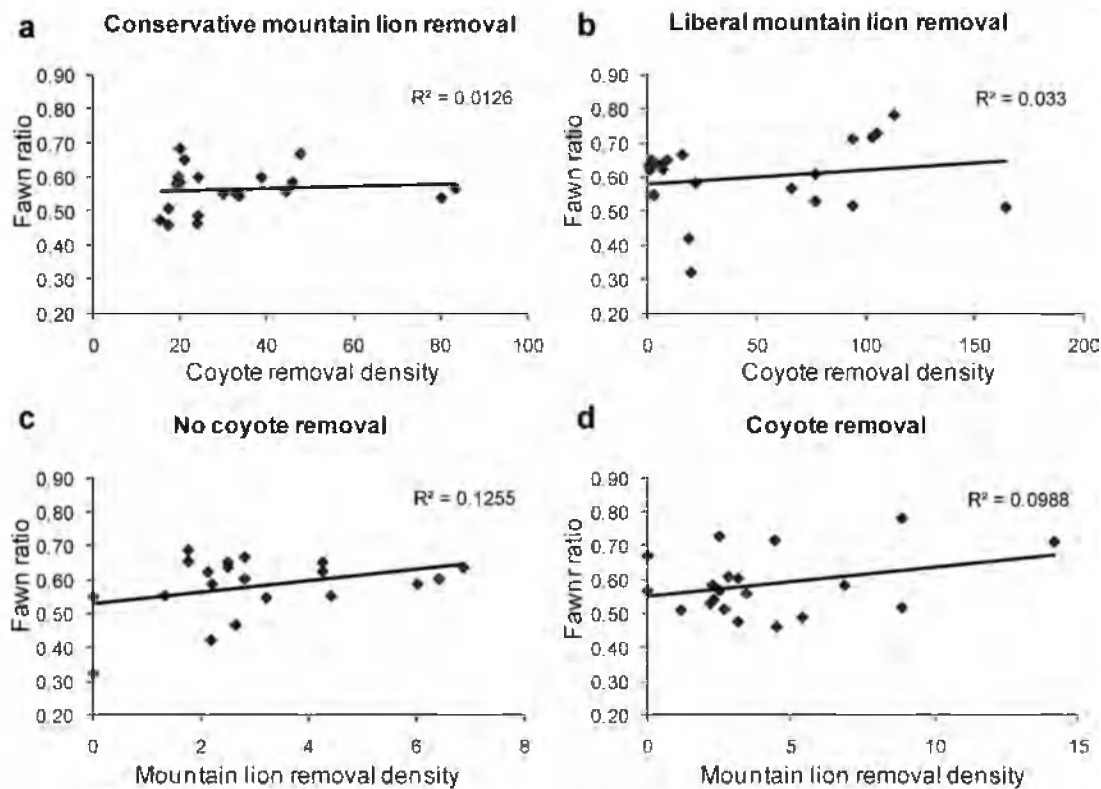


Figure 12. Relationship of fawn-to-adult female mule deer ratios versus (a) coyote removal density within the 4 game management units (GMUs) that did not receive a mountain lion removal treatment, (b) coyote removal density within the 4 GMUs that did receive a mountain lion removal treatment, (c) mountain lion removal density within the 4 GMUs that did not receive a coyote removal treatment, and (d) mountain lion removal density within the 4 GMUs that did receive a coyote removal treatment in southeastern Idaho, 1999–2003.

mountain lion removal. However, the effects of decreased mortality of fawns and adults were not manifested in population rate of increase, and our results suggest other factors, especially climate and the interaction between predation and primary productivity, regulate mule deer population dynamics in southern Idaho.

Predator Reduction

Effect sizes of our removal of mountain lions or coyotes were of sufficient magnitude and variation to provide a definitive test of the effects of predator removal on mule deer populations (Ballard et al. 2001), although predator-removal densities varied across study GMUs and year. We applied the maximum coyote-removal effort possible in a management context, mitigating the constraints of tracking conditions for helicopter removal and helicopter availability by assigning a Wildlife Services employee to each GMU for additional ground-removal efforts. For coyotes, our population estimates were similar to those reported elsewhere in the literature. Our initial density estimate for coyotes in the intensive-study GMUs was 0.22/km² adult or 0.15/km² breeding adults. This estimate was twice that of Clark's (1972) estimate of 0.114/km² adult coyotes or 0.08/km² breeding adult coyotes for the same area. Our estimate was similar to mean densities reported for the Missouri River Breaks (0.21 coyotes/km²) or prairie environments (0.14 coyotes/km²) in Montana (Hamlin et al. 1984, Pyrah 1984). Mean density estimates for a 2-yr period in Colorado were 0.205 coyotes/km² (Karki et al. 2007). The maximum estimated removal rate of 75% of the coyote population in GMU 73A in our study is similar to that reported by Karki et al. (2007), who observed a mean removal rate of 59.7% (range = 40.5–75%) also using helicopter-removal effort, but not trapping, in Colorado. Concordance of these studies with our data suggests our density estimate and corresponding removal rate were reasonably accurate.

