IDAHO DEPARTMENT OF FISH AND GAME

Cal Groen, Director

Project W-160-R-33

Subproject 51

Completion Report

SOUTHEAST MULE DEER ECOLOGY

Study I: Influence of Predators on Mule Deer Populations

Study II: Influence of Habitat Quality and Composition Changes to Productivity and Recruitment of Mule Deer

July 1, 2005 to June 30, 2006

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September 2007
Boise, Idaho

Findings in this report are preliminary in nature, are still in draft form, and not for publication without permission of the Director of the Idaho Department of Fish and Game.

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STUDY: I Mule Deer Populations

JOBS: 1-2

PERIOD COVERED: July 1, 2005 to June 30, 2006

INFLUENCE OF PREDATORS ON MULE DEER POPULATIONS

Abstract

We tested effects of removing coyotes (*Canis latrans*) and mountain lions (*Puma concolor*) on mule deer (*Odocoileus hemionus*) populations in 11 game management units (GMUs) in southeastern Idaho, USA, 1996-2006. From 1996 to 2002, we assigned 8 GMUs to treatments under a 2×2 factorial design (coyote removal, lion removal) with 2 replicates of each treatment or reference area combination. In a subsequent study, we assigned 8 GMUs to 3 levels of coyote removal. Mule deer populations were surveyed with a helicopter for young to adult female (fawn-to-doe) ratios in December and total population size in March, with estimates corrected for visibility bias. To determine survival and causes of mortality, 250 neonates, 284 6-month-old fawns, and 521 adult does were monitored with radio telemetry in 2 intensive study sites, one with coyote and mountain lion removal and one without. Pregnancy rates, fawn-at-heel ratios, population rates of increase, and previous population levels suggest these populations were below numerical carrying capacity (K) at the onset of the research. Important factors influencing survival of neonates were small mammal and lagomorph abundance, coyote removal, and weather conditions. Coyote removal increased neonate survival only when deer were apparently needed as alternate prey. Coyote removal did not influence the survival of 6-month-old fawns or adult females. Mountain lion removal increased the survival of adult females in winter. Weather variables were the dominant factor in most competing survival models for all age classes of mule deer. Fawn-to-doe ratios were significantly increased (up to 27%) at maximum rates of mountain lion removal across all GMUs. Coyote removal had no significant effect on fawn-to-doe ratios during 1997-2002. Coyote removal was weakly related to fawn-to-doe ratios for 3 years following a 50%, weather-related population reduction in 2002. We detected no significant effect of coyote or mountain lion removal on total population trend of mule deer, although populations increased at higher levels of mountain lion harvest. A regression analysis of removal rate of predators with deer population rate of increase was not significant, although the coefficients of the removal variables were positive. Winter severity was significantly related to mule deer population growth. The lack of fawn-to-doe ratio or mule deer population response indicates that decreased neonate mortality due to coyote removal is partially compensatory. The increased effect of coyote removal on fawn-to-doe ratios after a reduction in mule deer population size supports the conclusion of compensatory mortality at or approaching carrying capacity. The combination of primary prey numbers and weather conditions required for coyote removal to increase fawn survival indicates annual coyote removal programs will not be a cost-effective

method to increase mule deer populations. Coyote removal programs targeted when mule deer fawn mortality is additive and coyote removal conditions are optimal may influence mule deer population vital rates, but likely will not change direction of population trend. Mountain lion removal increased deer survival, fawn-to-doe ratios, and increased populations slightly at higher levels of removal. However, we were not able to statistically demonstrate changes in population direction related to our management level application of mountain lion removal. Benefits of predator removal appear to be marginal and short term, necessitating clear harvest goals for immediate use of increased mule deer populations.

Introduction

Mule deer have historically exhibited volatile population cycles in the intermountain west. Periods within low population cycles of this highly valued resource are often viewed as a crisis by both the public and wildlife professionals. During the 1900s, populations of mule deer in western United States followed essentially the same pattern; a gradual population increase beginning in the 1920s with peaks in the late 1940s to early 1960s, followed by a general decline during 1960s to mid-1970s (Denny 1976). In areas of southern Idaho, herds rebounded through the 1980s and then underwent a widespread decline in the 1990s (Idaho Department of Fish and Game 1999). Complex combination of factors that drive these population cycles is only partially understood. Even less clear are the consequences of management actions such as predator control, habitat improvement, and harvest strategies to reverse mule deer population direction.

Mule deer populations in southern Idaho declined significantly during winter 1992-1993. Mortality rates as high as 50% of the total population were attributed to dry conditions during the previous summer, resulting in minimal fat storage and fawn growth, followed by above average winter snowfall (Hurley and Unsworth 1998, Bishop et al. 2005). For the next 5 years, mule deer populations in southeast Idaho were stable or declining despite apparently favorable weather conditions (Hurley and Unsworth 1998). We hypothesize these populations were below carrying capacity during this period because winter malnutrition mortality was minimal, core winter ranges were used only moderately, and peripheral winter use areas were vacant. Adult deer mortality was reduced by elimination of antlerless deer harvest and reduction of antlered-only hunting opportunity beginning in 1994.

Most western states use fawn-to-doe ratios (fawns per 100 does observed during late Autumn or early winter aerial surveys) to index recruitment. Because adult doe survival remains relatively constant across years (Unsworth et al. 1999), these ratios are an important metric of mule deer population performance. Generally, fawn-to-doe ratios have declined over the past 20 years in most of the western states (Carpenter 1998, Mackie et al. 1998, Gill et al. 2001). Likewise, fawn-to-doe ratios in southeastern Idaho declined from an average of 89 (SE = 4.16) between 1988 and 1990 to an average of 66 (SE = 2.99) between 1994 and 1997. Density-dependence theory predicts that pregnancy rates and recruitment should have increased with reductions in deer density, provided carrying capacity (K) was unchanged. Robinette et al. (1977) observed that does on a higher nutritional plane have higher pregnancy and fetal rates than does on a lower nutritional plane. Between 1993 and 1997, fawn-to-doe ratios and population growth did not respond as expected with respect to previous years, indicating habitat and deer density may not have been limiting deer populations. Above average mortality of adults and/or fawns was a possible explanation for stagnant or declining mule deer populations in southeastern Idaho.

Major causes of mule deer mortality are weather, humans, and predation, whereas minor causes include parasites and disease (Connolly 1981*a*). The relative role of these factors may change depending on environmental conditions or degree of mortality that is compensatory. In southern Idaho, predation by mountain lions and coyotes is the major proximate cause of mule deer mortality during winter (Unsworth et al. 1999, Bishop et al. 2005). Bobcats (*Felis rufus)* are present, but exert little influence on deer populations (Hurley and Zager 2005).

The effect of predation on mule deer populations has been a controversial topic for decades in North America. The role of predation in population regulation is poorly understood because natural systems are complex. Extensive research into the effect of predators on mule deer populations has reached a common conclusion; predators can certainly limit or regulate deer populations under some circumstances. Connolly (1978*b*) cited 31 research efforts that tended to support 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 population that determine whether predation constitutes additive or compensatory mortality. Evidence in these reviews does not implicate predators in mule deer population declines, therefore the question shifts to limiting effects on population recovery after a decline.

Differing conclusions about the role of predation on ungulates are most likely because of complex interactions of environmental variables that influence prey population size, additive versus compensatory mortality, abundance of alternate prey species, and variability in the predator species complex (Theberge and Gauthier 1985). Peek (1980) restated 2 competing theories of ungulate regulation: (1) stability results from an interaction between animals and the plants they eat; (2) stability is imposed by predators. Peek (1980) and Caughley (1981) agreed that regulation by food and regulation by predators are not mutually exclusive and may be expected to act concomitantly. 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 (Caughley 1976, 1981; Keith 1974, 1983; Peek 1980). Theberge and Gauthier (1985) noted that 3 conditions must be met to assert that predators are limiting 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.

Controversial as the effect of predation may be, wildlife professionals often receive considerable pressure to reduce predator populations in an effort to increase mule deer populations. Indeed, several research efforts have documented the effectiveness of predator removal to increase recruitment in mule deer, white-tailed deer (*Odocoileus virginianus*), and pronghorn (*Antilocapra americana*) populations on a limited scale (Beasom 1974; Austin et al. 1977; Guthery and Beasom 1977; Stout 1982; Smith et al. 1986). Despite this evidence, predator removal is often ineffective for increasing mule deer populations because: (1) populations were at or near K, (2) predation was not a limiting factor, (3) predator populations were not sufficiently reduced, and (4) predator control efforts were dispersed over a large area (>1,000 km^2; Ballard et al. 2001). Overriding influences on implementation of removal programs usually include public opinion and questionable cost:benefit.

Ballard et al. (2001), "To date, all research (excluding that conducted on wolves) concerning predator removal programs to enhance deer populations has been conducted on small areas (i.e., <1,000 km^2)." Furthermore, most studies were conducted over relatively short time frames (1-3 years) and often failed to examine confounding or interacting variables. To enhance decision-making processes regarding predator removal, Ballard et al. (2001) suggested future research include a rigorous experimental approach; increased temporal scale to include favorable and severe weather conditions; and measurements of alternate prey, hunter harvest, and habitat condition.

We designed our research to evaluate predator reduction as a tool to increase mule deer populations at temporal and spatial scales relevant to wildlife managers. We addressed criteria identified by Ballard et al. (2001) with 1 major exception: the scale of predator removal. Through activity of Wildlife Services and sport hunters, we used existing management tools to affect predator reductions. From a management perspective, predator removal must affect the entire target deer population to be of value to the wildlife professionals who manage mule deer at the population or Game Management Unit level. By matching the scale of treatment effort to techniques used by mangers to monitor populations, we are more likely to detect a change related to predator removal. Large scale experimental tests of influences of predator removal are necessary to evaluate efficiency, logistical practicality, and cost of the removal effort with respect to actual increases in mule deer populations or hunter harvest.

Hypothesis and Experimental Design

We tested whether coyote and mountain lion removal would increase mule deer populations. We also investigated the influence of deer population characteristics, alternate prey abundance, and weather conditions on effectiveness of predator removal to alter mule deer populations. We monitored mule deer populations in 8 environmentally similar game management units (GMUs) in southeast Idaho. We removed coyotes from 4 randomly selected GMUs, whereas the other 4 were reference areas (no coyote removal). Through an adaptive management process, we also assigned 4 GMUs to mountain lion removal, completing the factorial design. Concurrently, radio telemetry was used to evaluate cause-specific mortality, age-specific survival, and recruitment of adult female and fawn mule deer on 2 intensive study GMUs with different levels of predator removal. Our research was expanded to test the influence of coyote removal on mule deer fawn-to-doe ratios after we documented a weather-related population decline in 2003. This event presented the opportunity to examine the effect of coyote removal on deer populations with minimal density-dependent influence.

<div align="center">

Study Area

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The 1997-2002 study area (Study Area 1) encompassed 14,700 km^2 and included Idaho Department of Fish and Game (IDFG) GMUs 54, 55, 56, 57, 71, 73A, 73 Elkhorn, and 73 Malad in southeastern Idaho (Figure 1a). The 2003-2006 study area (Study Area 2) encompassed 13,600 km^2 and included GMUs 56, 71, 72, 73A, 73 Elkhorn, 73 Malad, 76, and 78 (combined GMUs 75, 77, and 78) in southeastern Idaho (Figure 1b). The Study Area 2 mule deer populations were reduced during winter of 2001-2002. Elevation ranged from 1,060 m to 3,150 m. Topography was typified by several north-south mountain ranges separated by wide valleys.

Southeast Idaho is characterized by hot, dry summers; cool, dry winters; and warm, wet springs (Figure 2). Average annual weather variables for Study Area 1 included 29.8 cm precipitation and 86 growing degree days (10 C° base, AgriMet, Pacific Northwest Cooperative Agricultural Weather Network, U.S. Bureau of Reclamation, Boise, Idaho). Average annual precipitation for Study Area 2 was 34.5 cm. During most winters, snow accumulation on the valley floors was <20 cm for both study areas.

Vegetation at lower elevations was dominated by agricultural fields of dry-land grain and Conservation Reserve Program (CRP) perennial grasses, big sage (*Artemesia 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 U.S. 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.

Game Management Units 56, 71, 72, 73 Malad, 73 Elkhorn, 73A, 76, and 78 were managed with antlered-only hunting regulations. 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, antlerless hunting opportunity was not offered anywhere in the study area. Antlerless deer 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, 73 Elkhorn, and 73 Malad, whereas antlerless harvest in GMUs 55 and 57 represented <0.5% of the population. Antlerless harvest was reduced to <0.5% in all GMUs during 2003-2006.

Four years prior to our study, a wildfire in GMU 54 converted 60% of the traditional, mixed-shrub winter range to annual and perennial grassland. This habitat conversion may have changed the growth potential of the deer population in GMU 54.

Methods

Experimental Design

We used aerial surveys to monitor size of mule deer populations (Unsworth et al. 1994) and fawn-to-doe ratios across 8 GMUs of similar habitat to evaluate effects of coyote and mountain lion removal on mule deer population recruitment and growth, 1997-2002. Four GMUs were randomly assigned to coyote removal treatment and 4 GMUs were assigned to increased mountain lion harvest, 2 with coyote removal treatments and 2 without (Study Area 1). Combinations of coyote and mountain lion treatment resulted in a 2×2 factorial treatment design with 2 replicates each (Figure 1a). We estimated deer populations prior to the investigation with aerial surveys (Table 1). We also monitored cause-specific mortality and survival of adult females and fawns with radio telemetry in 2 intensive-study GMUs, 56 (reference) and 73A (treatment) (Figure 1a). These GMUs were situated near the center of Study Area 1 and provided year-long habitat for 2 distinct subpopulations of deer.

In a subsequent study, we used fawn-to-doe ratios derived from aerial surveys to evaluate the effects of coyote removal across 10 GMUs following a population reduction that occurred in 2002 (Study Area 2, Figure 1b). We assigned GMUs to 3 target levels of coyote removal (high = > 100/1000 km^2, medium = 60/1000 km^2, low = < 20/1000 km^2). We manipulated mountain lion harvest quotas to achieve similar lion removal rates across Study Area 2 during 2003-2006. Alternate hypotheses tested with this experiment included effects of predator removal as influenced by several covariates (Table 2).

Predator Manipulation

Coyote Population Index and Removal

Wildlife Services personnel removed coyotes by aerial shooting in the 4 treatment GMUs during winter and early spring 1997-2002 (Figure 1a) and 5 treatment GMUs during 2003-2005 (Figure 1b). Repeated, approximately weekly, flights continued through winter while snow cover provided acceptable tracking conditions. Beginning in 1999, additional ground efforts were implemented April through July, including trapping, calling and shooting, and pup removal at den sites. Wildlife Services only removed coyotes from reference GMUs to solve specific livestock depredation problems. Total number of coyotes removed from a GMU was converted to density of coyotes removed based on land area of the GMU (number removed/km^2). Coyote harvest was open year-round to licensed hunters and trappers throughout the study areas. We believe this relatively low, consistent, background harvest level across all GMUs did not compromise our experimental design. This assumption is well supported by Hamlin's (1997) analysis of coyote survival related to hunting and trapping during a period of very high pelt prices. Intensive harvest efforts by fur trappers and hunters resulted from the high economic incentive. Despite increased aerial and ground hunting methods, the coyote population continued to increase. Very low coyote pelt prices during our study period provided no economic incentive for the intense harvest pressure observed by Hamlin (1997).

We estimated diet composition for coyotes via analysis of stomach contents. Carcasses of coyotes killed during 1998 were collected and sent to the National Wildlife Research Center in Logan, Utah, for analysis (T. DeLiberto, 1998, unpublished data). Flight crews collected carcasses opportunistically when flight safety or efficiency was not compromised.

Mountain Lion Population Index and Removal

Mountain lion populations were indexed within intensive study GMUs from 1998 through 2001. We combined dust-track survey (Smallwood and Fitzhugh 1995) and aerial snow-track survey methods (Van Sickle and Lindsey 1991) to develop a ground snow track method. We divided GMU 56 and GMU 73A into 46-km^2 quadrats and then stratified the quadrats into high or low probability of finding a mountain lion track based on habitat type and expert opinion. A random sample of 25% of the quadrats in each stratum was drawn from both GMUs 56 and 73A. Two days after a snowfall of ≥5 cm, tracks were counted from snowmobiles along up to 32 km of snow-covered roads in each quadrat. Personnel traveled at 10-16 kph along routes in both directions. Stride length and track dimensions were measured for each mountain lion track observed on the transect (Smallwood and Fitzhugh 1993). The index was expressed as the number of unique tracks/km for all quadrats within a GMU.

We altered hunting season length or harvest quotas to manipulate mountain lion harvest in Study Area 1, 1998-2002. Mountain lion hunting seasons were closed 48 hours after licensed hunter harvest reached a predetermined quota. Structure of mountain lion seasons in liberal harvest (treatment) GMUs were changed from liberal female quota systems for the 1997-1998 seasons to no quota seasons in 1998-1999, then back to liberal quotas 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 check-in procedure required of all successful mountain lion hunters in Idaho. The total number of mountain lions removed from a GMU was converted to density (km^2) of lions removed based on affected land area.

During 2003-2005 in Study Area 2, harvest quotas of female mountain lions were manipulated to achieve similar equivalent harvest density across all GMUs to nullify the effect of removal. Harvest quotas were set, considering average harvest and vehicle access, to produce a target removal of 3 mountain lions/1,000 km^2 across the study GMUs. Our estimate of mountain lions removed included legal harvest, control actions, and other reported mortality.

Alternate Prey Abundance

Small Mammal Abundance

We indexed small mammal abundance in the intensive study area (GMUs 56 and 73A) annually during September and October (Trout 1978). Trap transects were established in each of the non-forested cover types: low elevation sagebrush, low- and mid-elevation perennial grasslands (CRP), and mid-elevation mountain shrub. Transects were randomly placed with respect to location and direction within stands representing cover types in GMUs 56 and 73A. Once established, transect end points were marked with wooden stakes and repeated each year. Each 300 m transect included 20 stations spaced 15 m apart, with 1 mouse snap-trap and 1 rat snap-trap per station. Traps were baited with a mixture of whole oats and peanut butter. Each station was examined and baited daily for 3 consecutive days. Upon capture, small mammal species was recorded and the trap was cleared and baited. One live trap in addition to the snap-traps was also set at each station in 1999, but catch rates were very low (<0.012 animals/trap night) and their use was discontinued. Trap nights were adjusted for snapped traps without capture as follows:

$$ATN = TN - S/2$$

where;

ATN = adjusted total trap nights;
TN = total trap nights for the trapping session;
S = number of traps snapped with no capture.

The cover type specific index was expressed as captures/100 trap nights ((Total captures/ATN)100). We derived an overall index to small mammal abundance by summing the catch rates across cover types. Because estimation of alternate prey abundance began in fall 1998, an index for fall 1997 was missing. This data was necessary to balance the covariate matrix for survival modeling in winter 1998. To obtain an estimate for the missing year (1997),

the small mammal index was regressed on total precipitation from the previous winter ($P = 0.15$, $R^2 = 0.54$, RMSE = 13.23). The model was:

Small mammal index = -20.718 + 10.84(previous precipitation).

We thus predicted an index value for small mammals in fall 1997 as 47.14.

Lagomorph Abundance

We used vehicle headlight surveys to estimate lagomorph abundance from 1998 to 2002 (Trout 1978). Surveys were initiated 1 hour 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 transect was proportional to the land area of the GMU, thus the transect in GMU 56 was approximately twice the length of the transect in GMU 73A (104 km vs. 56.2 km). Observers traveled secondary roads at 32-48 kph and recorded lagomorphs observed in vehicle headlight beams on the roadbed. Species of lagomorph (*Lepus americanus*, *L. californicus*, *L. townsendii*, or *Sylvilagus nuttallii*) and distance along transect were recorded. 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. A significant relationship between the index and precipitation was not sufficient to develop a model to predict an index for 1997 season. Therefore, the index for summer 1997 was replaced with the mean of lagomorph indices for all years.

Weather Conditions

We used data from the AgriMet weather station (AgriMet, Pacific Northwest Cooperative Agricultural Weather Network, U.S. Bureau of Reclamation, Boise, Idaho) in Malta, Idaho, USA, to quantify seasonal precipitation and temperature for survival modeling and fawn-to-doe ratio analysis, 1998-2002 (Figure 1a). 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. Precipitation for fawn-to-doe ratio analysis during 2003-2006 (Figure 1b) was a composite average of 4 weather stations: Malta, American Falls, McCammon, and Soda Springs (Western Regional Climate Center; http://www.wrcc.dri.edu). For analysis, summer and winter were identified based on season of plant growth (minimum temperature >-2 C°). The summer period, 16 April to 30 September, corresponded to the growing season, with most precipitation falling as rain. We considered 1 October to 15 April as winter, when most precipitation fell as snow. Total seasonal precipitation was included in survival and fawn-to-doe ratio modeling. To minimize the number of parameter in survival models, we combined the seasonal precipitation variables to reflect the extremes in weather related mule deer survival in Idaho; low summer precipitation + high winter precipitation = low winter survival (Bishop et al. 2005, Unsworth et al. 1999). We also hypothesized that high previous winter precipitation + low summer precipitation would decrease survival of fawns in summer. To estimate this biological process in 1 variable, we calculated a composite variable (combined precipitation) 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 is comparable across seasons. During winter season, a larger value of this variable indicates below average summer precipitation and

above average winter precipitation. The opposite is true during summer season when a larger value indicates below average winter precipitation and above average summer precipitation.