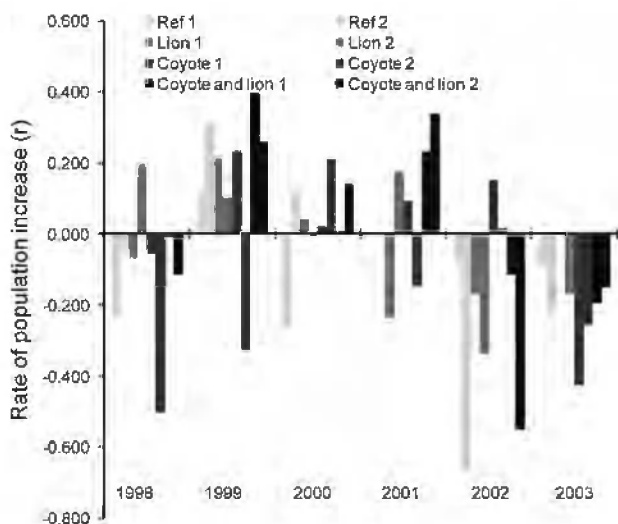


Figure 13. Spring mule deer population growth rate (r) for 8 subpopulations in southeastern Idaho, 1997–2003. We labeled each pair of replicates to depict coyote and mountain lion treatments, Ref = reference areas, Lion = experimental mountain lion removal, Coyote = experimental coyote removal, Coyote and lion = experimental coyote and mountain lion removal.

Table 15. Top model set (models 1–9) of selection results using Akaike Information Criteria (AIC_c) testing the main effects of coyote and mountain lion removal and winter severity^a on mule deer rate of population increase, 1997–2003, where $\Delta AIC_c = AIC_c$ units from the best model and $W =$ Akaike Information Criteria evidence weights.

Model rank	Model	K	AIC _c	ΔAIC_c	W
1	lionlag + wsi + wsilag + lionlag × wsi	5	-17.59	0	0.189
2	coyotelag + wsi + wsilag	4	-17.37	0.22	0.169
3	lionlag + wsi + wsilag	4	-17.28	0.31	0.161
4	wsi + wsilag	3	-16.84	0.75	0.130
5	coyotelag + wsi + wsilag + wsi × wsilag	5	-16.08	1.51	0.088
6	lionlag + coyote + wsi + wsilag	5	-15.41	2.18	0.063
7	coyote + wsi + wsilag	4	-15.22	2.37	0.058
8	lion + coyotelag + wsi + wsilag	5	-14.92	2.67	0.050
9	lionlag + coyotelag + wsi + wsilag	5	-14.77	2.82	0.046
10	wsilag	2	-13.40	4.19	0.023
11	lion + coyote + wsi + wsilag	5	-12.88	4.71	0.018
12	lionlag + wsi	3	-6.67	10.92	0.001

^a We evaluated the covariates including coyotes removed/1,000 km² (coyote), coyotes removed lagged 1 yr (coyotelag), mountain lions removed/1,000 km² (lion), mountain lions removed lagged 1 yr (lionlag), winter severity (wsi), and winter severity lagged 1 yr.

Table 16. Top 3 general linear models relating mule deer population rate of increase to removal of coyotes and mountain lions, and winter severity in southeastern Idaho, 1997–2003. Variables included in the model set were: lionlag = mountain lions removed in the previous year, wsi = winter severity, wsilag = winter severity in the previous year, coyotelag = coyotes removed in the previous year.

Model	Adjusted R ²	β_0	SE	β_1	SE	β_2	SE	β_3	SE	β_4	SE
lionlag + wsi + wsilag + lionlag × wsi	0.268	-0.11 ^a	0.044	0.01	0.011	-0.24 ^a	0.081	-0.20 ^a	0.052	0.03	0.018
coyotelag + wsi + wsilag	0.239	-0.07	0.042	0.001	0.0009	-0.11 ^a	0.049	-0.21 ^a	0.055		
lionlag + wsi + wsilage	0.244	-0.11 ^a	0.045	0.02	0.010	-0.14 ^a	0.051	-0.19 ^a	0.053		

^a Parameters where probability of $\beta = 0$ is <0.05.

Mountain lion removal was similarly high but variable in treatment GMUs compared to reference GMUs during the study period because of fluctuating hunter behavior and success rates. Despite this variation, harvest rates were quite high. For example, Holmes and Laundre (2000) estimated a population of 16–17 resident and independent mountain lions for GMU 73A through intensive capture and telemetry methods, 1997–1998. We documented 16 mountain lions removed from GMU 73A during 1998–1999, which would suggest a harvest rate of >94%. Laundre et al. (2007) estimated 11–15 independent mountain lions per 1,000 km² within their study area, which included GMUs 55 and 57 in our study area, during the period of study from 1997 to 2002. Applying our removal rates to these density estimates suggests we removed 0–94% of independent lions per GMU. This reduction was corroborated by our track indices, with the lowest observed values in 1999, 2 yr after removals were initiated. Furthermore, in all treatment areas except GMU 71, adult female harvest exceeded 25% of total harvest by 2000 and declined in 2001–2002, indicating a high harvest rate for 1998–2000 (Anderson and Lindzey 2005). Anderson and Lindzey (2005) estimated a density of 29 mountain lions/1,000 km² in the Snowy Range of Wyoming, and Choate et al. (2006) estimated densities of 12–32 mountain lions/1,000 km² in central Utah depending on duration of exploitation. These density estimates are based on high-quality mountain lion habitat, whereas we based our removal estimates on the entire area of the GMU and included low-quality mountain lion habitat. Our removal-rate estimate would increase if we confined the area estimate to more traditional mountain lion habitat.

As mountain lion populations decreased, hunting became more difficult and hunting pressure declined during the 2001–2002 general harvest seasons. Harvest was further reduced due to poor snow conditions and hunter success in 2001. Lindzey et al. (1992) reported a mountain lion population recovered to pre-removal numbers within 9 months following cessation of a 36% removal experiment. Logan and Sweanor (2001) found that a population recovered 31 months after a 47% removal effort. The work of these authors suggests that the lower rate of removal of mountain lions in the liberal harvest GMUs during the last 2 yr of the study may have allowed population recovery by 2002.