Average snow depth varied across winter ranges, and was related to elevation. To account for differential effects of snow depth and temperature on rate of increase of mule deer populations, we incorporated data from United States Geological Survey weather stations within or near each GMU (Figure 1a) to generate a winter-severity index (WSI). Missing values for individual weather stations were estimated by regressing monthly means of the chosen weather station with monthly means of the nearest weather station (Table 3). Total snowfall during December and January and monthly mean maximum temperature during November through March were used as indicators of winter severity. To create a standardized index of winter severity, we calculated Z-scores (Zar 1984) from these monthly values. These were expressed as number of standard deviations of that monthly value above or below the 50-year mean. A snow severity index (SSI) was estimated 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. The WSI was then calculated as: WSI = (SSI – TSI)/2.

Changes in Deer Survival

We used radio telemetry to evaluate the effect of predator removal on survival of individual deer within the intensive study area. Minimal coyote removal and conservative lion harvest occurred in the reference area (GMU 56), while both liberal mountain lion harvest and active coyote removal was focused in the treatment area (GMU 73A). We estimated survival (Pollock et al. 1989) of neonate (age birth to 6 months), 6-month-old fawns (age 6 to 12 months) and adult does (age >12 months) in each GMU.

Capture Methods

We used methods described by White et al. (1972), Smith (1983), and Riley and Dood (1984) to capture neonate fawns. Does exhibiting fawning behavior were observed until they fed their newborn fawns or otherwise identified fawn locations through body posturing (White et al. 1972). We searched the identified area and captured fawns by hand after the doe moved off. To minimize capture influences or predator attraction, latex gloves were used to handle the fawn, no blood was collected, and no ear tag inserted. To sample the entire reproductive unit and reduce capture bias, efforts were made to capture all fawns in a litter. Fawn mass, chest girth (directly behind shoulders on the exhale), hind foot length (tip of hoof to calcaneous), and growth ring of front hoof (Robinette et al. 1973) were measured to estimate age and condition. Fawns were fitted with brown or black expandable radio collars designed to break away 6-8 months after capture. Transmitters were equipped with mortality sensors (4-hour delay) and weighed 89 to 98 grams.

We used drive nets (87% of the captures), net guns (11%), and clover traps (2%) to capture adult deer and 6-month-old fawns during winter. In the first year, deer were captured from December through March. Thereafter, captures began in December and were completed by 22 January. Adult females and 6-month-old fawns were fitted with radio collars and ear tags. We measured hind foot length and chest girth of all animals. During the first year, transmitters deployed on

female fawns were permanently affixed and pleated to expand as the animal grew. Thereafter, all 6-month-old fawn collars were designed to break away within 1 year. We measured fawn mass to the nearest 0.4 kilogram with a calibrated spring scale. We estimated age of adult does from tooth eruption and wear patterns (Robinette et al. 1957). A blood sample was drawn from each adult female to determine pregnancy and assess blood serum serology. Blood serum was analyzed for pregnancy-specific Protein-B (PSPB) by Bio-Tracking Inc., Moscow, Idaho, USA (Sasser et al. 1986), and tested for standard respiratory diseases and other infectious blood borne diseases common to the western United States at Bureau of Animal Health Labs, Boise, Idaho, USA. Diseases antibodies tested for included; 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. pomona*. Idaho Department of Fish and Game Veterinarian or laboratory biologist was on site during most captures to assist with animal welfare and biological sampling.

Survival and Cause-Specific Mortality of Deer

Adult and 6-month-old deer were monitored every other day during winter and spring and approximately twice weekly during summer and autumn. Neonates were monitored at 1-2 day intervals throughout summer and twice weekly throughout autumn until collars were shed. When motion sensors indicated no movement, we investigated the site within 24 hr. We attempted to identify cause of death using criteria developed by O'Gara (unpublished manuscript). Whole carcasses of fawns were retrieved and delivered to the IDFG Wildlife Health Lab, Caldwell, Idaho, USA, for necropsies and disease sampling when practical. Adults and 6-month-old deer that died ≤5 days after capture were considered capture-related and were removed from further analysis.

We estimated survival rates (Kaplan and Meier 1958, Pollock et al.1989) and variances of neonates, 6-month-old fawns, and adult does. We tested for differences in survival rates by age group between GMUs 56 and 73A using log rank tests (Hosmer and Lemeshow 1999, Pollock et al.1989). We modeled relationships between instantaneous mortality rates and predator removal, alternate prey abundance, weather, and animal morphology using Cox's proportional hazards models (Cox and Oaks 1984). This semi-parametric method modeled the relationship between independent variables and the log of an unspecified, instantaneous mortality, or hazard rate. Hazard rate is calculated in terms of failure time, which is the number of days that an individual lived after marking. We calculated hazard ratios, often called risk ratios, for each predictor (Pollock et al. 1989, Hosmer and Lemeshow 1999, Harrell 2001). A hazard ratio >1 represents an increasing mortality rate as the predictor increases, whereas a hazard ratio <1 represents decreasing mortality rate as the predictor increases (Cantor 1997). Correlation between predictor variables was indicated when parameter estimates drastically changed when a new variable was added to the model (Harrell 2001). 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 explored this assumption graphically and used a test for proportionality to assess violations of the time by predictor interaction assumption (Therneau and Grambsch 2000). Conformity to all other assumptions was assessed graphically (Therneau and Grambsch 2000).

Flexibility of Kaplan-Meier method and Cox's proportional hazards models accommodated varying data structures for each mule deer population segment. Both methods allowed for left truncation (i.e., staggered entry where animals continually enter the analysis) and accommodated right censoring. Animals were right censored when we did not record a fate for that animal because the transmitter failed, the collar was shed, the animal left the study area, or the animal lived to the end of the study. Failure time for 6-month-old fawns and adults was calculated by counting the number of days between marking and death or censoring and then left truncated at the study period initiation date. The study period was initiated after the first capture in each unit. For neonates, failure time was the time between 4 days of age and age at death.

We used Akaike Information Criteria (AIC) for model comparison (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 variables considered using a forward type selection process (Klein and Moeschberger 2003). We limited the factors examined to main effects (coyote and lion removal), main and alternate prey, precipitation, and individual animal predictors (Table 3). We began by comparing AICs for all a-priori 1-factor models. Models having a ΔAIC <2 were considered competing models. All remaining variables were allowed to enter these competing models one at a time and in all possible combinations. Model building continued in this fashion until the AIC did not decrease with addition of new variables (Klein and Moeschberger 2003). At the final step, if differences between model AIC values were <2, they were deemed competing models and reported with the 1-factor models. Statistical analyses for survival were conducted using SAS Version 8.2 (2001) and R Version 1.8 (2003).

Primary treatment effects were quantified as coyote and mountain lion removal rate (number removed/1,000 km^2). We anticipated similar predator removal levels each year in the treatment GMU (73A), but annual variation in coyote removal by Wildlife Services and mountain lion hunter harvest resulted in varying coyote and mountain lion removal levels. Because no coyotes (for research purposes) and consistently few mountain lions were removed in the reference GMU (GMU 56), and varying levels were removed in GMU 73A, we separated analyses to better explore varying coyote and mountain lion removal levels. Because there was not "considerable overlap" of coyote removal density or lion removal density levels between GMUs, analyzing the GMUs together would violate analysis of covariance assumptions (Ott et al. 2000). We conducted separate survival analyses by age class (neonate fawns, 6-month-old fawns, and adults) for winter-spring (1 Dec-15 May) and summer-autumn (16 May-30 Nov). These dates coincided with winter use area through spring migration and summer use area through fall migration.

Individual animal predictors used in survival models included sex and mass of neonatal and 6-month-old fawns, number of neonate siblings, and age of adult does. Mass was explored as a predictor for neonates and 6-month-old fawns. Because animals were captured 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, mass differences were examined over time between sexes and among years. If a significant mass gain or loss was detected 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. Based upon residual plots, we only observed an important, linear relationship between survival and age for adults ≥6.5 years. For modeling purposes, we used a constant value for all adults ≤5.5 years and allowed all animals ≥6.5 years to age until death or censoring. Chest girth was initially considered as an individual predictor for adult does. We examined the relationship between age and chest girth with Von Bertalanffy growth models. Differences in growth rates between the 2 study GMUs were tested using likelihood ratio tests for 4 nested models. Chest girth was not included in any of the models because a specific adjustment date was not deemed reasonable. Missing values for individual measurements were nullified by using average values.

Changes in Deer Population Demographics

Neonate Fawn-at-heel Ratios

We used fawn-at-heel ratios to index fetal rates in mule deer. To estimate fawn-at heel ratios, we observed deer in fawning areas every 3-4 days, 25 May-25 June, 1998-2002. Distinct does with fawns were observed from a distant vantage point until the observer was confident all fawns with an individual doe were identified. Observation usually included a feeding and bedding cycle with fawns in plain view. Observations were verified with neonate capture attempts and repeated observations of does using the same habitat patch. Fawn-at-heel ratio (FDR) included only does with fawns and was calculated as:

$$FDR = \frac{\sum_{i=1}^{G} f_i}{\sum_{i=1}^{G} d_i},$$

where;

f_i = number of fawns in the ith animal group observed $(i = 1,\ldots,G)$;

d_i = number of does in the ith animal group observed $(i = 1,\ldots,G)$;

G = number of animal groups observed during time period.

Variance for fawn-at-heel ratios was calculated by cluster sampling where each group of deer was treated as a cluster:

$$V(\hat{R}) = \frac{1}{n\bar{x}\left(1 - \dfrac{n}{N}\right)} \frac{\sum (y_i - Rx_i)^2}{n - 1}$$

where;

y = number of fawns in group,

$\bar{x}$ = mean number of does per group,

R = ratio of fawns to does,
n = number of groups observed,
N = number of groups in the population.

Confidence intervals (95%) for fawn-at-heel ratios were calculated as:

$$\hat{R} \pm t_{n-1}\sqrt{V(\hat{R})}\,.$$

December sex and age ratios

We estimated mule deer population sex and age class structure in December and early January by surveying a representative sample of subunits using a Bell 47G3B helicopter, including all elevations and habitats that contained deer, until a sample of 500 deer or 50% of the estimated population was obtained (Unsworth et al. 1994). We classified deer as adult female ($\geq$1year old), fawn, yearling male (1-2 antler points/side), 3-point male, or $\geq$4-point male. Fawn-to-doe ratios (FDR) were computed for each GMU each year as previously. The variance of December FDR was estimated by:

$$\widehat{\mathrm{Var}}\left(\widehat{\mathrm{FDR}}\right) = \frac{\sum_{i=1}^{G}\left(f_i - d_i\left(\widehat{\mathrm{FDR}}\right)\right)^2}{\bar{d}^2 G(G-1)},$$

where,

$$\bar{d} = \frac{\sum_{i=1}^{G} d_i}{G}.$$

An asymptotic $(1-\alpha)\cdot 100\%$ confidence interval was calculated as:

$$\widehat{\mathrm{FDR}} \pm Z_{1-\frac{\alpha}{2}}\sqrt{\widehat{\mathrm{Var}}\left(\widehat{\mathrm{FDR}}\right)}.$$

Two alternative approaches were used to assess efficacy of predator removal on fawn-to-doe ratios, 1997-2003. A factorial design permitted tests of main effects of coyote removal, main effects of mountain lion removal, and their interaction (design based). Knowledge of removal density of coyotes and mountain lions from each GMU each year permitted an analysis based not only on presence or absence of a treatment, but also level of treatment (model based). Because predator removal rates varied over time and across replicate sites, use of actual treatment levels was a more realistic and accurate portrayal of treatments employed during the study.

The treatment design was a 2×2 factorial design based on presence or absence of coyote or mountain lion removal within a GMU. The experimental design was a randomized design with 2

replicated sites per treatment level. Additionally, the study consisted of a repeated-measure design where fawn-to-doe ratios were measured in a GMU for consecutive years.

The analysis was based on a general linear model (GLM) using a log-link and normal error structure. The response model was written as:

$$R = \mu \cdot Y_i \cdot C_j \cdot L_k \cdot CL_{jk} \cdot YCL_{ijk},$$ (1)

where;

μ = overall mean;
Y_i = effect of year i ($i = 1,\ldots, 6$);
C_j = effect of coyote removal treatment j ($j = 1, 2$);
L_k = effect of mountain lion removal treatment k ($k = 1, 2$);
CL_{jk} = interaction of the coyote j ($j = 1, 2$) and mountain lion removal k ($k = 1, 2$) treatments;
YCL_{ijk} = interaction between years and predator control treatments jk.

Because missing values in a factorial design can severely bias estimates of treatment effects and invalidate tests of main effects, we only included data for 1999-2003, when the data set was balanced and complete. Year-by-treatment interaction assesses whether the pattern of treatment effects is consistent across years. Some environmental interaction with predator effects or widely varying levels of predator removal within a treatment across time could induce an interaction.

Null hypotheses tested by the analysis of deviance (ANODEV) were that treatment main effects and interactions were zero. Because we expected predator removal to increase fawn-to-doe ratios, we used 1-tailed tests of the form:

$$H_o: \quad C_j \leq 0 \quad \forall_j$$
$$H_a: \quad C_j > 0 \quad \forall_j.$$

The second alternative analysis was model-based. Fawn-to-doe ratio is an expression of net fecundity; in other words, a function of reproductive rate and fawn survival. If coyote and mountain lion predation is heavily focused on young, reductions in predator density might be expected to be manifested in higher fawn survival, and consequently, higher fawn-to-doe ratios. Hence, fawn-to-doe ratios can be modeled as a function of survival processes:

$$E\left(\frac{f}{d}\right) = \text{Productivity} \cdot \text{Survival}_{\text{Fawn}}.$$ (2)

Productivity might also be expected to differ between years and locations due to natural variability. Hence, Equation 2 can be written as:

$$E\left(\frac{f}{d}\right) = \mu \cdot Y_i \cdot A_j \cdot \text{Survival}_{\text{Fawn}}, \qquad (3)$$

where;

μ = mean productivity;

A_j = effect of the jth area $(j = 1,...8)$;

Y_i = effect of the ith year $(i = 1,...,9)$.

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

$$S_{\text{Fawn}_{ij}} = S_{N_{ij}} \cdot S_{\text{Coyote}_{ij}} \cdot S_{\text{Lion}_{ij}}, \qquad (4)$$

where;

$S_{N_{ij}}$ = survival probability for fawns in the ith year at the jth site from non-predator effects,

$S_{\text{Coyote}_{ij}}$ = probability of surviving coyote predation in the ith year at the jth site,

$S_{\text{Lion}_{ij}}$ = probability of surviving mountain lion predation in the ith year at the jth site.

Equation 4 assumes sources of mortality act independently. In turn, predator survival parameters can be re-parameterized as:

$$S_{ij} = e^{-C\left(\text{predator density}_{ij} - \text{removal density}_{ij}\right)}, \qquad (5)$$

where,

C = vulnerability coefficient.

Equation 5 is equivalent to catch-effort models used to characterize fishery and hunting exploitation (Seber 1982:296). Combining Equations 3-5 and absorbing site- and time-specific predation densities into the location (A_j) and year (Y_i) effects, leads to the multiplicative response model:

$$E\left(\frac{f}{d}\right)_{ij} = \mu \cdot Y_i \cdot A_j \cdot e^{C_L(\text{Lion Removal Density})} e^{C_C(\text{Coyote Removal Density})} \qquad (6)$$

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

$$\ln E\left(\frac{f}{d}\right)_{ij} = \ln \mu + \ln Y_i + \ln A_j + C_L (\text{LRD})_{ij} + C_C (\text{CRD})_{ij} \qquad . \quad (7)$$

Equation 7 attempts to first describe any inherent differences in fawn-to-doe ratios that may be attributable to annual or location differences in productivity and baseline predator densities. Additional variation in fawn-to-doe ratios is then described by reductions in mountain lion and coyote densities. In model 7, vulnerability coefficients should be positive if predator removal increases fawn-to-doe ratios. Analysis was based on general linear models using a log-link and normal error structure. Weighted (W) analysis was used in the case of the design-based and model-based analyses:

$$W = \frac{1}{\text{Var}\left(\ln \widehat{\text{FDR}}\right)} \square \frac{1}{\left(\dfrac{\widehat{\text{FDR}}}{\text{SE}\left(\widehat{\text{FDR}}\right)}\right)^2} = \frac{1}{\text{CV}^2} , \qquad (8)$$

where CV = coefficient of variation in FDR.

The analytical methods employed to test the effects of coyote removal on fawn-to-doe ratios in the 2003-2006 (Study Area 2) were consistent with the earlier time period. Two approaches were used, a design-based and model-based analysis. In the design-based analysis, CRD was treated as a categorical variable. In the model-based approach, a hierarchical multiple regression model was constructed treating CRD as a continuous covariate.

Each of the 8 GMUs in Study Area 2 was assigned to 1 of 3 levels of coyote removal (low = < 20/1000 km^2 – 78, 71, 73 Malad; medium = 60/1000 km^2, – 72, 76; high = > 100/1000 km^2) – 56, 73A, 73 Elkhorn). The winter fawn survival (FS) covariate was used to adjust for habitat and predation differences that may affect productivity and any carryover effects from one year to the next. Because mule deer first reproduce as 2-year-olds in Idaho, high fawn survival the previous year will result in higher 1-year-old abundance the next year, which can depress FDR values. Fawn survival was estimated from the nearest of 2 winter fawn survival monitoring areas to the GMU of interest (Hurley and Zager 2005). This approach was used instead of a multivariate repeated-measures analysis to help preserve error degrees of freedom in this analysis with limited number of sample years.

In the model-based analysis, significance of CRD was tested using a hierarchical regression model, first incorporating other environmental variables considered potentially influential on FDR. These ancillary variables include mountain lion removal density (LRD), winter precipitation (WP), summer precipitation (SP), and prior-year fawn survival (FS). Although, mountain lion removal efforts were held as constant as possible, LRD was assessed to determine whether additional adjustment was necessary. The precipitation variables were used to adjust for any ambient changes that may affect predation on fawns and survival from year to year and site to site.

Population rate of change

We used aerial surveys to estimate mule deer population characteristics at a GMU scale during 1997-2003. Surveys were conducted 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. Winter ranges and major migration routes were included in search areas to account for differences in timing of migration. All subunits within search areas were sampled and estimates were adjusted for visibility bias (Unsworth et al. 1994).

Population estimates derived from aerial surveys were used to estimate rates of population change. We calculated annual rate of population change, expressed as an instantaneous rate of change r_t, for each unit as:

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

where N_t is the population at time t. We tested the effect of predator removal on rate of population change within the factorial design with analysis of variance (ANOVA) (SYSTAT Version 9, SPSS Inc., 233 S. Wacker Drive, Chicago, Illinois, USA). Multiple linear regression models were used to test effect of varying rates of predator removal on rate of deer population increase. Because of potential effects of winter severity on population growth, winter precipitation was replaced with a GMU-specific winter-severity index in models to control for varying effects of snow depth on winter survival and recruitment. Statistical tests were considered significant at the $\alpha = 0.10$ level.

Results

Coyote Manipulation and Food Habits

Coyote Removal

Coyotes were removed from 4 treatment areas within Study Area 1 (GMUs 55, 57, 73A, and 73 Elkhorn) winter through summer, 1997-2002 (Figure 1a, Table 4). Coyote removal density increased throughout the study period in response to increased effort and expenditures. We increased ground-based efforts in 2000 and 2001, when snow tracking conditions and helicopter availability hampered efforts. Coyotes were removed from treatment areas within Study Area 2, winter through summer 2003-2005, for analysis of fawn-to-doe ratios only (Table 5).

Coyote Food Habits

Wildlife Services collected 96 coyotes between 21 January and 1 April 1998. Coyote carcasses were collected between 21 January and 5 March in GMUs 73A and 73 Elkhorn, whereas coyotes in GMUs 55 and 57 were collected between 11 March and 1 April. Coyote stomach content analysis revealed 58% of 88 stomachs with prey items contained deer (Table 6). Coyote stomach contents shifted from ungulates to small mammals in March. Percent of coyote stomachs

containing deer was 64% in January, 72% in February to March 10, and 27% in March to early April.

Mountain Lion Manipulation and Demographics

Mountain Lion Removal

Removal rates for mountains lion varied across years and GMUs. Removal rates of mountain lions in combined liberal harvest (treatment) GMUs were greater than in conservative harvest (reference) GMUs during 1998-2001, but returned to previous levels in 2002 (Table 7). Mountain lion removal/1,000 km^2 in GMU 73A was 2 to 6 times greater than observed in GMU 56 (Table 8). Quotas were not met in any of the treatment GMUs from 1999-2002 and harvest seasons remained open through 31 March, essentially functioning as an unrestricted, 7-month harvest season. Proportionately high adult female harvest (>25% of total harvest) indicated a high harvest rate in treatment GMUs (1998-2000), except GMU 71. Female quotas were met in the reference GMUs resulting in season closure prior to March 31. Female mountain lion quotas were set to obtain a target harvest of 3/1,000 km^2 for the 2003 to 2006 study period in Study Area 2. Mean lion removal density was 3.13 (SE = 0.326), 2003-2005.

Mountain Lion Population Index

Lack of consistent snow conditions on our study area reduced usefulness of track surveys as a reliable index for mountain lions. Wind and warm temperatures melted fresh snow and snow rarely persisted the 48 hr required for this approach. Snow conditions were favorable in 1998, 1999, and 2001 (Table 9); however, low track encounter rates and a minimum number of completed transects precluded use of this index for rigorous comparison of populations. Index values from track transects in 1999, however, reflected increased mountain lion harvest in that year in GMU 73A. Track transects in 2001 and harvest summaries in 2002 indicated lion populations in liberal harvest GMUs had returned to pre-treatment levels.

Alternate Prey Abundance

Small Mammal Abundance

Small mammals (primarily *Peromyscus maniculatus*) were most abundant in 1998 and in 2002. Catch rates were lower along the low elevation transects in 1999-2001 (Table 10). Our highest catch rates occurred in the low elevation sagebrush type in 2002.

Lagomorph Abundance

We observed peak lagomorph index values in 1999 followed by the lowest population levels in 2000 (Table 11).

Mule Deer Capture and Pregnancy

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 (Table 12). Four 6-month-old fawns and 2 adult females died of capture-related injuries.

We collected blood from 95 adult does, 12 yearling does, and 4 female fawns within GMUs 56 and 73A in 1998. Blood serum was analyzed for pregnancy and disease profiles. During 1998, pregnancy rates were 98%, 83%, and 0% for females ≥ 2 years old, 1.5 years old, and fawns, respectively. In 1999, we sampled blood from 57 adult and 11 yearling does in 4 GMUs across Study Area 1 (GMUs 54, 56, 71, and 73A) and pregnancy rates were 91% for females ≥ 2 years old and 100% for yearlings. Serologic profiles were completed for 135 adult females (>1 year-old) within Study Area 1 and for 58 adult females in 4 other mule deer populations in central and southern Idaho. Disease prevalence (proportion positive for exposure) for GMUs within the study area are reported as disease = study area value (range of 4 other populations). Diseases documented in the study area and other areas in Idaho included; Anaplasmosis = 0 (range 0-0.76), Bluetongue = 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 (0-0.38), PI3 = 0.27 (range 0.33-0.88). Disease prevalence of mule deer in the study area was in the lower portion or below the ranges of other populations in Idaho with the exception of BRSV.

Mule Deer Mortality Causes

Cause-specific Mortality

Mortality causes pooled across 1998 -2002 varied between treatments and age classes (Table 13). Mortality-cause distributions were different between treatment and reference areas for fawns in both summer ($\chi^2_7 = 14.18$, $P = 0.048$) and winter ($\chi^2_7 = 13.86$, $P = 0.054$). In summer, total mortality and mountain lion-caused mortality was lower in the treatment area. Whereas, coyote-caused mortality was lower in the treatment area in winter. Mortality-cause distributions were not statistically different between treatment and reference GMUs for adult females in summer or winter ($P > 0.10$); however, mountain lion-caused mortality was lower in the treatment area during both seasons (Table 13). Coyote-caused mortality accounted for <1% of annual adult female fates (Table 13) and was not related to coyote removal treatment.

Mule Deer Survival Models

Neonate Fawns

Mass gain of neonates was significantly different among years ($F_{4, 225} = 3.67$, $P = 0.007$). Therefore, a different regression equation was calculated for each year to predict mass at age 4 and remove annual variation in growth rates (Figure 3).

During summer, survival 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 all years were combined (Figure 4). No best model explained survival of neonates for the reference area (GMU 56; Table 14). Ten models were competing (Δ AIC <2), all with AIC weights < 0.142.

The model with the lowest AIC suggests above average summer precipitation or below average previous winter precipitation (combined precipitation) and higher small mammal density will increase survival, but the risk ratio confidence intervals (95%) overlap 1 (Table 15).

Four competing models containing density of lagomorphs, coyote removal density, and presence of siblings provided significant explanations for neonatal mule deer survival in the treatment area (Table 14, Table 15). None of the risk ratio confidence intervals of the 4 parameters estimated in best model overlapped 1, indicating all contributed significantly to the model. This model predicts fawn survival will improve with increased coyote removal and increased lagomorph density. Survival will decrease with presence of siblings and higher precipitation levels in the winter preceding birth.

Six-month-old Fawns

Mass of 6-month-old fawns was greater for males ($F_{1, 269} = 32.80$, $P < 0.001$) and different between years ($F_{4, 266} = 5.26$, $P < 0.001$), but was not different between study areas ($F_{1, 269} = 1.20$, $P = 0.263$) (Table 16). A significant interaction of year and study area ($F_{4, 266} = 3.46$, $P = 0.009$) suggests the pattern of mass difference varied between study areas and years. Mass for all combinations of year, sex, and GMU did not change over the capture period ($F_{4, 266} = 0.50$, $P = 0.735$). Because mass did not change over time, measured mass at capture was used 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 all years were combined (Figure 5). One 3-parameter and two 4-parameter models yielded competing explanations for survival of 6-month-old-fawns in the reference area (Table 14). The significant parameters in these models included mass, lagomorph density, and combined precipitation (Table 17).

Additionally, there were 2 competing models explaining survival of 6-month-old fawns for the treatment area (Table 14). Mass, combined precipitation, sex, and lagomorph density or density of coyotes removed were important predictors of survival (Table 17). In all models of winter fawn survival, below average summer precipitation and above average winter precipitation (combined precipitation) decreased survival, higher mass increased survival, and female survival was higher than males. Contrary to expected results, increased lagomorph density or increased coyote removal predicted lower fawn survival.

Adult Females

Survival of adult female mule deer during summer was ≥0.93 in all years and study GMUs. During summer, adult female survival in the reference GMU (S = 0.950, SE = 0.015) was not significantly different ($\chi^2_1 = 1.33$, $P = 0.242$) from the treatment GMU (S = 0.970, SE = 0.009) when all years were combined (Figure 6). Precipitation in the previous winter was the best predictor of adult female survival in the reference area (Table 14, Table 18).

Two 3-parameter models explained survival in the treatment area (Table 14). Age was a highly significant predictor of survival ($P < 0.001$) for GMU 73A (treatment), but not for GMU 56 (reference; Table 18). The significance of age may be related to shifts in age structure resulting

from increased survival. Both lagomorphs and precipitation or previous precipitation were also included in the models for the treatment area.

During winter, adult female survival in the reference area (S = 0.932, SE = 0.017) was not significantly different (χ^2_1 = 0.583, P = 0.463) from the treatment area (S = 0.945, SE = 0.026) across years (Figure 7). Low previous summer precipitation combined with high winter precipitation was the best predictor of survival in the reference area (Table 14, Table 19). The best model for winter survival in the treatment area suggested survival of adult females increased with mountain lion removal and decreased with deer age over 5.5 years (Table 19).

Changes in Mule Deer Population Demographics

Neonate Fawn-at-heel Ratios

Based on June fawn-at-heel ratios, we believe twinning rates were high in GMUs 56 and 73A (Table 20). Ratios were similar between the treatment (73A) and reference (56) GMUs in 1998-1999. Observed ratios were lower during 2000-2002 in the treatment area, although only significantly lower (P < 0.05) in 2002.

Fawn-to-doe Ratios 1997-2002

Fawn-to-doe ratios (FDR) were calculated for each study area and each year of the study (Table 21). Ratios varied from 0.322 (SE = 0.029) to 0.839 (SE = 0.048). Average FDR across all surveys was 0.588 (SE = 0.013).

Factorial experimental designs are very sensitive to unbalanced factorial combinations. For this reason, only data from 1999 to 2003 were used in the analysis of deviance (ANODEV) (Table 21). Significant interactions between coyote and mountain lion removal treatments and between removal treatments and years of study were identified by a weighted ANODEV (Table 22). Treatment and year-by-treatment interactions were not conducive to simple interpretation or summary of the results. The widely varying pattern of effects might be partially explained by inconsistent levels of predator removal within treatment designations (Table 23).

Instead of including treatments at fixed levels as above, our model-based analysis uses actual predator removal densities to investigate relationships between FDR and predator removal. The analysis was hierarchical, first adjusting FDR for year and site effects prior to examining effects of predator removal. Year effects could be accounted for by using either an indicator variable or precipitation data considered important to fawn survival and adult fecundity. While year indicators explained 43% of the overall variability in FDR; summer precipitation, previous winter precipitation, and their interaction explained 41%. Summer precipitation ($F_{1, 27}$ = 8.05, P = 0.009) and previous winter precipitation ($F_{1, 27}$ = 5.91, P = 0.022) had significant negative effects on FDR, while a positive interaction existed ($F_{1, 27}$ = 14.43, P = 0.001). Because they were biologically meaningful, precipitation variables were subsequently used in lieu of year effects for modeling changes in FDRs.

Using an unweighted ANODEV, we observed no effect associated with coyote removal (P = 0.439, 1-tailed), whereas mountain lion removal had a significant positive effect (P = 0.018,

1-tailed) on FDRs (Table 24). Similarly, using a weighted ANODEV to account for sample precision, coyote removal ($P = 0.314$, 1-tailed) had no effect on FDR, but mountain lion removal had a significant positive effect ($P = 0.066$, 1-tailed) on FDR (Table 25). There was no significant interaction between coyote and mountain lion removals ($P > 0.72$) in either analysis. Hence, conclusions are robust whether FDR were weighted to account for sampling precision or not.

A residual analysis from the unweighted ANODEV indicates 7 of 40 observations (17.5%) had residuals with significant model deviation at $\alpha = 0.05$. Nominally, 5% of standardized residuals would have values greater than ± 2 (i.e., 2 of 40 observations). Therefore, there is some indication of lack-of-fit of the unweighted model ($\chi^2 = 8.42$, $P = 0.004$) to the data. Only 1 of 40 observations from the weighted ANODEV had a residual greater than ± 2. Therefore, the weighted model is the preferred interpretation.

Scatterplots illustrate effects of removing varying amounts of coyote or mountain lion density (Figure 8). As removal of mountain lions increased, FDR increased significantly, regardless of whether coyotes were removed ($P = 0.089$, 1-tailed; Figure 8d) or not ($P = 0.063$, 1-tailed; Figure 8c). Conversely, as removal density of coyotes increased, FDR did not increase significantly, regardless of whether mountain lions were removed ($P = 0.161$, 1-tailed; Figure 8b) or not ($P = 0.54$, 1-tailed; Figure 8a).

The weighted ANODEV estimates a vulnerability coefficient of $C_L = 0.01688$ for mountain lion predation. Hence, the FDR is expected to be modified by mountain lion removal by the quotient

$$e^{0.01688(\text{LRD})}.$$

Fawn-to-doe Ratios 2003-2006

Plots of coyote removal density profiles over time for each location indicate the high and low treatment sites segregate as expected (Figure 9). Nonetheless, removals for the medium-treatment level were less accurately applied and less consistent over time (Figure 9). This imperfect treatment application would add unacceptable variability in an analysis of variance where the independent variables are assumed to be sampled without error. To remedy the situation, only the 6 sites in the high and low treatment categories were used in the design-based analysis.

The 2-way ANOVA, adjusted for previous winter fawn survival (FS) ($F_{1, 11} = 2.34$, $P = 0.077$, 1-tailed) indicated FDR was not significantly different between coyote removal density (CRD) treatment levels ($F_{1, 11} = 0.008$, $P = 0.465$, 1-tailed), or years ($F_{2, 11} = 0.619$, $P = 0.556$); there was no treatment × year interaction ($F_{2, 11} = 0.848$, $P = 0.455$). An interaction plot indicates FDRs were lower in 2004, but there was no consistent pattern between treatment levels over time (Figure 10).

From this design-based analysis, one cannot conclude that coyote removal had a statistically significant effect on observed fawn-to-doe ratio. The variability in coyote removal application within a treatment could still be masking differences in FDRs. For this reason, a model-based

analysis using site-specific and year-specific CRD values was also performed. Considering single-variable models, only fawn survival of the previous year (FS) was significantly correlated with FDR ($F_{1, 22}$ = 3.75, P = 0.066). Neither winter precipitation (WP) (P = 0.380) nor summer precipitation (SP) (P = 0.278) was correlated with FDR. Therefore, only FS was incorporated in the hierarchical regression model. Subsequently, adding lion removal density (LRD) to the model was not significant (P = 0.906), due to the low, constant effort applied over time and locations.

Adding CRD to this hierarchical model (Table 26) resulted in CRD being weakly related to FDR ($F_{1, 21}$ = 1.72, P = 0.1019, 1-tailed). The fitted model was:

$$\ln \text{FDR} = \underset{(SE=0.1748)}{-0.4051} - \underset{(SE=0.2400)}{0.3811 \text{ FS}} + \underset{(SE=0.0009122)}{0.001196 \text{ CRD}}$$

The regression model indicates as the CRD increases, so does the FDR, consistent with the working hypothesis. Over the range of CRDs observed (0, 126.8), the FDR was estimated to increase by a factor of 1 to 1.16. Location effects were not statistically significant after adjusted for CRD (P = 0.206). The FS-plus-CRD model, however, explains only 21% of the total variability in fawn-to-doe ratios.

Population Rate of Change

Deer populations generally increased across the study area from 1997-2001 (Figure 11, Table 27). Populations in several study GMUs were severely impacted by a dry summer in 2001 followed by above average winter snowfall. Populations in the southernmost GMUs (56, 73 Elkhorn, and 73 Malad) declined 43-53% in 2002 (Table 27).

Mean rate of change for all deer populations in the study area from 1993 through 2003 was r = -0.019 (n = 63, SE = 0.134, range = -0.459 to 0.263) implying an overall finite rate of change of 0.98. The extremely variable annual rates of change in some of these populations complicated analyses. The population estimates in GMU 54 implausibly decreased 50% in 1 year (r_t =-0.36 from 1999 to 2000) and increased to previous levels the next year (r_t = 0.25 from 2000 to 2001; Table 27). In these instances, deer likely truncated their migration due to light snow conditions and wintered on transition range, outside of the survey area. This assessment is supported by observations that highest population estimates occurred during years of heavier snowfall. Therefore, we replaced 3 extreme decreases with average rates of change over 2-year intervals to eliminate the apparent impact of these behavioral changes on annual rates of change.

We observed declining average population trends (approximately -2.1%/year) in all GMUs before predator manipulation as well as in GMUs where predators where not removed during the study (Table 26). However, the rates of increase were opposite in the 2 reference GMUs; one increasing at 12% per year through 2001, the other declining at 10% per year through the study period (Figure 11). Deer herds in GMUs treated with either coyote control or mountain lion removal alone maintained a similar overall declining rate of increase. Only when both mountain lions and coyotes were removed was the trend reversed, producing an average positive rate of increase of 1.8% per year (Table 26). If coyote- and mountain lion-caused mortality were

additive, the expected rate of population increase when both were removed would have been only 0.8% in contrast to the observed rate of 1.8%. Regardless, rates of change in deer populations were not statistically different and treatments predicted only 5.4% of variation in growth rates. This a priori factorial analysis does not adequately explain the variance inherent in growth patterns of mule deer populations. As in this study, variable rates of increase across areas and extreme weather-related population reductions are common. We believed an a posteriori regression analysis would be more appropriate.

Regression analysis (ANCOVA) of mule deer population rates of increase with measured removal rates of coyotes and mountain lions also yielded a non-significant model ($R^2 = 0.05$, $F_{2, 64} = 1.65$, $P = 0.20$). Removal rate of mountain lions positively influence rate of increase ($t_{64} = 1.54$, $P = 0.064$, 1-tailed), but we observed no effect of coyote removal ($t_{64} = 0.481$, $P = 0.316$, 1-tailed).

Effect of winter severity was incorporated by performing analysis of covariance testing predator removal effects while using a winter severity index (WSI) as a covariate. The significant model ($F_{3, 63} = 4.37$, $P = 0.007$) explained 17% of the variation in mule deer population rates of increase. The WSI was highly correlated with die-offs ($t_{63} = 3.06$, $P = 0.003$) in severe winters, but the analysis of covariance did not substantially change results from the ANOVA described previously (Table 26). Neither coyote removal ($t_{63} = 0.92$, $P = 0.361$) or mountain lion removal ($t_{63} = 0.70$, $P = 0.487$) were significant when WSI was added as a covariate. The change in coefficients indicates that mountain lion removal was correlated with winter severity.

Discussion

Predator Manipulation

Coyote Removal

Effectiveness of coyote removal was variable temporally and spatially during the study period, as influenced by snow conditions, aircraft availability, effort, and methods. Aerial coyote removal was most effective during periods with 100% fresh snow cover. Unfortunately, availability of personnel and helicopters often did not coincide with optimal snow conditions. The result was differential removal of coyotes among treatment areas (study GMUs) and years. We mitigated for this variability by increasing ground removal efforts in spring and summer. Ground efforts were concentrated within fawning areas where neonates were especially vulnerable (Knowlton 1976). Different removal rates between treatment areas and among years prompted us to prefer a model-based analysis over the design-based analysis intended for the study of recruitment and mule deer population growth.

Coyote Food Habits

Analysis of coyote stomach contents indicated a significant switch from ungulate prey to small mammals in the last 2 weeks of March. This switch coincided with the emergence of ground squirrels (*Spermophilis* spp.) and increased vulnerability of other rodents due to snow melt. This prey switching pattern from mule deer to ground squirrels was also documented by Lingle (2000). February and March exhibited the highest coyote-caused mule deer mortality, but that

source of mortality declined significantly in April and May. Prey switching appears common in coyotes depending on primary prey density (Prugh 2005) or prey vulnerability (Patterson et al. 1998).

Coyote Demographics

Researchers have documented a direct positive relationship between coyote abundance and lagomorph abundance (Hoffman 1979, Todd and Keith 1983, Knowlton and Gese 1995). Clark (1972) reported that changes in coyote density in and adjacent to GMU 56 were correlated with density of black-tailed jackrabbits (*Lepus californicus*). He suggested a causal mechanism in which coyote reproductive rates (litter size and percentage of breeding females) increased in response to increased jackrabbit density. Increased density of staple prey likely resulted in immediate increases in coyote populations due to greater survival of young, young staying with the packs, and greater tolerance of transients during breeding seasons (Knowlton and Gese 1995, Gese 1995). This evidence suggests coyote populations followed the pattern of our lagomorph index and prey switching likely influenced mule deer survival and population growth results of this study.

Mountain Lion Removal

Mountain lion removal was variable in liberal harvest GMUs during the study period because of hunter behavior and success rates. 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 73A during 1998-1999, attesting to the high harvest rate. Adult female harvest exceeded 25% of total harvest by 2000 and declined in 2001-2002 indicating a high harvest rate in all treatment GMUs for 1998-2000, except GMU 71 (Anderson and Lindzey 2005). As mountain lion populations decreased, hunting became more difficult and hunting pressure declined during the 2000-2002 general harvest seasons. Harvest was further reduced due to poor snow conditions and hunter success in 2000 and 2001. Lindzey et al. (1992) observed a mountain lion population recover to pre-removal numbers within 9 months after removal ceased. The reduced number of mountain lions removed in the liberal harvest GMUs during the last 2 years of the study probably resulted in population recovery by 2002.

Pregnancy and Disease Factors

Pregnancy rate of adult and yearling females was high in the study areas. These rates are higher than most reported for similar habitats (Robinette et al. 1977, Anderson 1981). Fawn-at-heel ratios were also higher than most reported fetal rates (Anderson 1981). Therefore, observed below average recruitment rates in the study area were not likely a result of low pregnancy or fetal rates in these populations.

Low incidence of death caused by disease among fawns or adults and normal serology values, indicated these agents were not limiting mule deer populations in this area. Antibody prevalence for Anaplasmosis, Bluetongue, and Epizootic hemorrhagic disease were lower within the study area than prevalence reported by Chomel et al. (1994) and Hoff et al. (1973).

Deer Survival Factors

Factors Affecting Neonate Fawn Survival

Fawn body mass prior to winter is a good predictor of survival to recruitment (Bartmann et al. 1992, Unsworth et al. 1999, Bishop et al. 2005). Rate of mass gain was highest in 1998 when total summer precipitation was nearly twice that of other years. Rate of mass gain of neonates is dependent on doe nutrition and behavior (Robbinette et al. 1973), suggesting does in 1998 were on a higher nutritional plane than in other years. Thus, above average precipitation during the growing season should positively influence survival of fawns (Knowlton 1976). Conversely, exposure during cold, wet weather at birth can increase neonate mortality (Gilbert and Raedeke 2004, Pojar and Bowden 2004).

Overall neonate survival was higher in the treatment area than the reference area. Factors that influenced neonate survival to 6 months of age in the reference area (GMU 56) were summer and previous winter precipitation, birth mass, and density of small mammals. Even though these models were not significant, hazard ratios suggested that the factors affected survival as we hypothesized (Table 15). Higher growing season precipitation, lower winter precipitation, higher birth mass, and higher small mammal density all increased neonate survival. Weather conditions often will change prey vulnerability, density, or distribution, which may explain the lack of a significant model pattern. Hamlin et al. (1984) noted vegetation production and winter snow cover may have regulated microtine populations and were thereby changed coyote predation rates of fawns.