Factors Affecting Deer Productivity and Survival

Pregnancy rates of adult and yearling female mule deer were high in all study areas. These rates were higher than most reported for similar habitats in the Intermountain West (Robinette et al. 1977, Anderson 1981). Fawn-at-heel ratios were also higher than most fetal rates reported in a comprehensive review by Anderson (1981) and similar to recent work (Bishop et al. 2009). Therefore, observed below-average recruitment rates in the study areas were probably not the result of low pregnancy or fetal rates in these populations.

Low incidence of disease-related death among fawns or adults and normal serology values indicated these agents were not limiting vital rates of mule deer in southeast Idaho. Disease prevalence for mule deer in the study area was in the lower end or even below the ranges of prevalence in other populations in Idaho, with the exception of BRSV, which causes lower respiratory tract infections in young cattle. However, only 6% of adults sampled were positive for BSRV antibodies in our study

area. Antibody prevalence for anaplasmosis, bluetongue, and EHD were lower within the study area than reported for California (Chomel et al. 1994) and North Dakota (Hoff et al. 1973).

Neonatal fawn survival.—Few studies have tested the effect of predator removal on mortality of neonatal mule deer fawns (Austin et al. 1977, Smith and LeCount 1979, Trainer et al. 1981), and none at large landscape scales. In contrast, many studies have tested the effect of coyote removal on white-tailed deer mortality (Ballard et al. 2001). This distinction is important because mule and white-tailed deer have different anti-predator strategies (Lingle et al. 2005), likely differentiating the effect of reduced coyote density. Coyotes are less likely to attack mule deer fawns than white-tailed deer fawns and are less likely to kill mule deer fawns if attack is commenced. Defensive behavior by mule deer dams generally contributes to lower predation rates by coyotes (Lingle et al. 2005). Given these distinct species traits, it is not surprising that we did not observe the dramatic results seen with coyote-removal experiments on white-tailed deer (Beasom 1974, Kie and White 1985).

We documented decreased mortality of fawns from birth to 6 months old through coyote removal as hypothesized. Coyote-caused mortality of neonates in the reference area was 0.13, which is similar to other recent work, 0.13 (Pojar and Bowden 2004) and 0.12 (Bishop et al. 2009). Coyote-caused mortality rate across all years was lower in the treatment unit (0.11), but not significantly. Nevertheless, the effect of coyote removal was the most important predictor in our mortality models, suggesting specific conditions facilitate increased effect of coyote removal during some years. The generalist nature of coyote prey selection as influenced by vulnerability and availability of prey may lead to the inconsistent effect of coyote removal. Overall rates of mountain lion-caused mortality rates were lower in the treatment GMU (0.07) than the reference GMU (0.11), suggesting the effects of mountain lion removal may be somewhat confounded by the stronger predictor, coyote removal.

Coyote populations in our study probably mirrored their primary prey, lagomorphs, similar to other studies of coyote ecology (Hoffman 1979, Todd and Keith 1983, Gese 1995), with important implications for mule deer fawns, a secondary prey in our system. As lagomorph density increased, fawn mortality decreased (Table 8, second model), suggesting coyote predation may switch to mule deer at lower lagomorph densities. Furthermore, there was an interaction between coyote removals and lagomorph density (Table 8, first model), such that at high lagomorph densities the effects of coyote removal decreased fawn mortality even more than expected just based on main effects. The higher mortality of fawns during low lagomorph abundance was contrary to our expectations, although the coyote removal rate was close to median (113 coyotes removed/1,000 km²). The relative scarcity of primary prey may have increased coyote dependence on mule deer fawns for prey, thereby canceling the effect of reduced coyote density.

We hypothesize that coyote populations fluctuate with their main prey items, lagomorphs and small mammals, and when one of these prey populations is reduced, coyotes switch to deer fawns as alternate prey. Previous research has documented the influence of coyote/primary prey ratio on prey selection and survival of

ungulates. Hoffman (1979) reported that coyotes switched to mule deer during low jackrabbit abundance in the south portion of our reference area and adjoining northern Utah. Snowshoe hare (*L. americanus*) abundance explained 94% of the variation in coyote food habits in Alberta, Canada (Todd and Keith 1983), and greater abundance of snowshoe hare decreased the rate of coyote predation on white-tailed deer in Nova Scotia, Canada (Patterson and Messier 2000). Mortality of mule deer fawns attributed to coyotes was lowest when microtine rodent populations were high in Montana (Hamlin et al. 1984). Prugh (2005) observed that the ratio of Dall sheep (*Ovis dalli*) killed per coyote did not change as coyote populations increased with increasing snowshoe hare abundance (i.e., no prey switching), but the resultant increase in the coyote population led to more sheep killed. Because coyote and lagomorph populations can be highly correlated (Clark 1972, Hamlin and Mackie 1989, Knowlton and Gese 1995), we think our predator-prey ratio likely remained similar at all levels of lagomorph abundance until coyote removal changed the ratio. Thus, the benefits of increased lagomorphs to fawn survival would not be realized until a reduction in coyote populations increased the available food items per coyote. These results emphasize the key importance of understanding the community ecology of all prey species in predator-prey studies (DeCesare et al. 2010).

Fawn vulnerability also may have increased due to nutritional condition. As we observed, higher birth mass was associated with decreased neonatal mortality in mule deer (Lomas and Bender 2007, Bishop et al. 2009) and most other temperate ungulates (Gaillard et al. 2000). Rate of mass gain is another important aspect of neonatal fawn development because fawn body mass before winter is a reliable predictor of survival to recruitment (Bartmann et al. 1992, Unsworth et al. 1999, Lukacs et al. 2009). Mass gain is dependent on dam nutrition, behavior (Robinette et al. 1973), and nutritional resources available to the fawn (Parker et al. 2009). Rate of mass gain was highest in 1998 when total summer precipitation was nearly twice that of other years, suggesting that adult females in 1998 were on a higher nutritional plane than in other years. Forage quality has been linked to increased precipitation in arid climates such as prevails in our study area (Hamlin and Mackie 1989, Marshal et al. 2005). Thus, above-average precipitation during the growing season and increased mass gain should positively influence summer fawn survival (Knowlton 1976, Lomas and Bender 2007). Conversely, exposure to cold, wet weather shortly after birth can increase neonate mortality (Gilbert and Raedeke 2004, Pojar and Bowden 2004), as we observed death due to exposure following measurable snow falls in 3 of 12 (25%) fawns captured at birth sites.