Factors influencing neonate survival in the treatment area (GMU 73A) differed markedly from the reference area, possibly related to perturbations of the predator-prey ratio caused by predator reduction. Coyote removal density, lagomorph density, and number of siblings best explained neonate survival in this area. Increased density of coyotes removed, higher density of lagomorphs, and lower number of siblings increased fawn survival. Decreasing coyote density likely changed the coyote-primary prey ratio, possibly reducing the need for alternate prey, such as mule deer. Previous research has highlighted the importance of coyote-primary prey ratios to prey selection and survival of ungulates. Todd and Keith (1983) reported snowshoe hare (*Lepus americanus*) abundance explained 94% of the variation in coyote food habits. Abundance of snowshoe hare influenced the rate of coyote predation on white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada (Patterson and Messier 2000). Hamlin et al. (1984) noted that fawn mortality attributed to coyotes was lowest when microtine rodent populations were high. Prugh et al. (2004) observed the ratio of Dall sheep (*Ovis dalli*) killed per coyote did not change as coyote populations increased with increasing snowshoe hare abundance, but resultant increase in the coyote population led to a greater number of sheep killed. This body of research suggests a plausible explanation for the difference in importance of lagomorph density between survival models in reference and treatment areas. Because coyote and lagomorph populations may be highly correlated (Clark 1972, Hamlin and Mackie 1989, Knowlton and Gese 1995), the predator-prey ratio remains similar at all levels of lagomorph abundance until coyote removal changed the ratio. Thus, the benefits of increased primary prey abundance to fawn survival would not be realized until a reduction in coyote populations increased the available food items per coyote. In the absence of coyote removal, fawn survival would likely be influenced by other primary prey populations (e.g., small mammals), as we observed in the reference area. Increased

survival of single fawns may be explained by decreased competition for resources (milk) or more effective predator defense of a single fawn by the adult doe (Wenger 1981).

Inspection of observed predation rate on neonatal mule deer revealed some interesting patterns when viewed in relation to primary prey of coyotes. Coyote removal increased survival of neonates when the lagomorph index was high and the small mammal index low or vice versa. When both lagomorph and small mammal indices were high, survival of neonates was high and coyote removal had little effect on survival of young deer. When primary prey populations were low, survival of neonates was low and coyote removal did not increase survival. This is contradictory to expected, even though removal rate was high (94/1000 km^2). They scarcity of primary prey may have increase coyote dependence of mule deer fawns, thereby cancelling the effect reduced coyotes density. We hypothesize that coyote populations fluctuate with their main prey items, lagomorphs and small mammals, and when one of these prey populations are reduced, coyotes switch to deer fawns as alternate prey. Hoffman (1979) reported similar prey switching patterns within the south portion of the reference area and adjoining northern Utah.

Predicting Neonate Survival

We used models created in the survival analysis to estimate effects of each factor for the range of values observed in our study. By nullifying other parameters (setting variable values to 0) within significant models, we estimated the percent change in survival from baseline survival rate as influenced by the factor of interest.

In the reference area, low previous winter precipitation and high summer precipitation levels increased survival of neonates. We predicted precipitation combinations increase survival by 32% or decrease survival by 30% from baseline or average survival. The models further predicted that fawn survival would increase by up to 49% when small mammal populations were at observed maximum. This outcome suggests that vigorous small mammal populations and favorable weather conditions will increase neonate fawn survival in areas without active coyote removal.

Our best neonate fawn survival models for the treatment area included lagomorph abundance and coyote removal density. Interruption of the coyote-lagomorph ratio though coyote removal appeared to influence fawn survival. At our highest lagomorph index, we predicted fawn survival would increase 57%. The coefficient estimated for coyote removal density within this model predicted fawn survival from 0.86 to .98 for the observed range of coyote removal density (53 – 126 coyote removed/1000 km^2) in the treatment GMU. These survival estimates are considerably higher than the observed range of survival (S = 0.20 to0.77). Even though this coefficient and the parent model were significant, this outcome indicates a poorly fit model. Data inspection revealed a 15% increase in fawn survival, explained by changes in coyote caused mortality, if one of the coyote main prey populations (lagomorphs and small mammals) was high and the other was low. This prey combination occurred in 2 of 5 years.

Factors Affecting Survival of Fawns in Winter

Factors influencing fawn survival in winter were the same in the reference and treatment areas. In order of importance, these factors were previous summer precipitation, early winter mass,

winter precipitation, and lagomorph density. Higher summer precipitation, greater mass, and lower winter precipitation increased survival as hypothesized. Interestingly, the lowest survival we observed during the winter did not coincide with extremes in winter precipitation. During the year with the highest winter mortality, previous summer precipitation was the second lowest recorded, but winter precipitation equaled the median for all 5 years. Years with higher winter precipitation were associated with high precipitation during the previous summer indicating summer fat deposition may have mitigated severe winter weather conditions. Total season winter precipitation (1 Oct-15 Apr) used in this research may mask important time periods within winter season. For example, November and December snowfall and minimum temperature are important predictors of overwinter fawn survival (Bartmann et al. 1992, Hurley et al. *In Prep*). Contrary to our hypothesis, increased lagomorph density estimated during the previous summer-autumn resulted in predictions of decreased fawn survival. This relationship may have reflected increases in coyote population resulting from increased lagomorph food base. Several researchers have documented an increase in winter coyote populations with greater lagomorph density during the summer-autumn due to improved survival of young and decreased dispersal (Clark 1972, Knowlton 1976, Hoffman 1979, Messier and Barrette 1982, Prugh 2005). The ineffectiveness of predator removal on winter fawn survival in our study indicated we did not appreciably alter the predator-fawn dynamics in winter with predator removal, or coyote-caused mortality being compensatory during years when precipitation levels severely reduce fawn survival. Interestingly, significant factors in survival of fawns were different from the pooled cause-specific mortality presented in Table 13. This suggests that annual patterns in survival and treatment effects are not adequately explained in composite cause-specific mortality analyses.

Predicting 6-month-old Fawn Survival

Models of winter fawn survival were similar in both treatment and reference areas. Combinations of precipitation values predicted survival would increase ≤20% with a wet summer and dry winter or decrease ≤77% with a dry summer and wet winter. Models predicted a 16% increase in survival if fawn mass increased 4.55 kg, which was the maximum average difference between years. The predictions estimated from these models reaffirms the most important factors related to winter fawn survival are growth and fat deposition in summer-autumn and energy expenditure in winter-spring.

Factors Affecting Adult Survival in Summer

The most influential factor on adult survival in the reference area during summer was previous winter precipitation. Following severe winters, during which we observed high rates of juvenile and adult mortality, adult females continued to die from malnutrition into May and early June. In the treatment area, the best predictor of survival was age, followed by lagomorph density. Older adults died at a higher rate from both predation and other natural causes. Adult female survival increased as lagomorph numbers increased, indicating mountain lions may have been killing snowshoe hares and white-tailed jack rabbits (*Lepus townsendii*) as alternate prey.

Factors Affecting Adult Survival in Winter

Precipitation during the previous summer and current winter influenced adult female survival in the reference area. Low previous summer precipitation and high winter precipitation decreased

survival. Bender et al. (2007) also reported decreased condition and annual survival of adult female mule deer when growing season precipitation was below average. In the treatment area, age and mountain lion removal were significant predictors of adult survival. Upon predator population manipulation, a combination of mountain lion removal density and alternate prey density interact to influence annual adult mule deer survival. When predator populations are not manipulated, the influence of alternate prey appears secondary to precipitation levels. Deer typically dominate mountain lion diets, but prey switching is probable given the wide variety of prey items included in typical diets: lagomorphs, rodents, mesocarnivores, and vegetation (Robinette et al. 1959, Hornocker 1970, Toweill and Meslow 1977, Ackerman et al. 1984, Hemker et al. 1984). Spalding and Lesowski (1971) reported mule deer were the predominant food item of mountain lions in south-central British Columbia, but took advantage of alternate food sources when locally abundant, including snowshoe hares, moose (*Alces alces*), and domestic livestock. In southeastern Arizona, lagomorphs were the most numerous prey item killed by mountain lions and the importance of lagomorphs to mountain lion diets was often underestimated (Cunningham et al. 1999). Effects of age may be related to vulnerability to predation as indeed many researchers have found that mountain lions kill older deer of both sexes disproportionate to availability (Robinette et al. 1959, Hornocker 1970, Spalding and Lesowski 1971, Ackerman et al. 1984).

Increased mortality related to adult female age in the treatment area was likely a function of decreased mountain lion-caused mortality earlier in the study. To illustrate the effect of increased adult survival on age structure, we modeled populations in the intensive study GMUs (56 and 73A) using Leslie Matrices (Leslie 1945). We constructed a pretreatment age structure based on average survival in the reference GMU. Since our survival monitoring did not begin until 1 January 1998, we set 1997 summer survival of both GMUs to the documented 1998 summer survival of the reference GMU. We then held the recruitment in both GMUs constant at the average for the reference GMU, 1998-2002, to isolate the effects of changes in adult survival from changes in fawn survival. We then modeled the populations from 16 May 1997 to 15 May 2002 using the observed survival data of the adult females. Figure 12 includes: (a) the actual K-M survival curves of adult females captured in winter 1998, (b) observed survival of adult females as of 15 May, and (c) the modeled proportion of the adult (≥1 year old) females ≥6 years of age. The survival plots diverge in summer 1998 and converge again in winter 2001. Annual survival of adult females was higher in the treatment GMU, 1998-2000, coinciding with high mountain lion removal. By winter 2001, adult female survival was lower in the treatment area than the reference area. The modeled age structure also diverged at a rate of 2× annually during the same time period and then converges as survival in the treatment area declined. Although, the predicted differences in proportion of senescent adults were small (1.3%), the effect on mule deer populations with over 38% senescent adult females could be significant. The overall effect on the deer population was an initial increase in adult female survival related to mountain lion removal, followed by the development of an older age structure, and culminating in decreased survival in later years during severe weather conditions. Evidence of senescence was observed in 25 out of 59 mammal populations investigated by Gaillard et al. (1994). Senescence, manifested in increased mortality beginning at age 7, has been documented in bighorn sheep (*Ovis canadensis*), roe deer (*Capreolus capreolus*), and isard (*Rupicapra pyrenaica*) (Loison et al. 1999).

The females in the treatment area appeared to be less productive during the last 3 years of the study. Fawn-at-heel ratios were equal between treatment and reference areas during the first 2 years of investigation, followed by a trend toward lower ratios in the treatment area during the last 3 years. The difference, however, was only significant in 2002. This scenario indicates progressively lower fetal rates in the treatment area, possibly due to an increased number of older, less productive females or density-dependent reduction in overall condition of deer. In a summary of 10 investigations, Connolly (1981*b*) reported pregnancy rate and the number of fetuses per doe declined in the older age classes (≥7 years) of mule deer. Adult females in the more rapidly increasing treatment area population may have been affected by density-dependent reductions in body condition and pregnancy rate (Robinette et al. 1973, Stewart et al. 2005) earlier than the reference area.

Predicting Adult Female Survival

In the reference area, precipitation levels were the primary predictors of survival. In our summer models, maximum recorded precipitation during the previous winter would reduce survival 16%. This higher mortality was likely related to body condition of adult females entering the summer period (16 May) after a severe winter and experiencing continued mortality into June caused by malnutrition and stresses of parturition. Changes in winter survival rates based on combinations of previous summer and winter precipitation were predicted to range from +2.6% to -18%.

In the treatment area, increase in age, after a deer was >5.5 years old, was a significant negative predictor of survival. Our models predicted that an age increase of 2 years would decrease survival 4% during summer and 5.3% during winter (9.3% annually). Festa-Bianchet et al. (2003) supports our observation as they documented a 10-15% decrease in survival in senescent age classes of roe deer, bighorn sheep, and mountain goats (*Oreamnos americanus*). A model incorporating the maximum observed lagomorph index predicted a 2.9% increase in summer survival. The additional lagomorph biomass most likely acted as alternate prey for mountain lions. Our models predicted a 5.6% increase in adult female winter survival following the maximum mountain lion removal of 14/1,000 km^2.

Changes in Mule Deer Population Demographics

Factors Effecting Fawn-doe Ratios 1997-2002

We quantified fawn-to-doe ratios as a measure of changes in neonate fawn survival resulting from predator removal treatments and climatic conditions. Caughley (1974) has cautioned against the use of age ratios to explain population dynamics without supporting measures of population performance. Our consistently high summer survival of adults and lack of effect by coyote or mountain lion removal treatments (reference S = 0.95, treatment S = 0.97) provides a constant value for the ratios. Conversely, neonate survival was highly variable and different between reference (S = 0.28 to 0.64) and treatment areas (S = 0.20 to 0.77). These metrics provide a solid framework to interpret fawn-to-doe ratios within our study area. Any change in neonate survival will be reflected in fawn-to-doe ratios.
Among predator removal treatments, only mountain lion removal provided significant predictive value FDRs in all 8 populations. Interestingly, mountain lion removal was not a significant factor in neonate survival. Sample size may be a factor in the survival analysis as mountain lions killed

only 6 (4.5%) of the fawns in the treatment area. In the reference area, 13 (11%) were killed by mountain lions and the overall predation rate was significantly different between the 2 areas. Another way to visualize those data is with a 3-dimensional plot where observed FDRs were plotted against coyote and mountain lion removal densities (Figure 13). FDR values varied approximately 0.05 units as coyote removal density ranges from 0-120 and by approximately 0.15 units as mountain lion removal density ranges from 0-14. The regression model indicates that while a trend in FDR exists with mountain lion removal density, no trend or interaction was detected with coyote removal density.

The vulnerability coefficient estimated with the analysis of deviance predicts that under the average mountain lion removal density ($3.53/1,000$ km^2) we observed across the study GMUs, the FDR would be expected to increase by 6% over no removal. Fawn-to-doe ratios would be expected to increase by 27% at the maximum removal rate we observed ($14.84/1,000$ km^2) over that of no mountain lion removal. For example, a 27% increase in an FDR of 50 would equal 63.5 fawns/100 does.

Precipitation was the most significant factor for predicting fawn ratios. Greater previous winter precipitation and greater summer precipitation decreased FDRs in our study area. This relationship may seem contradictory to findings of increased survival of neonate fawns with increased precipitation, but timing (by months) of precipitation appeared important. Pojar and Bowden (2004) reported that higher June precipitation decreased FDR in Colorado. Similarly, Gilbert and Raedeke (2004), summarizing a 20-year data set on black-tailed deer, observed cold temperatures and high precipitation during the fawning period had a negative impact on fawn recruitment. Median age of fawns captured during this study was 4 days (range 0-19). Thus, our sample of fawns most vulnerable to inclement weather, <4 days old ($n = 74$), was limited. Nevertheless, we verified death due to exposure in 3 of 12 (25%) fawns captured at or near birth sites. Values used in neonate fawn survival and FDR models included precipitation during the entire growing season: 16 April-30 September. We speculate cold, wet weather in June could decrease FDRs, whereas increased precipitation in late summer could increase survival of fawns due to greater nutritional intake by adult females and fawns. For example, following above average winter precipitation that continued into the fawning period and high adult mortality in 2002, we documented the lowest fawn-at-heel ratio (mean = 1.36) in the treatment area, followed by the highest neonate fawn survival ($S = 0.77$) but still resulted in the lowest FDR in December (51 fawns/100 does) recorded for this GMU. The significance of in utero or early fawn mortality to FDRs is evident.

Factors Effecting Fawn-doe Ratios 2003-2006

Following the mule deer population declines in the groups of GMUs selected for this portion of the study, we assumed all of the study GMUs to be well below carrying capacity (K). Summer precipitation levels (8.46 cm 1997-2002 vs. 14.76 in 2003-2006) likely favored an increase in biomass production and K over the previous period. When lion removal effects were nullified in 2003-2006, coyote removal had a positive effect on FDRs. The variability in FDRs, however, is better explained by inherent site differences ($r^2 = 0.5649$) than CRD levels. The model explains 21% of the total variability in FDR and much of that is attributable to the prior year's fawn survival. Considering the model correct, maximum CRD of $126.8/1,000$ km^2 increased the FDR by 16%. Average CRD exerted over the course of the study (i.e., 54.4 coyotes removed/1,000

km^2) would increase FDR 6.7%. For example, if the FDR is 54.0 fawns/100 does under no coyote removal, it would increase to a value to 57.6 fawns/100 does under average coyote removal effort to a maximum of 62.6 fawns/100 does under maximum observed removal effort. The increasing effect of coyote removal on mule deer fawn-to-doe ratios as populations were reduced below K suggests coyote-caused mortality had an increasing additive effect at lower mule deer densities. This conclusion is well supported by Ballard et al. (2001) review of literature. Their summary suggested that the lower a mule deer population is in relation to K, predator removal would more likely increase survival, because mortality in more likely to be additive

Factors Effecting Population Rate of Increase

Weather conditions were the most significant factors explaining mule deer population growth. Incorporation of a winter severity index in the model-based analysis explained 17% of the variation in deer population rate of increase for the 6 years of complete data. Essentially, the WSI-driven model described the outcome for the one year in which we observed severe weather conditions.

The highest rates of mule deer population increase prior to 2002 were in 2 GMUs with high mountain lion removal, one with coyote removal and one without. Data from these 2 GMUs contributed to the results of the model-testing effect of mountain lion removal on deer population rates of increase. The third highest rate of increase, however, occurred in an area where no predators were removed (GMU 56). From 1997 through 2001, average rates of increase were positive in the 3 GMUs where mountain lion removal was effectively increased. Removal of mountain lions from GMU 71 (a designated removal GMU) did not increase over the conservative harvest levels despite liberalized mountain lion harvest regulations. Logan and Sweanor (2001) found that mountain lion predation can suppress deer population growth. Bleich and Taylor (1998) reported predation accounted for > 70% of the known adult female mule deer deaths that mountain lions responsible for 90% of those. Given that mountain lions caused 74% of the known mortality of adult does in our study, any reduction in this mortality cause would have implications for population growth. We observed no relationship between coyote removal and population rate of increase in our research.

Effects of Environmental Conditions and Density on Population Growth

Mule deer populations in southeast Idaho are likely regulated by weather conditions within the context of habitat conditions. In our study area, annual forage quality and quantity is related to summer precipitation. We have shown that summer precipitation and fawn mass are highly correlated and 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). With low summer precipitation, fawns will experience above average winter mortality even in low snowfall winters. We have observed extreme fawn (95%) and adult (30%) mortality rates in winter following low summer precipitation and average winter precipitation. Predators, although a significant mortality agent, were not regulating the populations that we investigated. We observed slight changes in population parameters with predator removal, but not changes in population trend.

The effect of mountain lion removal on population performance provided some insight during our investigation. We demonstrated that mountain lion removal can increase adult female survival and increase fawn-to-doe ratios. Furthermore, we observed a weak, positive relationship between mountain lion removal and deer population rate of increase during the first 4 years of this research. The short term success of improved vital rates should be tempered with observed decline in fawn-at heel ratios and increased mortality of adult females in predator removal areas during the final years of study. We caution that long term (10 years) intensive removal of mountain lions may decrease fitness of a deer population by altering the age structure, thereby decreasing survival, productivity, and ultimately recruitment.

Density-dependent effects on survival and population growth of ungulates has received considerable research effort 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 influence of density on vital rates: juvenile survival, age at first breeding, reproductive rates, and adult survival proposed by previous authors (McCullough 1979, Eberhardt 1985). Festa-Bianchet et al. (2003), however, cautions that many determinations of density dependence may be confounded by changes in adult age structure. Attempts to quantify density-dependent effects in southern Idaho mule deer populations have been difficult due to the annual weather-related changes in K. Even at the lowest measured population levels, precipitation conditions may lower nutritive quality of the habitat below metabolic maintenance levels in summer. To further confound our understanding of density in mule deer populations, typical management action following a population decline is to eliminate adult female harvest, thereby increasing the female age structure. The frequency of weather-related population reductions (~10 years) precludes identification of density-dependent trends in vital rates. However, local density on fawning range appears to exhibit a density dependant reduction in fawn survival as quality fawn-rearing habitat is filled and subdominant females attempt to rear fawns in high risk habitat. The importance of local habitat density has been documented for red deer calves by Coulson et al. (1997).

Compensatory vs. Additive Mortality of Predation

We noted that primary prey densities need to fall within relatively specific levels in order to realize any increase in survival of fawns from birth to 6 months via coyote removal. Specifically, we predict coyote removal will not effect neonate survival unless: 1) lagomorph density is high and small mammal density is low, or 2) lagomorph density is low and small mammal density is high. In either of these situations, coyote predation on neonate fawns appears to be additive, provided mule deer populations are below K, because fawns are required as alternate prey to maintain a relatively high coyote population. Removing coyotes when total primary prey abundance was low did not appear to reduce fawn mortality in our study. Low prey abundance coincided with (or was caused by) drought conditions and fawn mortality from all causes increased. Coyote predation on fawns could be either additive or compensatory in this situation. Coyote-caused mortality is mostly compensatory during years of severe weather conditions, which cause greater than average winter fawn mortality. Even in mild winters, we found that fawns killed by coyotes were in poorer condition than fawns killed by mountain lions. The compensatory nature of coyote predation on mule deer is best explained by the combined mule deer vital and population rates we measured. We documented increased survival of neonate fawns as a result of coyote removal, a slight positive effect on fawn ratios when deer populations

were well below K but not when populations were approaching maximum levels, and were unable to detect an effect of coyote removal in mule deer population rate of increase. This is strong evidence that increased survival of neonate fawns is compensated by other forms of mortality prior to contributing to a measurable 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 high mule deer populations shifted the mortality cause of fawn from coyotes to malnutrition, suggesting a compensatory density-dependent response (Bartmann et al. 1992). Reducing coyote-caused mortality appears to be mostly compensatory in this deer population 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 improved population parameters following mountain lion removal. Although, variable juvenile survival with constant adult survival will often drive population rates of increase (Gaillard et al. 1998), small changes in adult survival will have extreme population consequences. Seven of 9 African ungulate species studied declined primarily as a result of adult survival (Owen-Smith and Mason 2005). They suggested 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 partially compensatory in a longer time frame. The increased age structure and population size realized after reducing predation for several years may increase the vulnerability of adults to predation and weather events.