Survival of fawns in winter.—Mortality of 6-month-old fawns in winter decreased with higher summer precipitation, greater mass, and lower winter precipitation, as hypothesized. Fawn mortality followed the pattern of mountain lion removal, but not coyote removal, as evidenced by mortality models. Unexpectedly, the highest winter mortality we observed did not coincide with extremes in winter precipitation. During the year with the highest winter mortality (2002), winter precipitation equaled the median for all 5 yr, but precipitation during the 2 previous summers (2000 and 2001) was low (Fig. 2), validating the role of summer nutrition and fat deposition for mitigating

winter weather conditions. The importance of summer and autumn nutrition and resulting mass gain in temperate environments has been highlighted in mule deer (Hobbs 1989, Bartmann et al. 1992, Unsworth et al. 1999), elk (*Cervus elaphus*, Cook et al. 2004), and most other ungulates (Parker et al. 2009). Furthermore, total winter (1 Oct–15 Apr) precipitation may mask important time periods within winter. For example, November and December snowfall and minimum temperature are important predictors of over-winter fawn survival in Colorado (Bartmann et al. 1992) and Idaho (M. Hurley, Idaho Department of Fish and Game, unpublished data).

Adult female deer survival.—The most influential factors on adult mortality during summer were precipitation during the previous winter and age. This higher mortality was likely related to poor body condition of adult females entering summer (16 May) following a winter with above-average precipitation or low precipitation the previous summer. Malnutrition mortality of adult females was not consistent across years, as 6 of 9 losses were in 2002, similar to Bishop et al. (2005), where all adult female losses to malnutrition occurred in 1 yr of a 5-yr study. Natural mortality of adult females ($n = 9$, Table 12) occurred between 1 March and 15 August, 3 of which died after the start of summer when stresses due to gestation and lactation were highest (Parker et al. 2009). The high cost of lactation caused adult female caribou to continue to lose mass for 3 weeks after parturition (Parker et al. 1990), a situation that could increase mortality into the summer. Bender et al. (2007) also reported decreased body condition and annual survival of adult female mule deer when the previous growing-season precipitation was below average.

The effect of age was important in both summer and winter. Age may increase vulnerability to predation as mountain lions kill older deer of both sexes disproportionate to availability (Hornocker 1970, Spalding and Lesowski 1971, Ackerman et al. 1984, Kunkel et al. 1999). We observed that mountain lions killed older adult females than were available in the population in the treatment GMU, but not the reference GMU, suggesting increased availability of this age class. In addition, we hypothesize that increased mortality related to adult female age in the treatment area may be a function of decreased mountain lion-caused mortality earlier in our study. Increased mortality from natural, non-predatory causes in the treatment area (Table 12) suggested compensatory mortality as the senescent portion of the treatment population expanded. Evidence of senescence was observed in 25 of 59 mammal populations investigated by Gaillard et al. (1994). Senescence, manifested in increased mortality beginning at 7 yr of age, has been documented in bighorn sheep (*Ovis canadensis*), roe deer (*C. capreolus*), isard (*Rupicapra pyrenaica*, Loison et al. 1999), and mule deer (Bishop et al. 2009). Festa-Bianchet et al. (2003) observed a 10–15% decrease in survival in senescent age classes of roe deer, bighorn sheep, and mountain goats (*Oreamnos americanus*).

Factors Affecting Mule Deer Fawn Ratios and Population Growth Rate

Fawn-to-adult female ratios.—Females in the treatment area appeared to be less productive during the last 3 yr of our study.

Fawn-at-heel ratios were equal between treatment and reference areas during the first 2 yr of investigation, followed by a trend toward lower ratios in the treatment areas during the last 3 yr (Fig. 11). This scenario indicates progressively lower fetal rates in the intensive treatment area, possibly due to an increased number of older and younger (yearlings), less productive females, or a density-dependent reduction in overall condition and pregnancy or fetal rate of deer (Robinette et al. 1973, Stewart et al. 2005). Bishop et al. (2009) documented an over-winter increase in fetal survival with increased adult nutrition. In a summary of 10 investigations, Connolly (1981) reported pregnancy rate and the number of fetuses per adult female declined in the older age classes (≥ 7 yr) of mule deer.

December fawn ratios are widely used by wildlife managers to index recruitment to 6 months of age as the ratios integrate pregnancy, fetal, and fawn survival rates. Caughley (1974) cautioned against the use of age ratios to explain population dynamics without supporting measures of population performance. Our consistently high summer survival of adults provides a constant value for the ratios, whereas neonate survival was highly variable to December. As previously noted, variation in fawn ratios could be because of variation in pregnancy rates or survival rates, clouding interpretation of mechanisms of changes in recruitment. Despite this uncertainty, December fawn ratios provided a useful metric to interpret fawn ratios within our study area, as changes in neonatal survival were reflected in fawn-to-adult female ratios.

Among predator-removal treatments, only mountain lion removal provided significant predictive value for fawn ratios in all 8 populations. However, mountain lion removal was a weak predictor of neonate survival. Sample size may be a factor in the survival analysis as mountain lions killed only 6 (CIF = 0.07) neonate fawns in the treatment area and 13 (CIF = 0.11) in the reference area. Our mortality rates from mountain lions were higher than Pojar and Bowden's (2004) felid predation rate of 0.032, but lower than Tatman (2009) where 8 of 44 (18%) fawns died of mountain lion predation.