Management Implications

Mule deer population status has again risen to top priority for state wildlife managers in the West. Predator removal always emerges during the search for management techniques to increase mule deer populations. Professionals and the public will ask questions regarding effectiveness, cost, and probability of success. Our intent was to enable managers to predict the effects of management action or environmental changes on mule deer populations. We attempted to conduct an experiment with tools readily available at temporal and spatial scales relevant to wildlife managers.

Key Findings Related to Coyote Removal

1. Coyote removal increased neonate fawn survival under specific coyote-prey ratios.
2. Coyote removal did not increase winter fawn survival or adult survival.
3. Coyote removal had a weak positive effect on fawn-to-doe ratios when deer populations were below K.
4. Effect of coyote removal on population growth rate was undetectable.

Coyote ecology confounds every attempt to completely understand the effects of their removal on mule deer populations. For example, increased primary prey (lagomorphs and small mammals) of coyotes will reduce the need for mule deer fawns as alternate prey, increasing mule deer survival, but will also increase survival of coyote young and increase the coyote population. If density of a primary prey declines or is unavailable, the greater number of coyotes will need deer as alternate prey. Hence, the same ecological change that increased survival in one season,

may decrease survival in the next. Coyote removal when deer are not needed as alternate prey will not likely be effective. Also, increased fawn survival related to coyote removal during periods of high non-predator mortality, such as dry summers or severe winter conditions, will likely be compensatory.

We noted that coyote removal had the greatest effect on neonate fawns in the summer with average or above rainfall, when fawns were needed as alternate prey, and when deer populations are well below K. Therefore, for maximum effect, coyotes should be removed from fawning-summer range of mule deer in years when density of one primary prey species for coyotes is low, and immediately after a mule deer population reduction.

Cost Analysis of Coyote Removal

To estimate the cost-per-deer produced of coyote removal programs, we deterministically modeled the increase in fawn survival as observed in GMU 73A for 10 years (fawn survival increased 15% in 4 of 10 years). We applied average survival rates for adult females and adult males in typical male-only general season hunt scenario in this area. We then applied the average annual cost of coyote removal for GMU 73A during this study to yield a cost-per-deer-produced estimate. In 10 years, 335 additional deer were added to the population due to increased survival of fawns at a cost of $307 per deer. Focusing specifically on harvestable deer, 65 additional yearling males were produced at $1,581 per deer or six 4-year-old males at $17,093 per deer. The preceding example of coyote removal illustrates the maximum effect, minimum cost scenario under an annual coyote removal program for the conditions we observed. The cost could be decreased by systematically applying coyote removals based on prey populations of coyotes, provided decreased deer mortality was not compensatory. Conversely, the cost would increase if mortality was compensatory. This analysis would only apply if the increased neonate fawn survival produced a measurable effect in population parameters. Given, we measured a weak effect in fawn-doe ratios only when mule deer populations were below K; low population levels would be important criteria in this scenario. Estimated cost could be reduced up to 60% if coyote removal was employed in optimal years (removal increased survival every year); when deer populations below K, primary coyote prey was low, precipitation favored neonate survival (low winter, high summer), and coyote hunting conditions were favorable.

Our aerial coyote removal efforts were curtailed when additional expenditure would not significantly increase removal. Ground removal efforts continued until approximately 1 August. The 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 much touted and often misunderstood 70% coyote removal rate needed to maintain reduced coyote population (Connolly and Longhurst 1975, Connolly 1978*a*, 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.

Key Findings Related to Mountain Lion Removal

1. Mountain lion removal increased adult female survival.
2. Mountain lion removal increased fawn-doe ratios.

3. Mountain lion removal had a weak positive effect on mule deer population rates of increase.

Because mountain lions are obligate predators of mule deer, results of removal were different than with coyotes, an opportunistic predator, as expected. Mountain lion removal at the highest levels we recorded predicted adult female survival to increase 2.8% annually (5.6% winter + 0% summer) and increase fawn-to-doe ratios 27% during less than optimal precipitation conditions. Unfortunately, in an effort to sort out the effects of coyotes during the later study period, we were unable to test the effect of mountain lion removal immediately after a mule deer population decrease.

Cost Analysis of Mountain Lion Control

A cost analysis for the effects of mountain lion removal on mule deer is difficult to assess. Maintenance of effort may be a limiting factor in achieving a target long-term removal rate. The actual removals were conducted by licensed hunters that 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 would not favor paid killing of mountain lions to increase mule deer populations.

Mule Deer Population Ecology and Predator Removal

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. Amount of precipitation, likely related to plant phenology and winter energy expenditure, has 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 weather-related changes in habitat carrying capacity and alternate prey populations. These changes in carrying capacity or increases in deer numbers will ultimately dictate the degree to which predation is compensatory.

The benefits of predator removal appear to be short term when considering mule deer ecology. If predator removal does increase mule deer populations, density-independent effects, such as weather, or density-dependent effects will reduce populations in a short time period. The conditions in which predator removal is effective are stringent and often not predicable prior to the ideal removal period. This is likely why annual predator removal programs are costly and may fail to increase mule deer populations.

through some extremely trying political times. L. Kuck was invaluable in the conception and implementation of this project. Colleagues C. Anderson, B. Compton, M. Scott, D. Meints, R. Smith, H. Miyasaki, A. Seglund, and C. Bishop tirelessly provided field assistance, logistical support, and analytical critiques for the benefit of this project. G. J. Gunnell, J. Muir, P. Nyland, and M. Thomas were excellent field assistants. J. Mulholland, M. A. Clemens, and M. Drew provided wildlife laboratory support. T. Deliberto provided coyote food habits analysis. We thank T. Bowyer, T. Keegan, and G. Pauley for extensive reviews which improved this manuscript. Finally, our deepest appreciation for wildlife pilots D. Savage and C. Anderson for their dedication to quality data and bringing us home every night.