Precipitation was the most significant factor for predicting fawn ratios. Fawn ratios in our study areas declined with increased previous winter precipitation and increased summer precipitation, but the significant interaction between these variables makes interpretation difficult. This relationship may seem contradictory to findings of increased survival of neonate fawns with increased summer precipitation, but timing (by months) of precipitation appeared important. Pojar and Bowden (2004) reported that fawn ratios declined with higher June precipitation in Colorado. Similarly, Gilbert and Raedeke (2004), summarizing a 20-yr data set on black-tailed deer (*O. hemionus*), observed cold temperatures and high precipitation during the fawning period had a negative impact on fawn recruitment. Our sample of fawns most vulnerable to inclement weather, <4 days old ($n = 74$), was limited. Nevertheless, we verified death due to exposure following measurable snow falls in 3 of 12 (25%) fawns captured at birth sites.

We speculate that the winter-summer precipitation interaction on fawn ratios was a result of early neonatal mortality caused by inadequate adult nutritional condition at parturition (winter precipitation, Bishop et al. 2009) or direct mortality due to

exposure (summer precipitation). However, increased precipitation in late summer may increase forage quality and nutritional intake by adult females and fawns, thus decreasing late-summer mortality and explaining the positive interaction.

Population growth.—Growth rates of mule deer populations in southeastern Idaho appeared to be limited by annual climate variation, within the context of habitat conditions, but were not strongly limited by predation. Winter severity was the most significant factor limiting mule deer population growth. It was not unexpected that the 1-yr lagged effects of winter severity and predator removal were more important predictors than current effects. Models with lagged predator removal were ranked higher than with weather severity alone, suggesting the effect of mountain lion removal in the previous year may partially offset a decrease in survival caused by severe weather conditions. Although we did not find strong evidence of mountain lion removal on mule deer population growth, Logan and Swenor (2001) found that mountain lion predation can suppress deer population growth during poor forage quality years. Bleich and Taylor (1998) reported that predation accounted for >70% of known deaths of adult female mule deer and that mountain lions were responsible for 90% of those. Given that mountain lions caused 60% of the known mortality of adult females in our study, any reduction in this mortality cause should increase population growth.

Annual forage quality and quantity in our study area was likely related to summer precipitation, as shown in other arid environments (Mackie et al. 1998, Marshal et al. 2005). We found that summer precipitation and fawn mass were correlated and were significant predictors of winter survival. Mass of mule deer fawns was positively related to winter survival in other studies (Bartmann et al. 1992, Unsworth et al. 1999, Bishop et al. 2005, Lukacs et al. 2009). With low summer precipitation, fawns experienced above-average mortality during the ensuing winter, even in low-snowfall winters. We observed extreme fawn (92%) and adult (26%) mortality rates during a winter (2002) with average precipitation following low precipitation during the 2 previous summers. Predators, although a significant mortality agent, were not regulating the populations we investigated. We observed slight changes in population parameters, but not population trend, with predator removal. We demonstrated effects of mountain lion removal to increase adult female survival and fawn-to-adult female ratios. Furthermore, we observed a weak positive relationship between mountain lion removal and deer population rate of increase. However, the minimal short-term improvement in vital rates was tempered with the observed decline in fawn-at-heel ratios and increased mortality of adult females in predator-removal areas during the final years of study.

The variability of mule deer populations in the northern portions of their range limits the evaluation of trophic cascades caused by removal of top predators. Although coyotes and mountain lions are important mortality agents, the magnitude and frequency of weather-caused mortality events overwhelms the effects of predators for population regulation of mule deer in this study area. Short-term modification of mule deer behavior is plausible through predator removal as observed in elk-wolf (Kauffman et al. 2007) and marine systems (Wirsing et al. 2008). For example, increased use of high-density coyote

habitat (mid-elevation shrubland) following removals may increase landscape carrying capacity for mule deer within this study area.

The degree to which density-dependence affects survival and population growth of ungulates has received considerable attention in recent years as data sets broaden to include comparative sites or true manipulative experiments (Gaillard et al. 1993, Coulson et al. 1997, Stewart et al. 2005, Kjellander et al. 2006, Wang et al. 2006). These works and others generally support the key role of density on vital rates, such as juvenile survival, age at first breeding, reproductive rates, and adult survival proposed by previous authors (McCullough 1979, Eberhardt 1985). Local habitat density is also important for red deer calves if resources are limited (Coulson et al. 1997). Festa-Bianchet et al. (2003), however, cautioned that many determinations of density dependence may be confounded by changes in adult age structure. Wang et al. (2009) also demonstrated that density dependence was only evident in ungulate populations without large carnivores and in areas of low spatial or climate heterogeneity. Density dependence, age structure, or climate variability may have influenced our interpretation of the effect of predator removal on mule deer population growth. As examples of these influences, mule deer populations doubled in some GMUs during the study period, age structure likely changed where predator removal increased survival rates, and we observed a 3-fold annual variation in precipitation. Although any of these changes may mimic a density-dependent response as outlined above, the pervasive effect of weather conditions on most of our measured vital rates highlights the importance of weather in mule deer population growth.

McLeod (1997) suggested that the concept of a food-based carrying capacity is not useful in estimating herbivore dynamics in highly variable environments. Mule deer populations in southern Idaho were compromised by annual weather-related changes in K and the frequency of weather-related population reductions (approx. 10-yr intervals) limits identification of density-dependent trends in vital rates. Even at the lowest population levels of mule deer we measured, drought conditions may reduce the nutritive quality of the habitat below required levels for growth and lactation in summer and maintenance in winter (Parker et al. 1999, Lomas and Bender 2007, Parker et al. 2009), decreasing fawn survival. As evidence, Bishop et al. (2009) documented improvements in most vital rates with increased nutrition in the winter. Annual changes in forage quality and their subsequent effects on nutritional carrying capacity (Hobbs and Swift 1985) need to be considered when estimating or modeling the effects of density on deer population growth (Hobbs 1989) or vital rate changes may be interpreted as a density-dependent signal when the effect is caused by forage quality, irrespective of density. In highly variable environments in Montana, mule deer populations grew during periods of favorable weather conditions and declined in unfavorable conditions irrespective of density (Mackie et al. 1998). In the variable and patchy habitats of the Missouri Breaks study area, population growth and recruitment did not follow density-dependent theory. Coulson et al. (2001) determined that dynamics of Soay sheep (*Ovis aries*) populations were independent of population size and depended largely on the interaction of weather patterns with age and sex structure. Mule deer

populations in our study area and others that experience high climatic variation appear to fluctuate independent of density.

Other variables also may have affected the power of our experiment. For example, climatic variation could influence aerial population surveys. We observed considerable spatial variation between years in counts of population abundance that were related to climate conditions and migration timing, likely increasing sampling variance of these surveys. Therefore, we observed increased variability as the metric scaled-up from individual survival to population surveys. The effect size of mountain lion removal that we observed on survival estimates may not have been large enough to overcome the sampling variance in our population surveys. Another possible limit to effect size was the lingering effects of medium mountain lion removal levels in conservative harvest areas before our experiment (Table 5). Harvest was reduced in 1998 (Table 5) when GMUs were assigned as reference areas. We tested current and 1-yr lagged mountain lion removal in population growth models, but a latent effect of the previous higher harvest rate could introduce variance in the models if mountain lion populations took >2 yr to recover.

Compensatory versus additive mortality of predation.—The compensatory nature of coyote predation on mule deer was best explained by the combined vital and population rates we measured. We documented increased survival of neonatal fawns, negligible change in fawn ratios, and no effect on mule deer population rate of increase as a result of coyote removal. These are strong clues that increased survival of neonatal fawns is compensated by other forms of later mortality before manifesting in a measurable increase in population growth rate. Eberhardt (1985) suggested juvenile survival of ungulates was more sensitive to density-dependent effects and environmental variation than adults. Removing coyotes during periods of increasing mule deer populations shifted the mortality cause of fawns from coyotes to malnutrition, suggesting a compensatory response in winter (Bartmann et al. 1992). In winter, we observed higher coyote-caused mortality in the reference area but no difference in mortality of fawns between the reference and treatment areas, again suggesting compensatory mortality. Also, because we did not observe appreciable disease-related mortality or high disease prevalence, disease is unlikely to be the compensatory mortality mechanism. Coyote-caused mortality appears to be mostly compensatory in the deer populations we studied, as in other areas of the western United States (Ogle 1971, Bartmann et al. 1992).

Mountain lion-caused mortality appears to be mostly additive in the short-term, as evidenced by increased survival of adults and 6-month-old fawns and by fawn ratios following mountain lion removal. Although variable juvenile survival with constant adult survival will often drive population rates of increase (Gaillard et al. 1998), these rates are very sensitive to small changes in adult survival. Seven of 9 African ungulate species studied declined primarily as a result of adult survival (Owen-Smith and Mason 2005), leading the authors to observe that lowering adult survival by 0.1 transformed a growing population into a declining population for 5 of these species. Predation by mountain lions, however, also appears compensatory in a longer time frame. Although mountain lion-caused mortality was reduced in the treatment area, mortality due to natural causes (malnutrition or unknown

whole carcasses) increased and overall survival decreased in winter during the last 3 yr of our study.

MANAGEMENT IMPLICATIONS

Understanding mule deer population dynamics is a priority for state wildlife managers in the West. Predator removal always emerges during the search for management techniques to increase mule deer populations, prompting professionals and the public to question effectiveness, cost, and probability of success. Our intent was to enable managers to predict the effects of predator-removal programs within a variety of environmental conditions on mule deer population demographics. We conducted an experiment with tools readily available at temporal and spatial scales relevant to wildlife managers.

We noted that coyote removal had the greatest effect on neonatal fawns in summers when fawns were needed as alternate prey. Therefore, if there was a population-level effect of coyote removal, it would be expected to be maximized through coyote removal from fawning-summer range of mule deer in years when density of one primary prey species for coyotes is low. Monitoring lagomorphs and small mammals in late April may provide a low-cost method to assess when coyote removal may have a possibility of success.

To estimate the cost-per-deer produced of coyote-removal programs, we conducted a simple post hoc analysis using a deterministic age-based Leslie matrix (Leslie 1948) to model a 10-yr population increase resulting from an increase in fawn survival as observed in GMU 73A (fawn survival increased 15% in 2 of 5 yr as a result of coyote removal). We randomly selected 4 yr of the 10 to increase survival by 0.15 to mimic what we observed in GMU 73A. We applied average survival rates for adult females (0.89) in the reference area and adult males in a typical male-only (0.40 annual survival), general-season hunt scenario in this area. Initial age structure was modeled with the pattern of survival indicated by our mortality models, decreasing adult survival by 3% each year (survival was set to 0 at age 15). The number of adults in the initial 73A population survey was assigned to an age based on this decreasing survival until the overall adult population survival was 0.89. Recruitment was set to the mean of the reference area with a 1:1 sex ratio at birth. We allowed the age structure to stabilize for 20 iterations and after resetting the initial population to the 73A population size, allowed recruitment to vary to reflect increased survival of neonate fawns in 4 randomly selected years. We then applied the average annual cost of coyote removal for GMU 73A during this study (\$10,276) to yield a cost-per-deer-produced estimate. In 10 yr, 335 additional deer would be added to the population due to increased survival of fawns at a cost of \$307 per deer (\$102,761/335 deer). Focusing specifically on harvestable deer, 65 additional yearling males would be produced at \$1,581 per deer over the entire 10-yr period. If increased trophy harvest were the objective, we estimated that 6 additional 4-yr-old males would survive to harvestable age over 10 yr at a cost of \$102,845, or \$17,127 per deer.