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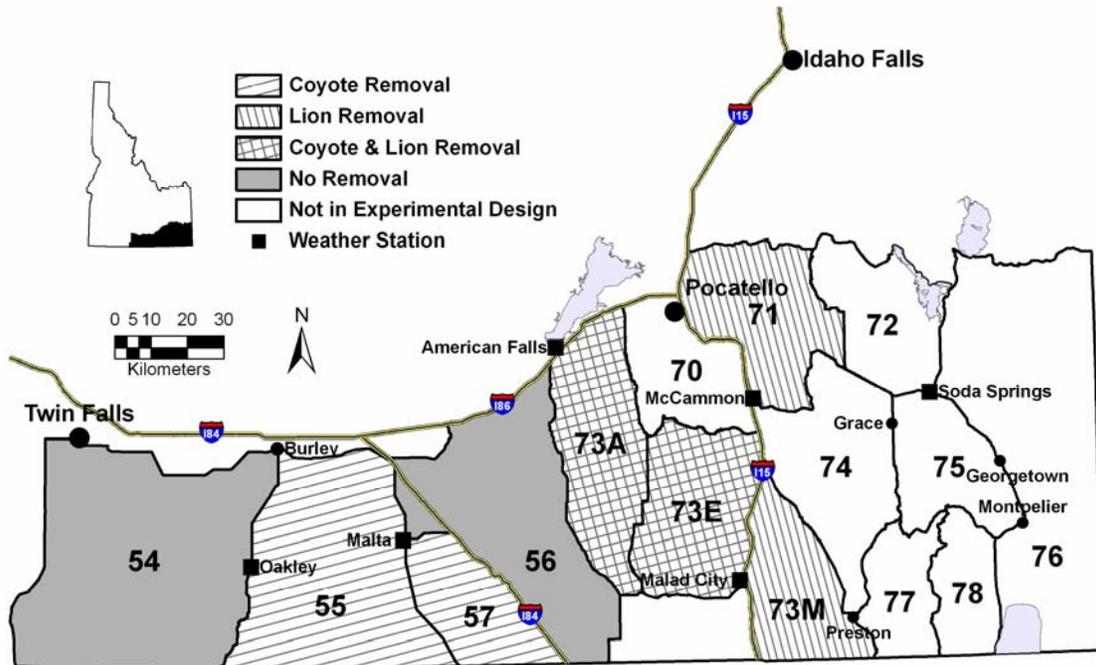
Figure 1a. Study Area 1 in southeastern Idaho where mule deer were monitored under different predator removal regimes, 1997-2002. Labels indicate game management units (GMUs). Intensive study units were GMU 56 and GMU 73A.
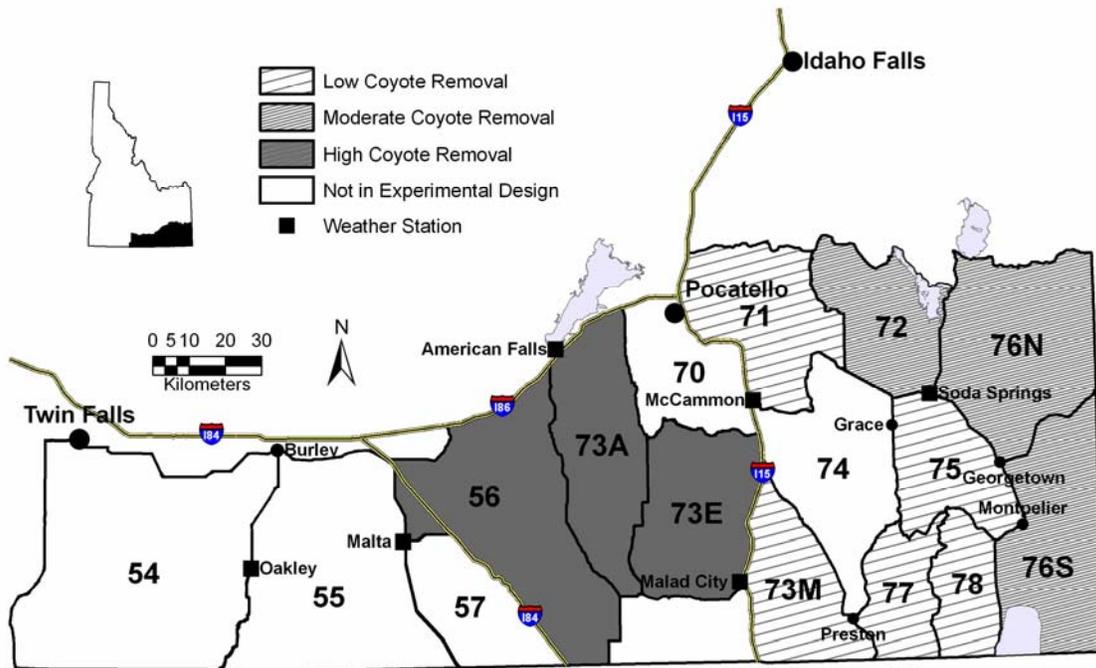
Figure 1b. Study Area 2 in southeastern Idaho where mule deer were monitored under different coyote removal regimes, 2003-2006. Labels indicate game management units (GMUs).
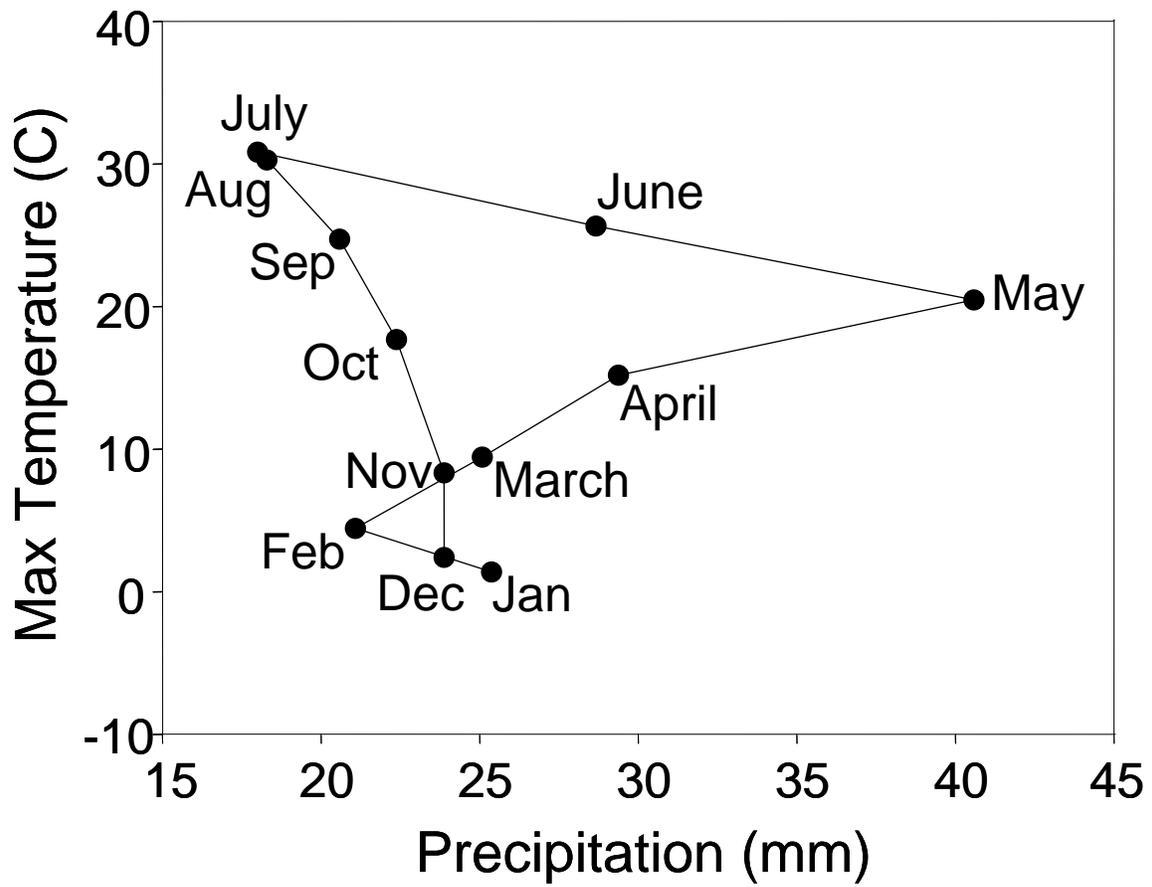
Figure 2. Climograph of study area, southeast Idaho, 1948-2003. Values are a composite of all weather stations in the study area.
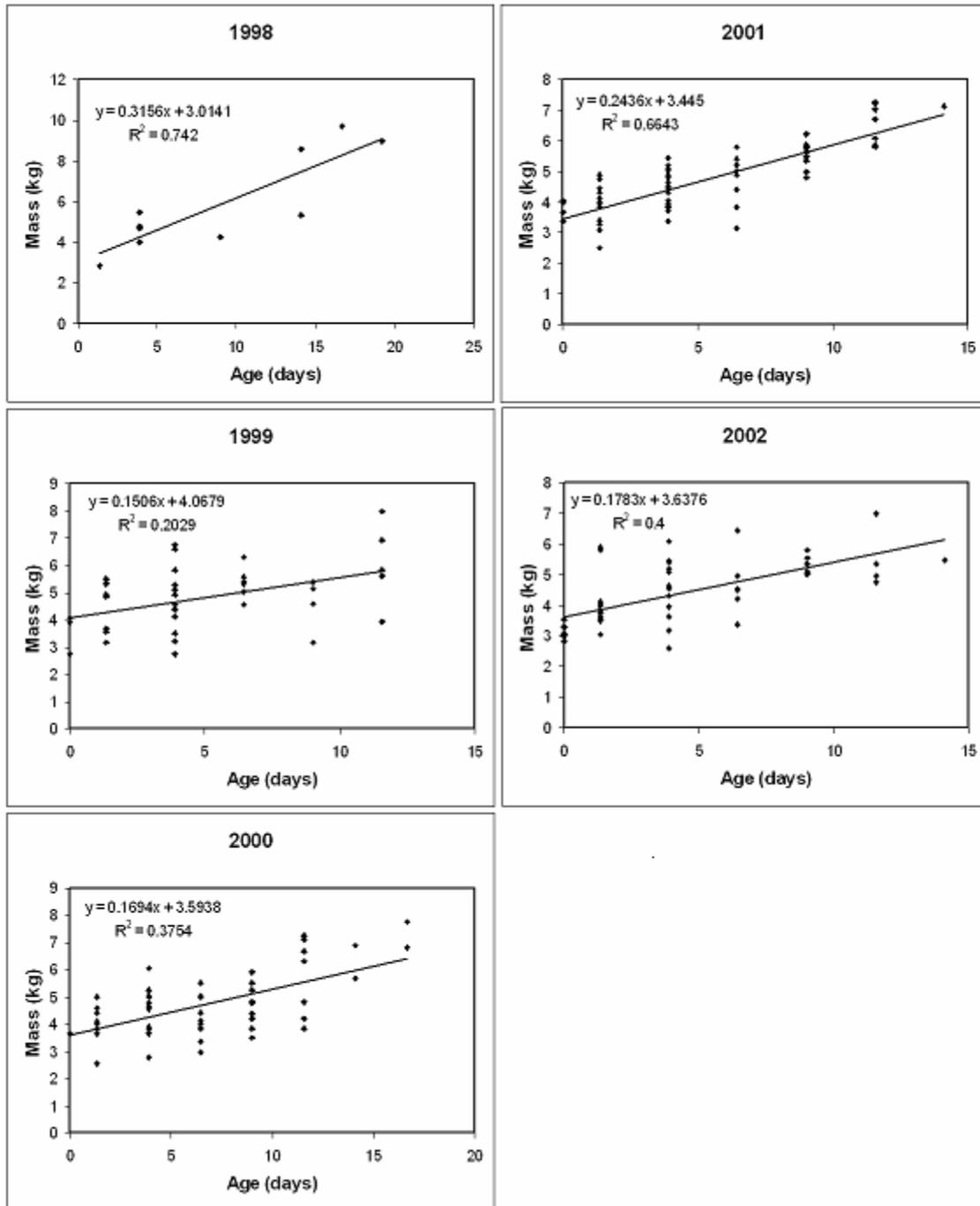
Figure 3. Linear regressions of neonate fawn mass gain versus age for predicting mass at 4 days of age, southeastern Idaho, 1998-2002.
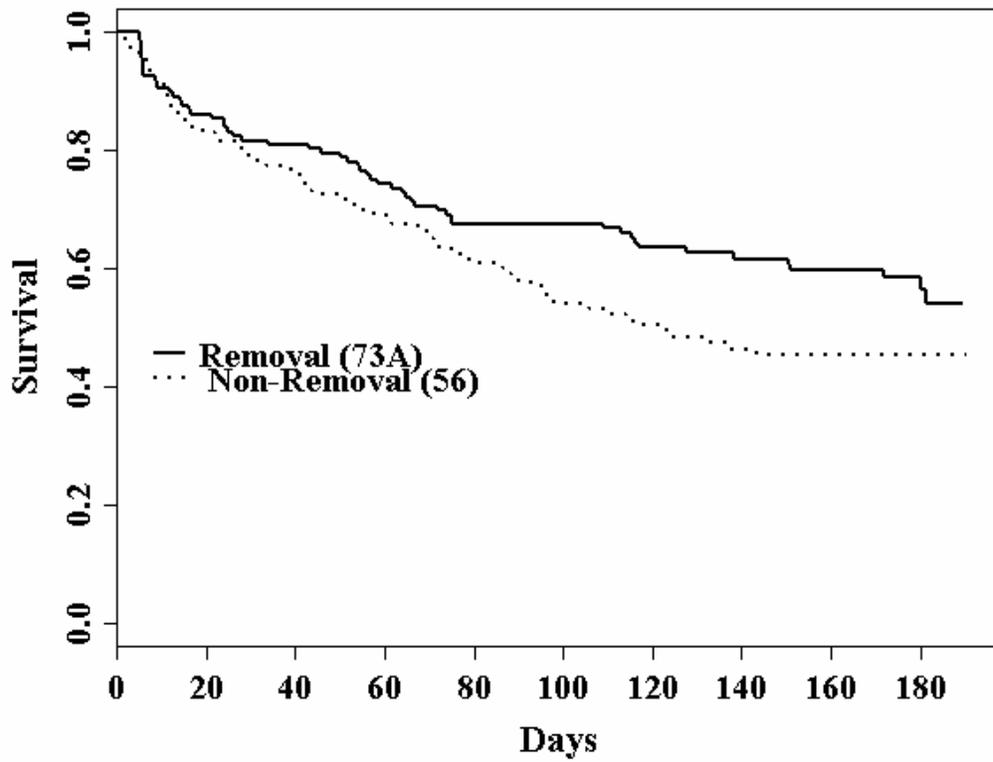
Figure 4. Kaplan-Meier survival curves for neonate mule deer fawns in summer-fall, GMU 56 (reference, *n* = 118) and GMU 73A (treatment, *n* = 132), southeastern Idaho, 16 May to 30 November, 1998-2002.
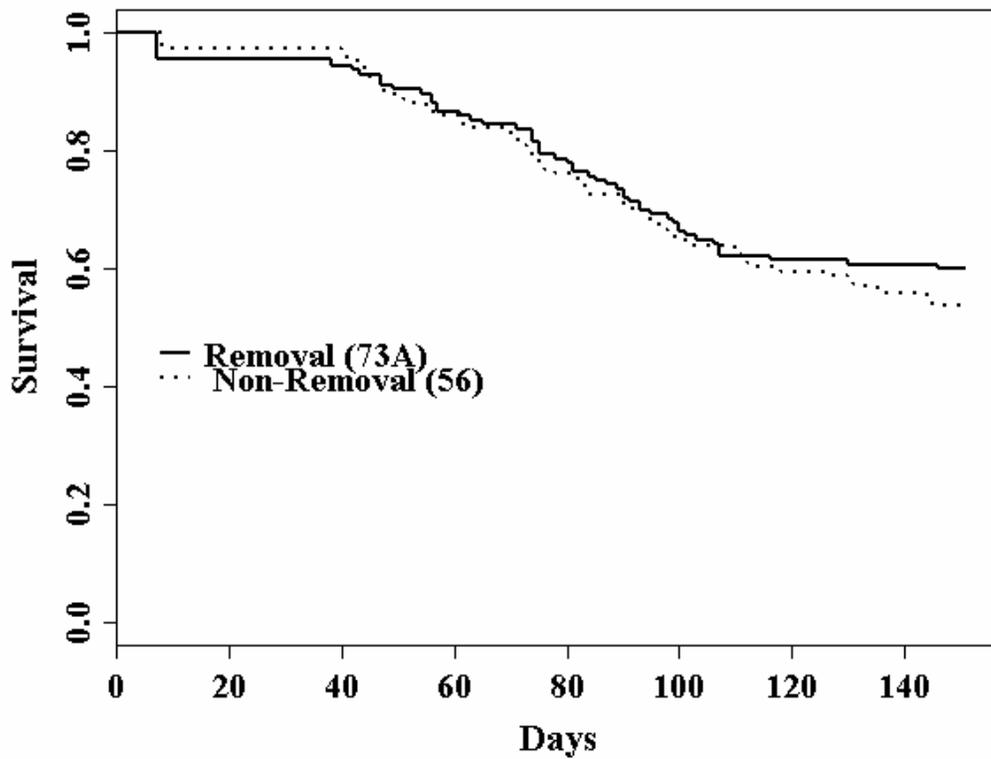
Figure 5. Kaplan-Meier survival curves for 6-month-old mule deer fawns in winter-spring, GMU 56 (reference, $n = 143$) and GMU 73A (treatment, $n = 139$), southeastern Idaho, 16 December to 15 May, 1997-2002.
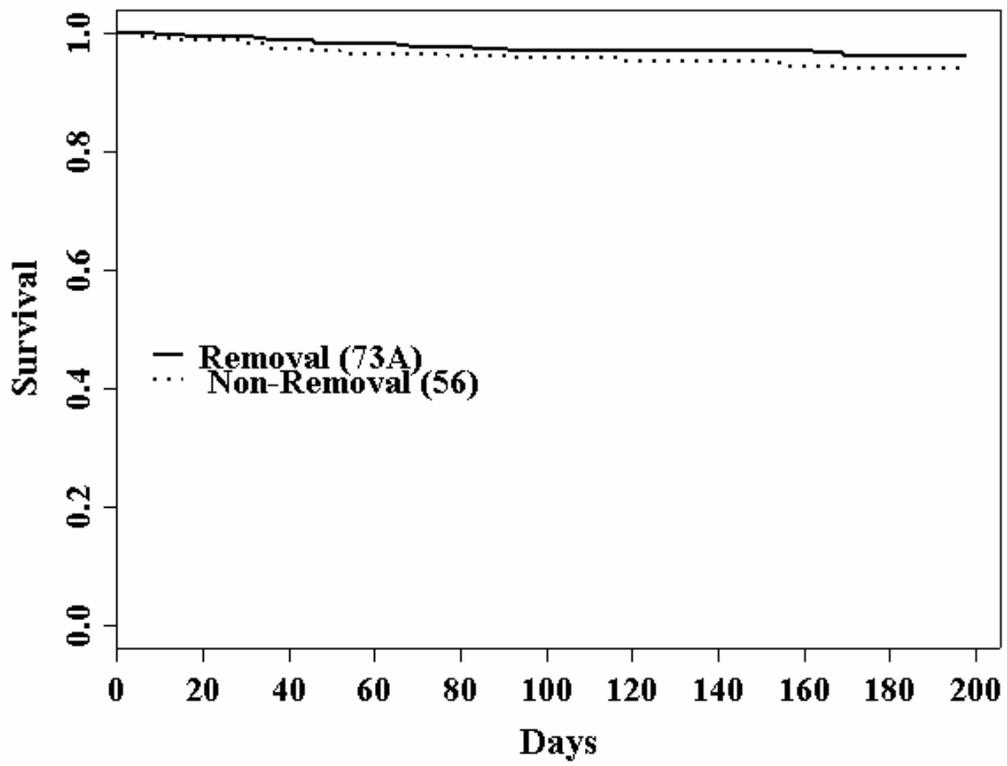
Figure 6. Kaplan-Meier survival curves for adult female mule deer in summer-fall, GMU 56 (reference, $n = 256$) and GMU 73A (treatment, $n = 296$), southeastern Idaho, 16 May to 30 November, 1998-2002.
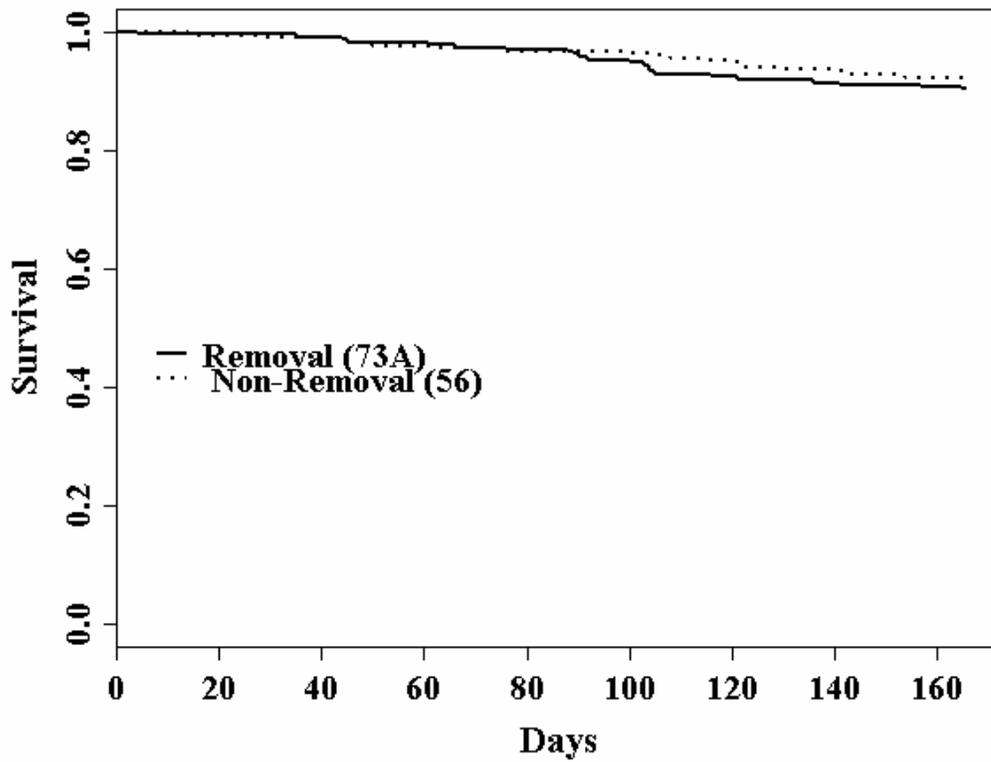
Figure 7. Kaplan-Meier survival curves for adult mule deer does in winter-spring, GMU 56 (reference, *n* = 270) and GMU 73A (treatment, *n* = 283), southeastern Idaho, 16 December to 15 May,1997-2002.
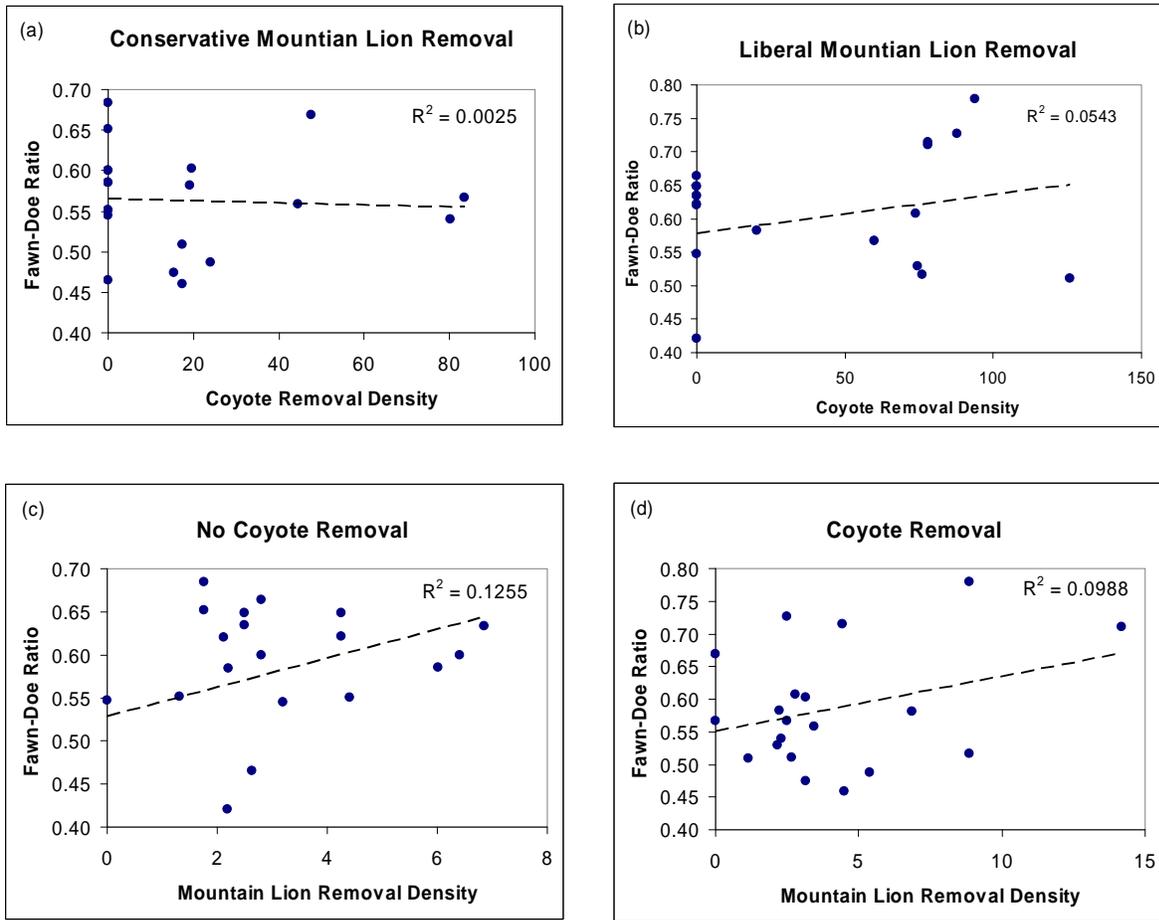
Figure 8. Scatterplots of fawn-to-doe ratios versus removal density of one predator while holding removal treatment constant for the other predator.
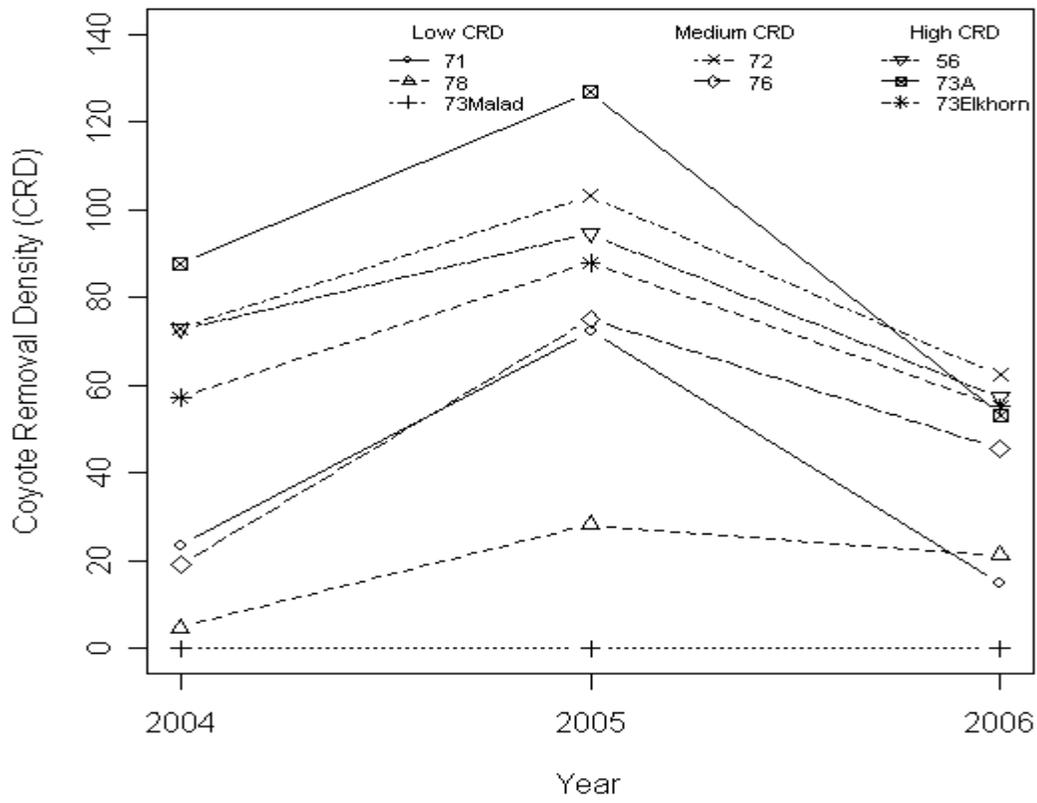
Figure 9. Time profiles of coyote removal density (coyotes removed / 1000 km^2) in Study Area 2, southeastern Idaho, 2003-2006.
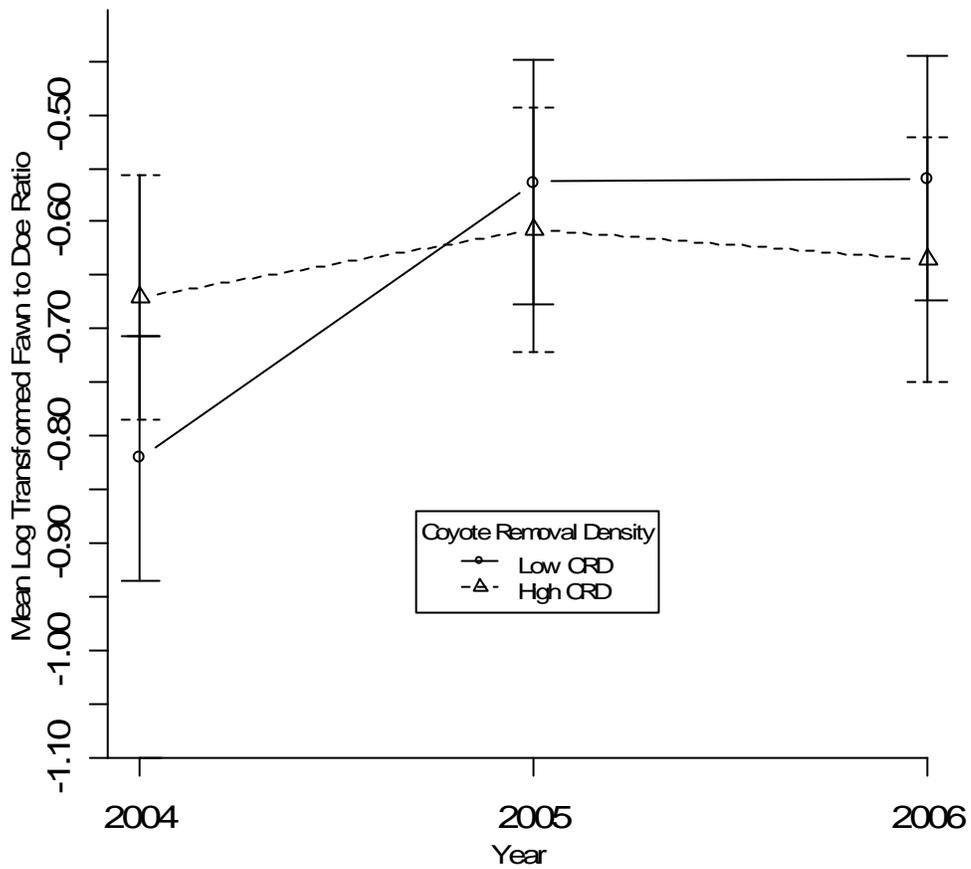
Figure 10. Plots of mean ln FDR by year and high/low treatment levels of coyote removal density, southeastern Idaho, 2003-2006. Error bars indicate 95% confidence intervals.
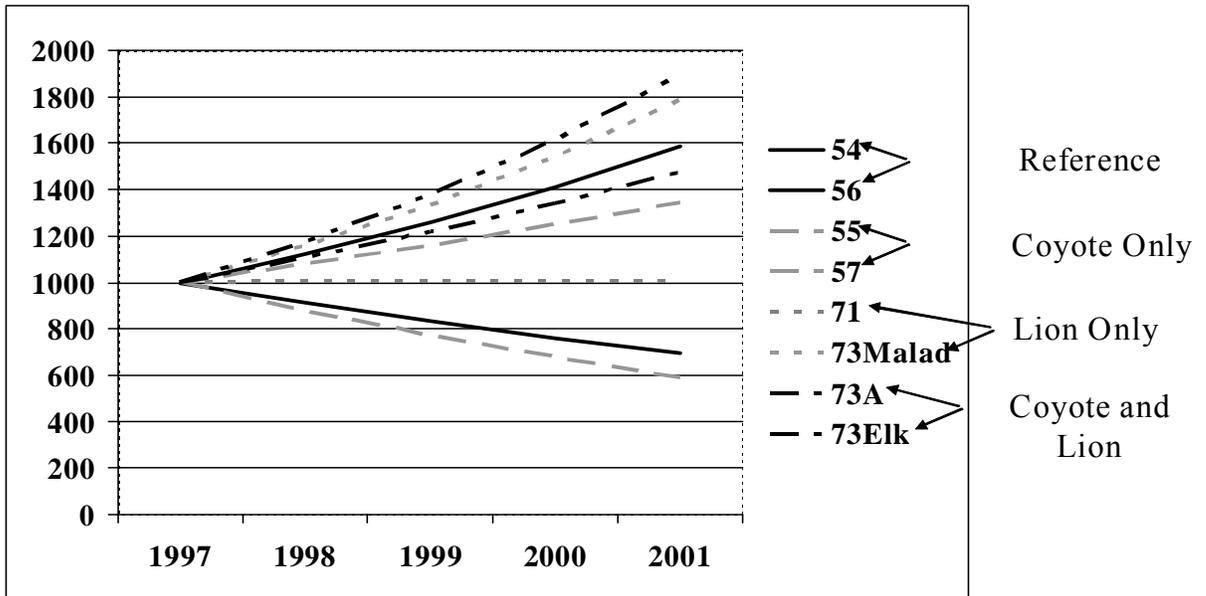
Figure 11. Average rate of population increase of 8 mule deer populations, southeastern Idaho, 1997-2001. Populations have been standardized to 1,000 animals and labeled to depict coyote and mountain lion treatments.
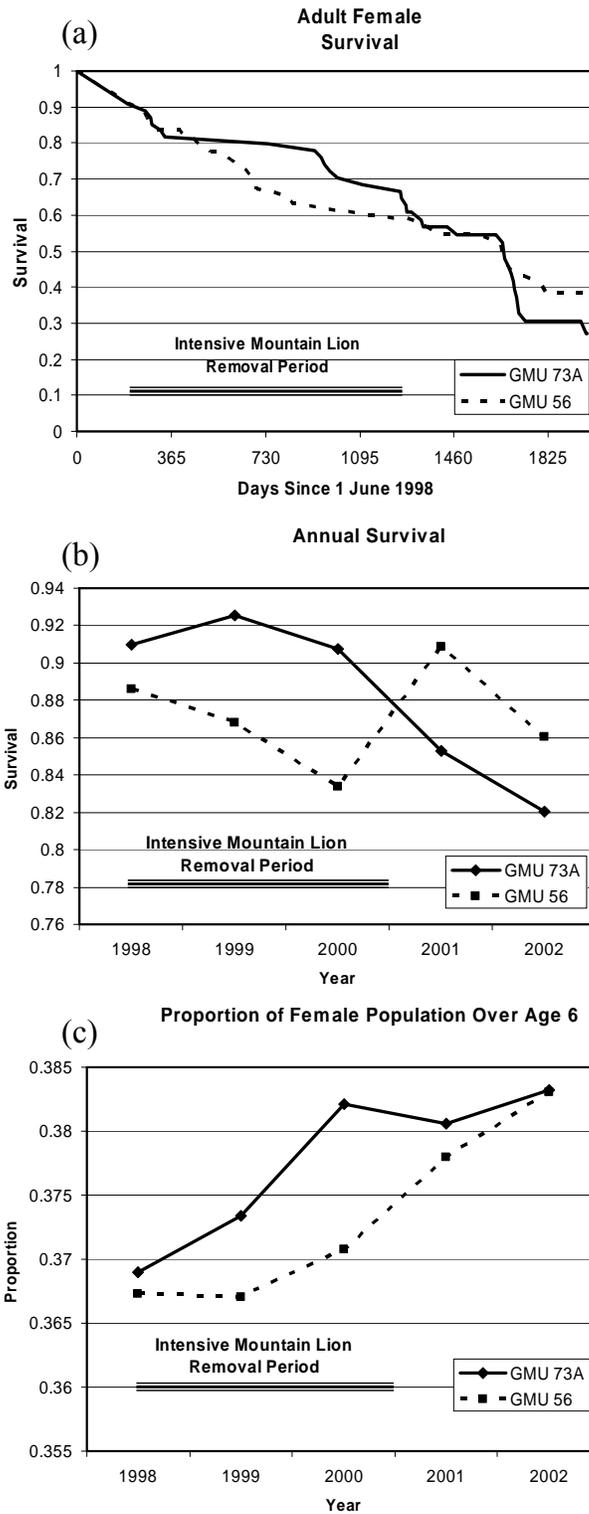
Figure 12. Adult female survival and age structure modeled with observed survival rates for treatment (GMU 73A) and reference (GMU 56) areas for the entire 5-year study period 1998-2002. Summer survival in 1997 (pretreatment) for both areas was set to the observed 1998 summer survival in the reference area. Figure (a) actual K-M survival curves of adult females captured in winter 1998, (b) observed survival of adult females as of 15 May, and (c) the modeled proportion of the adult females (≥1 year-old) ≥6 years of age.
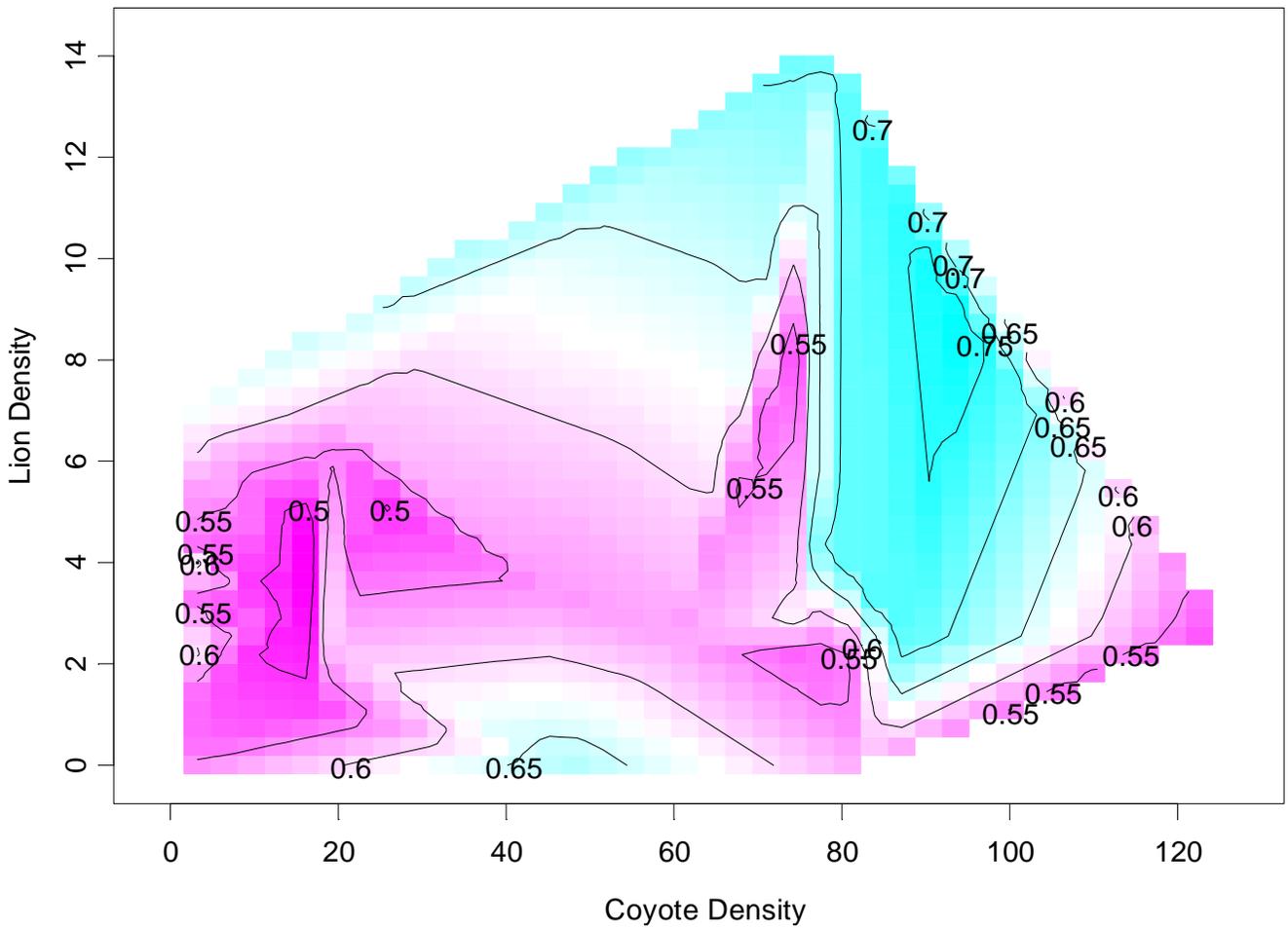
Figure 13. Isopleths of observed fawn-to-doe ratios (FDR) as a function of coyote and mountain lion removal densities, southeastern Idaho, 1999-2003. The FDR values may be confounded with location and year effects not explained by predator control.

Table 1. Mule deer population estimates (90% bound) from initial aerial surveys (Unsworth et al. 1994) within trend areas, southeastern Idaho, 1995-1998.

GMU	Survey year	Estimate (±90% bound)
54	1996	2,445 (159)
55	1995	785 (89)
56	1998	2,561 (256)
57	1997	717[a]
71	1996	1,003 (120)
73A	1996	1,324 (97)
73 Elkhorn	1996	908 (104)
73 Malad	1996	962 (270)

[a] No population estimate available, applied correction factor for population estimate in subsequent years (1.35) to raw count of 531.

Table 2. Predicted influences of predator removal treatments and covariates on mule deer survival and population growth, southeastern Idaho, 1997-2006.

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 small mammal and 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 small mammal and 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 doe and fawn.
	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. Predator swamping near peak fawning will increase survival, whereas inclement weather will decrease survival of early fawns and delayed maturity will decrease survival of late fawns.
	4. Neonate siblings will divide the available nutrients and predator defense from the dam, decreasing survival.

Table 3. Definitions and variable abbreviations of factors incorporated into survival models.

Abbreviation	Definition
CRD	Coyotes removed / 1000 km^2 annually in Game Management Unit
LRD	Mountain lions removed / 1000 km^2 annually in Game Management Unit
Lags	Annual lagomorph population index for the intensive study GMUs 56 and 73A
SMammal	Annual small mammal population index for the intensive study GMUs 56 and 73A
Precip	Total precipitation (cm) for the current season
PPrecip	Total precipitation (cm) for the previous season
CPrecip	Z-score of current season precipitation minus Z-score of previous season precipitation
Mass	Estimated mass (kg) of neonate fawns at age 4 days and mass (kg) of 6-month-old fawns at capture
Sex	Used in fawn models only
BirthTime	Timing of neonate fawn birth in relation to median birth date for cohort
Siblings	Presence of siblings with neonate fawn

Table 4. Coyotes removed (*n*) and density of coyotes removed per 1,000 km^2 (CRD) from GMUs 55, 57, 73 Elkhorn, and 73A in Study Area 1 and cost (U.S. dollars) of removals, 1997-2002. Cost includes contract aircraft, ground operating expense, and personnel time.

Year	GMU 55			GMU 57			GMU 73A			GMU 73 Elkhorn		
	n	CRD	Cost	*n*	CRD	Cost	*n*	CRD	Cost	*n*	CRD	Cost
1997	81	30.52	15,208	27	29.25	6,632	60	53.19	5,534	50	34.87	6,732
	51	19.22	15,094	16	17.34	5,842	86	76.24	11,797	59	59.97	7,536
	46	17.33	7,234	41	44.42	5,158	88	78.01	11,656	29	20.22	3,163
	52	19.59	12,107	44	47.67	10,871	106	93.97	10,547	126	87.87	13,727
	41	15.45	11,043	77	83.42	13,163	88	78.01	11,199	106	73.92	15,604
	64	24.12	9,784	74	80.17	13,319	142	125.89	10,924	107	74.62	15,092
	335		70,470	279		54,985	570		61,657	477		61,854

Table 5. Coyotes removed (*n*) and density of coyotes removed per 1,000 km^2 (CRD) from all GMUs in Study Area 2, 2003-2005.

GMU	2003		2004		2005	
	n	CRD	*n*	CRD	*n*	CRD
71	22	23.38	68	72.26	14	14.88
73 Malad	0	0	0	0	0	0
78	11	4.77	65	28.16	49	21.23
72	197	73.04	278	103.08	168	62.29
76	33	19.19	130	75.06	79	45.61
56	170	72.71	221	94.53	134	57.31
73A	99	87.77	143	126.77	60	53.19
73 Elkhorn	82	57.18	126	87.87	79	55.09

Table 6. Stomach contents (% occurrence) of coyotes experimentally harvested from coyote removal GMUs in southeastern Idaho, 1998. Values percent of coyote stomachs containing each food item.

GMU	*n*	Collection dates	Cattle	Deer	Rodent	Rabbit	Pheasant	Other
73A	44	21 Jan to 5 Mar	34	77	25	0	0	7
73 Elkhorn	18	21 Jan to 5 Mar	50	56	11	0	11	11
55	11	11 Mar to 1 Apr	36	18	36	27	0	0
57	15	11 Mar to 1 Apr	20	33	67	20	0	6
Total	88		25	58	30	7	2	7

Table 7. Mountain lions removed per 1,000 km^2 (LRD) in conservative harvest units (GMUs 54, 56, 55, 57[a]; 8,650 km^2 [b] total area) and liberal harvest units (GMUs 70, 71, 73 Elkhorn, 73 Malad, 73A; 7,115 km^2 total area), southeastern Idaho, 1993-2002.

Year	Conservative harvest GMUs					Liberal harvest GMUs			
	54	56	55	57		71	73 Malad	73A	73 Elkhorn
1993	5.208	0.000	1.347	0.000		0	0.935	0	0.935
1994	5.208	1.760	0.449	1.147		0	1.559	0	1.559
1995	6.410	1.320	3.592	1.147		0	0.623	0	0.623
1996	4.808	3.080	5.388	1.147		0	0.623	1.773	0.623
1997	6.811	3.520	4.041	3.440		0	1.559	3.546	1.559
1998	6.410	1.760	2.245	1.147		0	2.494	8.865	2.494
1999	2.804	2.640	4.490	3.440		2.125	6.858	14.184	6.858
2000	6.010	1.760	3.143	0.000		4.251	2.494	8.865	2.494[c]
2001	3.205	2.200	3.143	0.000		4.251	2.805	4.433	2.805
2002	4.407	1.320	5.388	2.294		0	2.182	2.660	2.182

[a] Identified as conservative mountain lion harvest starting in 1998.
[b] Excludes 900 km^2 of non-mountain lion habitat.
[c] Excludes 5 kittens removed from GMU 73.

Table 8. Mountain lions removed from intensive study GMUs used for survival analysis, southeastern Idaho, 1997-2002. Land area of GMU 56 = 2,273 km^2 and GMU 73A = 1,128 km^2.

Year	Reference GMU 56[a]		Treatment GMU 73A	
	# removed	# removed/ 1,000 km^2	# removed	# removed/ 1,000 km^2
1997	8	3.52	4	3.56
1998	4	1.76	10	8.87
1999	6	2.64	16	14.18
2000	4	1.76	10	8.87
2001	5	2.21	5	4.43
2002	3	1.32	3	2.66

[a] Identified as conservative mountain lion harvest starting in 1988.

Table 9. Mountain lion track indices, GMUs 56 (reference) and 73A (treatment), southeastern Idaho, 1998-2001.

	GMU 56[a]				GMU 73A			
Year	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
2000[b]	4	74.4	0	0.00	4	48.6	1	2.06
2001	5	138.9	3	2.16	5	131.4	2	1.52

[a] Identified as conservative mountain lion harvest starting in 1988.
[b] Snow conditions limited track counts to high-elevation, low-density mountain lion areas.

Table 10. Small mammals captured/100 trap nights along permanent snap trap transects in the intensive study GMUs (56 and 73A), southeastern Idaho, 1998-2002. Captures were summed across cover types to create the combined index.

Year	High-elevation perennial grass	Low-elevation sagebrush	High-elevation mountain brush	Combined index
1998	5.15	31.20	6.11	42.46
1999	8.18	2.52	4.26	14.96
2000	0.85	2.81	5.10	8.78
2001	1.76	2.65	9.17	13.58
2002	0.85	41.95	0.84	43.64

Table 11. Lagomorphs observed (*n*) in headlight surveys in GMUs 56 (reference) and 73A (treatment), southeastern Idaho, 1998-2002.

| | GMU 56 | | | GMU 73A | | | Combined |
Year	Km surveyed	*n*	No./ 100 km	Km surveyed	*n*	No./ 100 km	index 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

Table 12. Number of mule deer equipped with radio collars, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002.

| | Neonate fawns | | 6-month-old fawns | | Adult females | |
Year	GMU 56	GMU 73A	GMU 56	GMU 73A	GMU 56	GMU 73A
1998	8	12	24	21	53	54
1999	20	29	29	34	52	61
2000	32	30	30	29	44	55
2001	30	31	32	25	51	61
2002	28	30	30	30	48	42

Table 13. Fate of radio collared mule deer by age class, southeastern Idaho, 1998-2002. Data is pooled across years to calculate proportions. χ^2 test of distributional differences in fates between treatment and reference GMUs.

Age class Fate	Treatment GMU 73A				Reference GMU 56			
	n	Proportion	95% CI lower	95% CI upper	n	Proportion	95% CI lower	95% CI upper
Neonate fawns (birth to 30 Nov)								
Alive	82	0.621	0.536	0.699	58	0.492	0.403	0.581
Bobcat	4	0.030	0.012	0.075	4	0.034	0.013	0.084
Coyote	13	0.098	0.058	0.161	15	0.127	0.079	0.199
Lion	6	0.045	0.021	0.096	13	0.110	0.066	0.179
Natural[a]	13	0.098	0.058	0.161	11	0.093	0.053	0.159
Other	3	0.023	0.008	0.065	4	0.034	0.013	0.084
Predation[b]	6	0.045	0.021	0.096	9	0.076	0.041	0.139
Unknown	5	0.038	0.016	0.086	4	0.034	0.013	0.084
Total	132				118			
$\chi^2 = 14.175$, DF = 7, $P = 0.048$								
6-month-old fawns (16 Dec to 15 May)								
Alive	90	0.647	0.565	0.722	82	0.573	0.491	0.652
Bobcat	3	0.022	0.007	0.062	1	0.007	0.001	0.039
Coyote	15	0.108	0.066	0.170	23	0.161	0.110	0.230
Lion	18	0.129	0.084	0.195	16	0.112	0.070	0.174
Malnutrition	9	0.065	0.034	0.118	10	0.070	0.038	0.124
Other	1	0.007	0.001	0.040	2	0.014	0.004	0.050
Predation	1	0.007	0.001	0.040	1	0.007	0.001	0.039
Unknown	2	0.014	0.004	0.051	8	0.056	0.029	0.107
Total	139				143			
$\chi^2 = 13.860$, DF = 7, $P = 0.054$								
Adult female summer (16 May to 30 Nov)								
Alive	258	0.963	0.933	0.980	230	0.947	0.911	0.968
Lion	5	0.019	0.008	0.043	10	0.041	0.023	0.074
Malnutrition	1	0.004	0.001	0.021	1	0.004	0.001	0.023
Unknown	4	0.015	0.006	0.038	2	0.008	0.002	0.030
Total	268				243			
$\chi^2 = 5.456$, DF = 3, $P = 0.141$								
Adult females winter (1 Dec to 15 May)								
Alive	232	0.917	0.876	0.945	235	0.925	0.886	0.952
Coyote	4	0.016	0.006	0.040	1	0.004	0.001	0.022
Lion	7	0.028	0.013	0.056	10	0.039	0.022	0.071
Malnutrition	2	0.008	0.002	0.028	2	0.008	0.002	0.028
Predation	3	0.012	0.004	0.034	1	0.004	0.001	0.022
Unknown	5	0.020	0.008	0.045	5	0.020	0.008	0.045
Total	253				254			
$\chi^2 = 8.510$, DF = 5, $P = 0.130$								

[a] Natural = malnutrition, disease, or other non-predatory natural cause.
[b] Predation = Confirmed predation, but species of predator not identified.

Table 14. Cox's proportional hazard survival models for fawns and adult females by season in southeast Idaho, 1998-2002. We included models with AIC values within 2 ΔAIC of the overall best model after determining models in forward stepwise procedure. Lower order models including the factors from the finals models included.

Model rank	Model	K	AIC	ΔAIC	W
Neonate fawns (birth to 30 Nov)					
Reference (GMU 56)					
2	CPrecip	1	523.83	0.39	0.117
3	Mass	1	524.53	1.09	0.083
7	Precip	1	525.31	1.88	0.056
9	SMammal	1	525.37	1.94	0.054
11	Sex	1	525.54	2.09	0.050
12	BirthTime	1	525.57	2.13	0.049
13	Siblings	1	525.59	2.15	0.049
14	PPrecip	1	525.60	2.16	0.048
15	Lags	1	525.71	2.27	0.046
1	CPrecip + SMammal	2	523.44	0.00	0.142
5	CPrecip + Mass	2	524.99	1.54	0.066
4	CPrecip + SMammal + Mass	3	524.70	1.26	0.076
6	CPrecip + SMammal + Lags	3	525.27	1.86	0.057
8	CPrecip + SMammal + Sex	3	525.36	1.92	0.055
10	CPrecip + SMammal + BirthTime	3	525.42	1.97	0.053
Treatment (GMU 73A)					
11	Lags	1	446.27	9.09	0.003
12	Siblings	1	446.50	9.32	0.003
13	CRD	1	446.71	9.54	0.002
14	Mass	1	447.07	9.89	0.002
15	CPrecip	1	447.99	10.81	0.001
5	CRD + Lags	2	439.54	2.36	0.080
4	CRD + Lags + Siblings	3	439.03	1.85	0.110
6	CRD + Lags + CPrecip	3	440.10	2.92	0.064
7	CRD + Lags + PPrecip	3	440.31	3.13	0.057
8	CRD + Lags + LRD	3	440.32	3.14	0.057
9	CRD + Lags + Mass	3	440.43	3.25	0.054

Table 14. Continued.

Model rank	Model	K	AIC	ΔAIC	W
10	CRD + Lags + Precip	3	441.00	3.82	0.041
1	CRD + Lags + Siblings + PPrecip	4	437.18	0.00	0.274
2	CRD + Lags + Siblings + Precip	4	438.52	1.34	0.140
3	CRD + Lags + Siblings + SMammal	4	439.02	1.85	0.109
6-month-old fawns (16 Dec to 15 May)					
Reference (GMU 56)					
5	Mass	1	549.51	8.16	0.007
6	Lags	1	550.28	8.93	0.005
4	Lags + CPrecip	2	544.73	3.38	0.073
1	Lags + Cprecip + Mass	3	541.35	0.00	0.396
2	Lags + Cprecip + Mass + Sex	4	541.81	0.45	0.316
3	Lags + Cprecip + Mass + Smammal	4	542.68	1.32	0.204
Treatment (GMU 73A)					
8	CPrecip	1	420.25	9.10	0.004
6	Cprecip + Mass	2	415.52	4.38	0.039
7	Cprecip + CRD	2	417.51	6.37	0.014
3	Cprecip + Mass + CRD	3	413.12	1.98	0.128
4	Cprecip + Mass + Sex	3	413.70	2.56	0.096
5	Cprecip + Mass + Lags	3	413.72	2.58	0.095
1	Cprecip + Mass + CRD + Sex	4	411.14	0.00	0.344
2	Cprecip + Mass + Sex + Lags	4	411.55	0.41	0.281
Adult female summer (16 May to 30 Nov)					
Reference (GMU 56)					
1	PPrecip	1	161.99	0.00	0.413
2	PPrecip + Lags	2	163.22	1.24	0.223
3	PPrecip + Age	2	163.52	1.53	0.192
4	PPrecip + SMammal	2	163.73	1.74	0.173
Treatment (GMU 73A)					
11	Age	1	118.83	4.21	0.028
7	Age + Lags	2	116.99	2.37	0.070
8	Age + SMammal	2	116.99	2.37	0.070
9	Age + Precip	2	117.80	3.17	0.047

Table 14. Continued.