This example illustrates the maximum effect, minimum-cost scenario under an annual coyote removal program for the conditions we observed. The cost per coyote removed would increase exponentially if increased effort was applied to our study areas.

The cost could be decreased by systematically applying coyote removals based on primary prey populations, but cost would increase by required surveys of primary prey. Conversely, the cost would increase if mortality was compensatory, as we observed. This analysis would only apply if the increase in neonatal fawn survival produced a measurable effect in population parameters, a result we did not observe in our study. Estimated cost could be reduced up to 60% if coyote removal was employed in optimal years (removal increased survival each year), when deer populations were below K , primary coyote prey was low, precipitation favored neonatal survival (low winter, high summer), and coyote hunting conditions were favorable. Regardless, these simple cost comparisons demonstrate the significant costs of predator control to increase harvestable mule deer, ignoring the weak overall support we found for these population-level increases.

Our removal goal was a simple numerical reduction of coyotes with an immediate, comparative decrease in predation rate of mule deer. We were not attempting to reduce the coyote populations for an extended period. Thus, the often-misunderstood 70% coyote removal rate needed to maintain reduced coyote population (Connolly and Longhurst 1975, Connolly 1978a, Pitt et al. 2001) does not apply to our research. Increased expenditure on coyote removal was not likely to improve the cost-per-deer beyond our modeling efforts. On the contrary, it would likely have increased cost exponentially.

We did not conduct a cost analysis for the effects of mountain lion removal on mule deer due to its inherent difficulty. Maintenance of effort may be a limiting factor in achieving a target long-term removal rate. Actual removals were conducted by licensed hunters who purchased a mountain lion tag. Interest in mountain lion hunting fades with declining populations or poor hunter success. In these instances, professionals such as Wildlife Services staff may be required to strategically remove lions. Realistically, public attitudes in many western states may not favor paid killing of mountain lions to increase mule deer populations.

The political and biological realities of wildlife management are often mutually exclusive. Nowhere is this more evident than in the arena of predator removal to increase game populations. In the context of population dynamics, our research provided little evidence that predator removal changed the overall population status of mule deer, especially with coyote removal. Amount and timing of precipitation, likely related to plant phenology and winter energy expenditure, had a greater influence on population vital rates. Predation is a significant limiting factor of mule deer populations; however, the effect on rate of increase is unpredictable due to yearly variation in climate-linked habitat carrying capacity and alternate prey populations. These changes in carrying capacity or increases in deer numbers will ultimately dictate the role of predation in mule deer population dynamics.

The limited effects of predator removal from this study and the pervasive effects of enhanced nutrition from Bishop et al. (2009) lead us to logically conclude that enhanced nutrition will increase mule deer populations more effectively and predictably than predator removal. The challenge now is to determine cost-effective methods of enhancing quality of naturally occurring forage in mule deer range in areas where increasing mule deer populations is an important goal. Research to answer this question for winter

range is currently underway in Colorado, but research documenting the effects of enhanced nutrition on summer range is needed.

SUMMARY

Coyote Removal

1. Neonatal fawn survival increased after coyote removal. Effectiveness of removal was dependent on the abundance of primary prey (lagomorphs) for coyotes because coyotes appeared to switch to mule deer fawns at low lagomorph densities.
2. Winter fawn survival and adult survival did not increase following coyote removal.
3. The effect of coyote removal on population growth rate was undetectable.

Mountain Lion Removal

1. Mountain lion removal increased winter fawn survival.
2. Adult female mule deer survival increased with mountain lion removal, up to 5.5% annually at maximum removal rates.
3. Fawn-to-adult female ratios increased with mountain lion removal. We predicted a 6% increase at average removal and up to 27% at maximum mountain lion removal.
4. Mountain lion removal had a minimal, positive effect on mule deer population growth rates.

Factors Affecting Mule Deer Vital Rates

1. Pregnancy rates of adult females were high (91–98%).
2. Fawn-at-heel ratios in June were high (1.62–1.81) in normal climate years.
3. Disease was not a factor in mule deer survival.
4. Age was an important factor in adult mortality.
5. Climate was the most important factor explaining survival of fawns in winter, adult females in summer, fawn ratios, and population growth rate.