Model rank	Model	K	AIC	ΔAIC	W
10	Age + Pprecip	2	118.72	4.10	0.030
1	Age + Lags + Precip	3	114.62	0.00	0.230
3	Age + Lags + Pprecip	3	115.90	1.28	0.121
5	Age + Lags + Smammal	3	116.47	1.85	0.091
2	Age + Lags + Smammal + Cprecip	4	115.83	1.21	0.125
4	Age + Lags + Precip + LRD	4	116.24	1.62	0.102
6	Age + Lags + Precip + Smammal	4	116.62	1.99	0.085
Adult females winter (1 Dec to 15 May)					
Reference (GMU 56)					
1	CPrecip	1	203.84	0.00	0.427
2	Cprecip + Age	2	204.48	0.65	0.309
3	Cprecip + Lags	2	204.80	0.96	0.264
Treatment (GMU 73A)					
4	LRD	1	245.07	7.6	0.009
1	LRD + Age	2	237.38	0.0	0.440
2	LRD + Age + Lags	3	237.75	0.3	0.365
3	LRD + Age + CPrecip	3	239.11	1.7	0.185

Table 15. Best competing survival models in order of ranking as identified by AIC (Table 14) for fawns in summer-fall, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002. Strength of association with survival time for each model was evaluated with partial likelihood ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	-2Log	Model χ^2	DF	Model P	Parameter estimate	Parameter P-value	Hazard ratio	95% hazard ratio CI
Reference (GMU 56)								
Combined precipitation	519.44	4.29	2	0.117	-0.597	0.058	0.55	0.30-1.02
Small mammal					-0.016	0.126	0.98	0.96-1.01
Combined precipitation	521.83	1.89	1	0.169	-0.343	0.177	0.71	0.43-1.17
Mass	522.53	1.20	1	0.274	-0.177	0.273	0.84	0.62-1.13
Combined precipitation	518.70	5.02	3	0.170	-0.563	0.077	0.57	0.31-1.06
Small mammal					-0.015	0.136	0.99	0.97-1.01
Mass					-0.137	0.391	0.87	0.65-1.17
Treatment (GMU 73A)								
Coyote removal	429.18	18.23	4	0.001	-0.030	0.002	0.97	0.95-0.99
Lagomorphs					-0.193	0.000	0.82	0.74-0.91
Siblings					0.770	0.030	2.16	1.08-4.33
Previous precipitation					0.136	0.045	1.14	1.01-1.30
Coyote removal	430.52	16.89	4	0.002	-0.022	0.027	0.98	0.96-0.99
Lagomorphs					-0.181	0.001	0.83	0.75-0.93
Siblings					0.722	0.042	2.06	1.03-4.14
Precipitation					0.076	0.104	1.08	0.99-1.17
Coyote removal	433.02	14.37	3	0.003	-0.034	0.001	0.97	0.95-0.99
Lagomorphs					-0.164	0.002	0.85	0.77-0.94
Siblings					0.689	0.050	1.99	0.10-3.97
Coyote removal	431.03	16.38	4	0.002	-0.026	0.010	0.97	0.96-0.99
Lagomorphs					-0.151	0.003	0.86	0.78-0.95
Siblings					0.476	0.124	1.61	0.88-2.95
Small mammals					0.018	0.148	1.02	0.99-1.04

Table 16. Mean mass (kg) by sex of 6 month-old fawns, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002.

| | GMU 56 | | | | | | GMU 73A | | | | | |
| | Females | | | Males | | | Females | | | Males | | |
Year	n	Mass	SE	n	Mass	SE	n	Mass	SE	n	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

Table 17. Best competing survival models in order of ranking as identified by AIC (Table 14) for fawns in winter-spring, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002. Strength of association with survival time for each model was evaluated with partial likelihood ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	-2Log	Model χ^2	DF	Model P	Parameter estimate	Parameter P-value	Hazard ratio	95% hazard ratio CI
Reference (GMU 56)								
Lagomorphs	535.35	16.71	3	0.001	0.145	0.002	1.16	1.05-1.27
Combined precipitation					0.651	0.002	1.92	1.26-2.91
Mass					-0.071	0.020	0.93	0.88-0.99
Lagomorphs	533.81	18.26	4	0.001	0.143	0.003	1.15	1.05-1.27
Combined precipitation					0.626	0.003	1.87	1.23-2.84
Mass					-0.084	0.009	0.92	0.86-0.98
Sex					0.345	0.216	1.41	0.82-2.44
Lagomorphs	534.68	17.38	4	0.002	0.156	0.002	1.17	1.06-1.29
Combined precipitation					0.689	0.002	1.99	1.29-3.08
Mass					-0.080	0.014	0.92	0.87-0.98
Small mammals					-0.008	0.407	1.01	0.99-1.03
Lagomorphs	540.73	11.33	2	0.004	0.145	0.003	1.16	1.05-1.27
Combined precipitation					0.614	0.004	1.85	1.21-2.82
Treatment (GMU 73A)								
Combined precipitation	403.14	44.20	4	0.000	0.870	0.011	2.39	1.22-4.67
Mass					-0.094	0.014	0.91	0.84-0.98
Coyote removal					0.020	0.029	1.02	1.00-1.04
Sex					0.615	0.046	1.85	1.01-3.37
Combined precipitation	403.55	43.70	4	0.000	1.508	0.000	4.52	2.69-7.58
Mass					-0.096	0.013	0.91	0.84-0.98
Sex					0.629	0.041	1.88	1.03-3.43
Lagomorphs					0.118	0.040	1.13	1.00-1.26

Table 17. Continued.

Factor	-2Log	Model χ^2	DF	Model P	Parameter estimate	Parameter P-value	Hazard ratio	95% hazard ratio CI
Combined precipitation	407.12	41.20	3	0.000	0.840	0.014	2.32	1.18-4.54
Mass					-0.068	0.067	0.93	0.87-1.00
Coyote removal					0.020	0.032	1.02	1.00-1.04
Combined precipitation	407.72	40.70	3	0.000	1.459	0.000	4.30	2.39-7.75
Mass					-0.096	0.010	0.91	0.84-0.98
Sex					0.591	0.050	1.81	1.00-3.26

Table 18. Best competing survival models in order of ranking as identified by AIC (Table 14) for adult female mule deer in summer-fall, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002. Strength of association with survival time for each model was evaluated with partial likelihood ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	-2Log	Model χ^2	DF	Model P	Parameter estimate	Parameter P-value	Hazard ratio	95% hazard ratio CI
Reference (GMU 56)								
Previous precipitation	159.99	4.93	1	0.026	0.226	0.038	1.25	1.01-1.55
Previous precipitation	159.22	5.69	2	0.058	0.233	0.045	1.26	1.01-1.59
Lagomorphs					0.063	0.370	1.21	0.80-1.85
Previous precipitation	159.52	5.39	2	0.067	0.242	0.033	1.27	1.02-1.59
Age					0.105	0.476	1.23	0.69-2.19
Previous precipitation	159.73	5.19	2	0.075	0..283	0.071	1.33	0.98-1.80
Small mammal					-0.013	0.61	0.69	0.17-2.84
Treatment (GMU 73A)								
Age	108.62	15.66	3	0.001	0.431	0.001	1.54	1.20-1.97
Lagomorphs					-0.297	0.072	0.74	0.54-1.03
Precipitation					0.123	0.033	1.13	1.01-1.27
Age	107.83	16.45	4	0.003	0.424	0.001	1.53	1.17-1.96
Lagomorphs					-0.370	0.120	0.69	0.34-1.10
Small mammals					0.039	0.056	1.04	0.99-1.08
Combined precipitation					1.242	0.137	3.46	0.67-17.80
Age	109.90	14.38	3	0.002	0.410	0.001	1.51	1.18-1.92
Lagomorphs					-0.264	0.082	0.77	0.57-1.03
Previous precipitation					0.195	0.082	1.22	0.98-1.15
Age	108.24	16.04	4	0.003	0.417	0.001	1.52	1.18-1.95
Lagomorphs					-0.320	0.120	0.73	0.49-1.08
Precipitation					0.138	0.037	1.15	1.01-1.31
Lion removal					-0.076	0.53	0.93	0.72-1.19

Table 19. Best competing survival models in order of ranking as identified by AIC (Table 14) for adult female mule deer in winter-spring, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002. Strength of association with survival time for each model was evaluated with partial likelihood ratio tests for the fitted model and individual parameter tests of $\beta \neq 0$.

Factor	-2Log	Model χ^2	DF	Model P	Parameter estimate	Parameter P-value	Hazard ratio	95% hazard ratio CI
Reference (GMU 56)								
Combined precipitation	201.84	5.65	1	0.018	0.960	0.024	1.28	1.03-1.59
Combined precipitation	200.48	7.00	2	0.030	0.861	0.044	1.25	1.01-1.55
Age					0.159	0.216	1.17	0.91-1.51
Combined precipitation	200.80	6.68	2	0.035	0.984	0.010	1.29	1.06-1.56
Lagomorphs					0.092	0.307	1.32	0.77-2.27
Treatment (GMU 73A)								
Lion removal	233.38	31.05	2	0.000	-0.277	0.001	0.29	0.14-0.60
Age					0.303	0.000	1.35	1.14-1.61
Lion removal	233.75	32.67	3	0.000	-0.308	0.000	0.26	0.12-0.54
Age					0.296	0.001	1.34	1.13-1.60
Lagomorphs					0.091	0.210	1.32	0.86-2.03
Lion removal	233.11	31.31	3	0.000	-0.337	0.031	0.22	0.06-0.87
Age					0.302	0.001	1.35	1.14-1.61
Combined precipitation					-0.293	0.621	0.93	0.69-1.25

Table 20. Fawn-at-heel ratios during June for mule deer does observed with fawns, GMU 56 (reference) and GMU 73A (treatment), southeastern Idaho, 1998-2002.

	GMU 56			GMU 73A		
Year	n[a]	Fawns/doe	95% CI	n[a]	Fawns/doe	95% CI
1998	21	1.62	1.39-1.85	21	1.62	1.39-1.85
1999	17	1.76	1.54-1.99	21	1.81	1.54-2.08
2000	24	1.83	1.67-1.99	30	1.70	1.48-1.92
2001	21	1.81	1.58-2.04	23	1.70	1.45-1.94
2002	22	1.68	1.43-1.93	28	1.36[b]	1.14-1.57

[a] Number of family groups.
[b] Significant difference between removal and non-removal GMUs.

Table 21. Mule deer fawn:doe ratios (FDR) during December-January (SE), southeastern Idaho , 1997-2003. Shaded area indicates data used in tests of hypotheses.

Winter of year	Unit 54		Unit 55		Unit 56		Unit 57		Unit 71		Unit 73 Elkhorn		Unit 73 Malad		Unit 73A	
	FDR	SE (FDR)	FDR	SE (FDR)	FDR	SE (FDR)	FDR	SE (FDR)	FDR	SE (FDR)	FDR	SE (FDR)	FDR	SE (FDR)	FDR	SE (FDR)
1994	0.6435	(0.0515)														
1995																
1996											0.5479	(0.0674)	0.5955	(0.0832)	0.6154	(0.0486)
1997									0.7364	NA	0.6810	NA	0.7357	NA	0.8387	(0.0481)
1998			0.5588	(0.0474)	0.6426	(0.0385)	0.5385	(0.0710)			0.7733	(0.0718)	0.5000	(0.0882)	0.5765	(0.0365)
1999	0.6000	(0.0543)	0.5822	(0.0478)	0.6519	(0.0344)	0.5091	(0.0555)	0.5472	(0.0508)	0.5667	(0.0966)	0.6349	(0.0585)	0.5162	(0.0331)
2000	0.6000	(0.0408)	0.4597	(0.0410)	0.4652	(0.0258)	0.5585	(0.0446)	0.6204	(0.0444)	0.5820	(0.0658)	0.6338	(0.0598)	0.7105	(0.0509)
2001	0.5855	(0.0437)	0.6027	(0.0548)	0.6842	(0.0312)	0.6692	(0.0517)	0.6218	(0.0373)	0.7267	(0.0522)	0.6491	(0.0464)	0.7796	(0.0323)
2002	0.5448	(0.0365)	0.4743	(0.0347)	0.5849	(0.0246)	0.5669	(0.0539)	0.6485	(0.0329)	0.6074	(0.0339)	0.6641	(0.0421)	0.7150	(0.0373)
2003	0.5506	(0.0425)	0.4873	(0.0342)	0.5514	(0.0358)	0.5397	(0.0902)	0.3219	(0.0285)	0.5290	(0.0319)	0.4209	(0.0386)	0.5115	(0.0296)
2004									0.5266	(0.0403)	0.3873	(0.0308)	0.4251	(0.0321)	0.5198	(0.0519)

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Table 22. Weighted ANODEV for mule deer fawn:doe ratios, based on main effects of coyote and/or mountain lion removal, southeastern Idaho, 1999-2003.

Source	DF	Dev	MDev	F	P
Total$_{Cor}$	39	73.662			
Year	4	33.79			
Main Effects					
Coyote	1	1.3317	1.3317	$F_{1,20} = 2.4857$	0.1306
Mountain Lion	1	4.811	4.811	$F_{1,20} = 8.9799$	0.0071
Coyote × Mountain Lion	1	4.318	4.318	$F_{1,20} = 8.0597$	0.0101
Year × Main Effects	12	18.69	1.5575	$F_{12,20} = 2.9071$	0.0169
Error	20	10.715	0.53575		

Table 23. Coyote and mountain lion treatments, mean removal density (No./1000 km^2), and the coefficient of variation (CV) as applied to the factorial treatment design, southeastern Idaho, 1997-2002.

GMU	Coyote removal	CRD		Mountain lion removal	LRD	
		$\bar{x}$	CV		$\bar{x}$	CV
54, 56	No	0	0	No	3.25	0.5500
55, 57	Yes	36.87	0.7125	No	2.53	0.7029
71, 73 Malad	No	0	0	Yes	2.75	0.7419
73A, 73 Elkhorn	Yes	76.87	0.3449	Yes	5.58	0.7198

Table 24. Unweighted ANODEV for fawn-to-doe ratios based on covariates for coyote and/or mountain lion removal densities, southeastern Idaho, 1999-2003.

Source	DF	Dev	MDev	F	P
Total$_{Cor}$	39	0.31058			
Year effects					
Summer precipitation	1	0.01412	0.01412	$F_{1,27} = 2.7259$	0.1103
Winter precipitation	1	0.03507	0.03507	$F_{1,27} = 6.7703$	0.0149
Summer × winter precip.	1	0.04651	0.04651	$F_{1,27} = 8.9788$	0.0058
Site	7	0.04997	0.0071		
Coyote removal	1	0.000126	0.000126	$F_{1,27} = 0.0243$	0.8772
Mountain lion removal	1	0.02502	0.02502	$F_{1,27} = 4.8301$	0.0367
Error	27	0.13977	0.00518		

Table 25. Weighted ANODEV for fawn-to-doe ratios based on covariates for coyote and/or mountain lion removal densities, southeastern Idaho, 1999-2003.

Source	DF	Dev	MDev	F	*P*
Total$_{Cor}$	39	73.662			
Year effects					
Summer precipitation	1	8.525	8.525	$F_{1,27} = 8.0478$	0.0085
Winter precipitation	1	6.293	6.293	$F_{1,27} = 5.9124$	0.0219
Summer $\times$ winter precip.	1	15.28	15.28	$F_{1,27} = 14.4246$	0.0008
Site	7	12.14			
Coyote removal	1	0.2560	0.2560	$F_{1,27} = 0.2417$	0.6271
Mountain lion removal	1	2.571	2.571	$F_{1,27} = 2.4271$	0.1309
Error	27	28.601	1.0593		

Table 26. Mean instantaneous, annual rates of change (SE) of mule deer populations in GMUs experimentally treated under a 2×2 factorial design to remove mountain lions, coyotes, or both, southeastern Idaho, 1993-2003.

		Coyote treatment	
		Non-removal	Removed
Mountain lion treatment	Non-removal	-0.021 (0.018)	-0.015 (0.025)
		n = 27	*n* = 14
	Removed	-0.022 (0.014)	0.018 (0.038)
		n = 9	*n* = 10

ANOVA , 1998-2003   Coyote removal $F_{1,33} = 1.27$, *P* = 0.269
                            Mountain lion removal $F_{1,33} = 0.66$, *P* = 0.977

Table 27. Mule deer population estimates and 90% bound (±) from aerial sightability surveys, southeastern Idaho, 1993-2003.

Year	GMU 54	±	GMU 56	±	GMU 71	±	GMU 73 Malad	±	GMU 55	±	GMU 57	±	GMU 73A	±	GMU 73 Elkhorn	±
1993					1,908	341							2,330	680	2,228	817
1994	2,435	140			976	228	761	171					1,392	130	731	91
1995	2,654	130					711	179	785	89					760	58
1996	2,445	159			1,003	120							1,324	97	908	104
1997	2,144	176	2,682[a]	NA	978	112	701	84	773	124	NA	NA	1,033	71	929	161
1998	1,106	92	2,561	256	978	119	947	141	699	93	522	117	1,121	142	787	117
1999	1,678	125	3,338	400	1,097	82	942	88	809	76	374	98	1,578	148	958	132
2000	1,251	33	3,509	190	1,118	92	885	66	1,022	145	418	96	1,528	95	980	89
2001	1,306	66	4,214	429	920	89	1,622	300	935	114	337	73	2,100	193	1,387	101
2002	1,112	60	2,248	284	889	165	761	73	1,301	171	343	70	2,016	194	794	76
2003	1,133	69	1,608	182	840	107	717	213	927	191	304	117	1,734	200	762	142

[a] Estimated from partial survey – not included in analysis.

Submitted by:

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Approved by:

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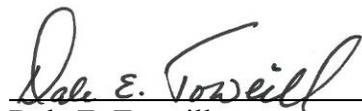
Dale E. Toweill
Wildlife Program Coordinator
Federal Aid Coordinator

James W. Unsworth, Chief
Bureau of Wildlife
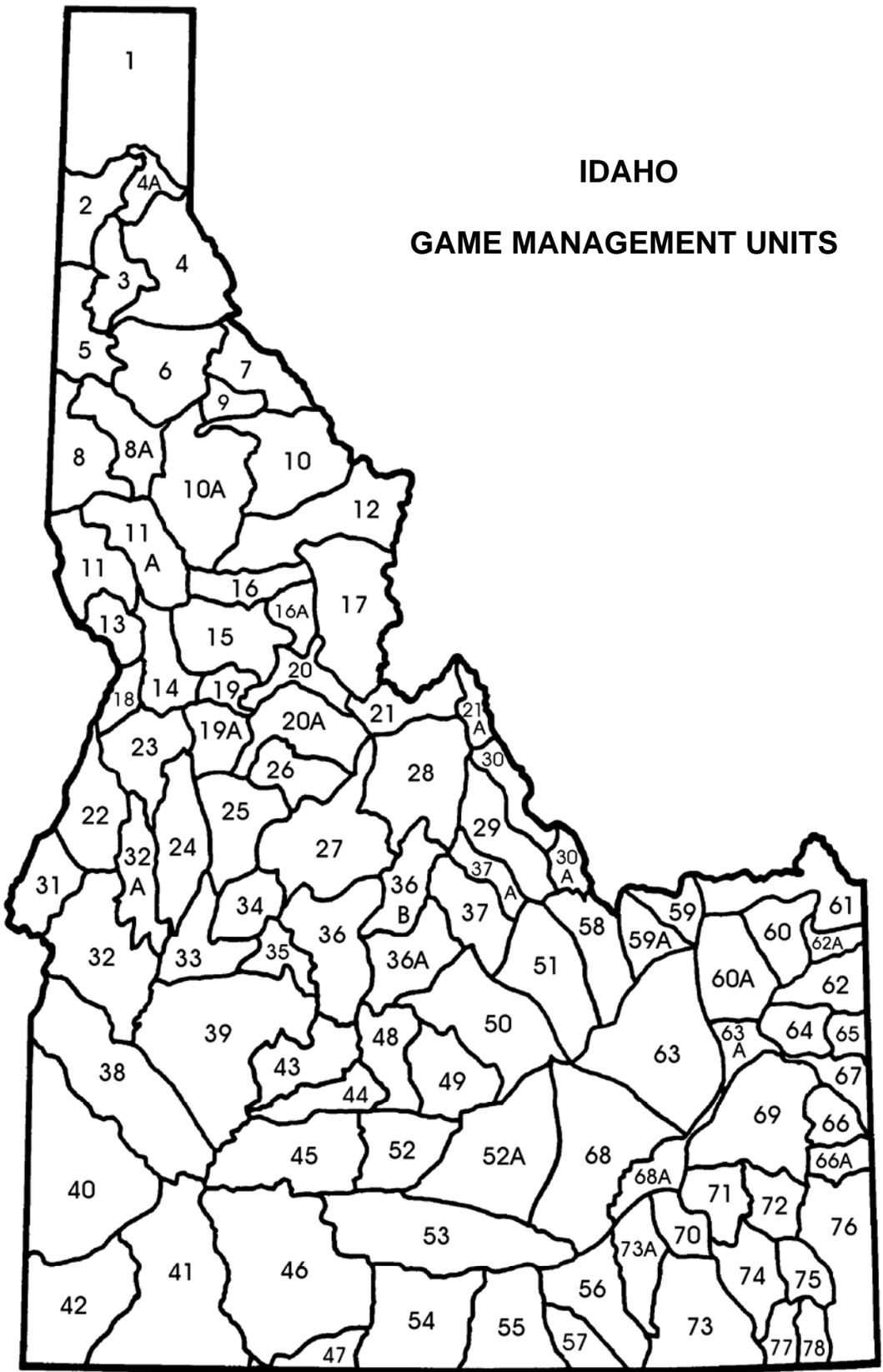
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GAME MANAGEMENT UNITS

FEDERAL AID IN WILDLIFE RESTORATION

The Federal Aid in Wildlife Restoration Program consists of funds from a 10% to 11% manufacturer's excise tax collected from the sale of handguns, sporting rifles, shotguns, ammunition, and archery equipment. The Federal Aid program then allots the funds back to states through a formula based on each state's geographic area and the number of paid hunting license holders in the state. The Idaho Department of Fish and Game uses the funds to help restore, conserve, manage, and enhance wild birds and mammals for the public benefit. These funds are also used to educate hunters to develop the skills, knowledge, and attitudes necessary to be responsible, ethical hunters. Seventy-five percent of the funds for this project are from Federal Aid. The other 25% comes from license-generated funds.