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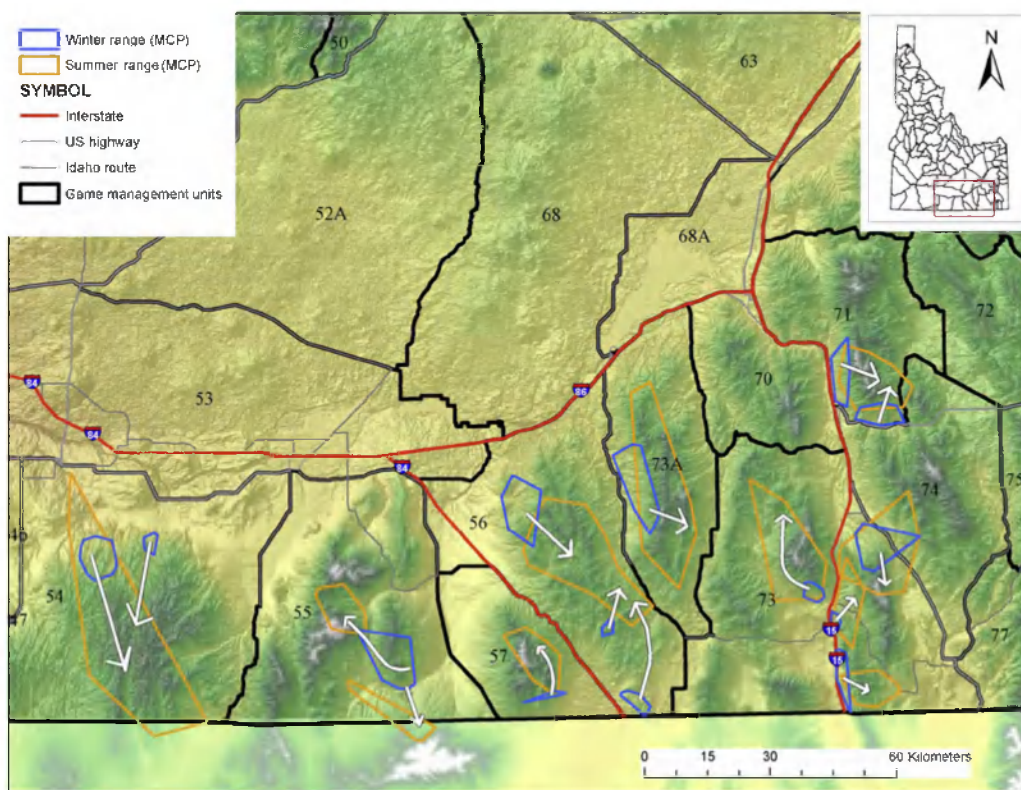
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Appendix A. Minimum population use polygons (MCP, 95% minimum convex polygons) of radiocollared mule deer outlining terminal winter ranges and summer ranges of distinct subpopulations. Arrows depict movement direction from winter to summer range. Locations were collected by the Idaho Department of Fish and Game for other investigations from 1999 to 2008 and seasonal sample sizes were variable (range from 6 to 126), thus polygon size should not be considered to encompass subpopulation home range sizes.

Appendix B. Cox's proportional hazard mortality models for fawns and adult female mule deer by season in southeast Idaho, during 1998–2002. We included models with Akaike Information Criteria (AIC_c) values within 4 AIC_c units of the best model (ΔAIC_c) of the overall best model after determining models in forward stepwise procedure. *W* = Akaike Information Criteria evidence weights. We display single-factor models of variables included in the competing model set to assess relative contributions to complex models. Variables included in models of the top model set were: CRD = coyote removal density, Mass = mass at capture or at 4 days old for neonates, Area = study area, Lagomorphs = lagomorph index, LRD = lion removal density, Z-Precip = standardized composite of summer and winter precipitation, Previous Precip = total precipitation in the previous season, Precipitation = precipitation during modeled season.

Model rank	Model	<i>K</i>	AIC _c	ΔAIC _c	<i>W</i>
Neonatal fawns (birth to 30 Nov)					
1	CRD + Mass + Area + Lagomorphs + CRD × Lago	5	1,116.92	0.00	0.398
2	CRD + Mass + Area + Lagomorphs	4	1,118.79	1.87	0.156
3	CRD + Mass	2	1,119.34	2.42	0.119
4	CRD + Mass + Area	3	1,119.34	2.42	0.118
5	CRD + Mass + Lagomorphs	3	1,120.16	3.24	0.079
6	CRD + Mass + LRD	3	1,120.60	3.68	0.063
7	CRD	1	1,121.41	4.49	0.042
8	Area	1	1,124.31	7.39	0.010
9	Mass	1	1,124.65	7.73	0.008
10	Lagomorphs	1	1,125.66	8.74	0.005
11	LRD	1	1,127.27	10.35	0.002
6-month-old fawns (16 Dec–15 May)					
1	Z-Precip + Mass + LRD + Sex	4	1,121.86	0.00	0.508
2	Z-Precip + Mass + LRD	3	1,123.12	1.26	0.270
3	Z-Precip + Mass + Sex	3	1,124.25	2.39	0.154
4	Z-Precip + Mass	2	1,125.89	4.04	0.068
5	Z-Precip	1	1,135.69	13.83	0.001
6	LRD	1	1,144.78	22.92	0.000
7	Mass	1	1,145.10	23.25	0.000
8	Sex	1	1,158.43	36.57	0.000
Adult females summer (16 May–30 Nov)					
1	Previous Precip + Age + LRD + Age × LRD	4	317.10	0.00	0.290
2	Previous Precip + Age + LRD	3	317.17	0.07	0.280
3	Previous Precip + Age	2	317.96	0.87	0.188
4	Previous Precip + Age + Lagomorphs	3	319.53	2.43	0.086
5	Previous Precip + Z-Precip	2	319.90	2.80	0.071
6	Previous Precip + LRD	2	320.92	3.83	0.043
7	Previous Precip	1	322.28	5.18	0.022
8	Age	1	323.45	6.35	0.012
9	LRD	1	325.67	8.57	0.004
10	Z-Precip	1	327.73	10.64	0.001
11	Lagomorphs	1	327.80	10.71	0.001
Adult females winter (1 Dec–15 May)					
1	Age + LRD + Area	3	514.95	0.00	0.372
2	Age + LRD + Area + Precipitation	4	515.83	0.88	0.239
3	Age + LRD + Area + Z-Precip	4	516.03	1.08	0.217
4	Age + LRD + Area + Previous Precip	4	516.52	1.57	0.170
5	Age	1	527.38	12.43	0.001
6	Z-Precip	1	529.95	15.00	0.000
7	LRD	1	534.91	19.96	0.000
8	Previous Precip	1	537.76	22.81	0.000
9	Area	1	541.97	27.02	0.000
10	Precipitation	1	542.45	27.50	0.000