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ELK ECOLOGY

Study IV: Factors Influencing Elk Calf Recruitment

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COMPLETION REPORT
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FACTORS INFLUENCING ELK CALF RECRUITMENT

Abstract

We evaluated survival and cause-specific mortality of elk (*Cervus elaphus*) calves on 2 contrasting study areas in north-central Idaho from 1997 to 2004. Recruitment was adequate and stable on the South Fork study area, and inadequate and declining on the Lochsa study area. We examined the effects of landscape structure, predator harvest levels, and biological factors on calf survival from birth through 31 August. The primary proximate cause of calf mortality on both study areas was predation by black bear (*Ursus americanus*) and mountain lion (*Puma concolor*). Annual calf survival ranged from 0.06-0.46 on the Lochsa study area and from 0.18-0.57 on the South Fork study area. Our models predict that calf survival was influenced both by the landscape structure surrounding calf locations and by predator harvest levels. All competing models included the percentage of forest with 33-66% canopy cover surrounding calf locations, the manipulation of predator harvest levels, the age of calves at capture, and the gender of calves. Other landscape features were influential in predicting calf survival but did not appear in all competing models. Our models also identified limits to our ability to impact calf survival through predator harvest, and demonstrated that landscape influences calf survival. Information presented here is in draft form and a completed manuscript is expected by 2007.

Elk recruitment has declined markedly in north-central Idaho since the late 1980s and early 1990s (Gratson and Zager 1997). Low or declining calf:cow ratios appeared to be a common event throughout the northwestern states (Gratson and Johnson 1995). Several factors could ultimately impact recruitment such as elk density, habitat condition, nutrition, weather, breeding condition, calf condition, and predation. The effects of these factors may be manifested through a number of demographic parameters such as pregnancy rates, birth rates, birth timing, birth mass, growth rate, and calf survival (Gratson and Zager 1997).

Research is demonstrating the relationships between ultimate factors and demographic parameters. For example, recent work by Cook et al. (2001) has found that poor nutrition can lead to delayed breeding in elk (Cook et al. 2001) which results in late-born young. Subsequently, late-born young might be predisposed to higher rates of mortality (Rearden 2005). As another example, it has also been demonstrated that mother's condition and nutritional intake during pregnancy (Verme 1962, Thorne et al. 1976) and weather during the last trimester (Smith et al. 1997) influence juvenile birth mass. Furthermore, growth rate may be suppressed by low birth mass (Cook et al. 2004).

Likely, no single factor is responsible for declining recruitment (i.e., calf survival). For example, the effects of calf condition may interact significantly with predation. Keech et al. (2000) demonstrated this when they found that birth mass of moose calves strongly influenced the subsequent likelihood of bear and wolf predation. Similarly, Singer et al. (1997) found a relationship between predation rates and birth mass of elk calves.

To better understand the reasons for low and declining recruitment in elk populations in Idaho, we investigated calf survival and cause-specific mortality. We experimentally manipulated black bear and mountain lions harvest levels. We predicted that calf survival would improve with increasing predator harvest and decline with reductions in predator harvest. Further, we quantify what influence predator removal, habitat (i.e., landscape structure), birth mass, and other biological parameters had on calf survival.

Study Areas

We selected 2 contrasting study areas in north-central Idaho to investigate factors potentially affecting elk calf survival, and eventual recruitment, to the population. The 2,032 km^2 Lochsa study area is comprised of the Lochsa River (GMU 12) and the North Fork of the Clearwater River (GMU 10) drainages in north-central Idaho. The area is characterized by mountainous terrain rising from approximately 425 m to 2,030 m. Vegetation types range from seral shrubfields that resulted from wildfires and some small prescribed burns (Leege 1969) to low-elevation ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) stands, to western hemlock (*Tsuga heterophylla*)/western red cedar (*Thuja plicata*) stands, and Engelmann spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*) stands at higher elevations. The Lochsa study area is entirely within the Clearwater National Forest with some scattered private parcels. Further details can be found in Unsworth et al. (1993).

The Lochsa study area is further characterized by poor calf recruitment, moderate access, possibly stagnant habitats, and apparently high predator densities (Gratson and Zager 2000). In 1997, calf:cow ratios were low (<15 calves:100 cows) in GMUs 10 and 12 and had been declining since the early 1990s. Cow elk densities were approximately 0.8-1.2/km^2. Since the early 1990s, annual bear harvest was 100-140 (1.6-2.3 bears harvested/100 km^2) in GMUs 10 and 12, and mountain lion harvest was 30-54 (0.5-0.9 lion harvested/100 km^2) (Gratson and Zager 1999). There was approximately 0.3 km of open road (open to motorized vehicles)/km^2 on the Lochsa study area (Gratson and Zager 1999).

The 1,931 km^2 South Fork of the Clearwater River (South Fork) study area (GMU 15) lies entirely within the Nez Perce National Forest with some scattered private parcels. Elevations range from 540 m to 2,000 m. Topography and terrain are generally less rugged and more rolling than on the Lochsa study area. Similarly, vegetation types on the South Fork are the same as those occurring on the Lochsa study area, but with less seral shrubfields and more grass rangeland cover types. The higher elevations on the eastern portion of the study area are characterized by grand fir (*A. grandis*) and subalpine fir habitat types that grade into Douglas-fir and ponderosa pine on drier, warmer sites on the lower western portion (Cooper et al. 1991).

Grand fir habitat types are the most common on the study area. Much of the study area has been logged since the early 1990s, producing a patchwork pattern of logged and unlogged sites (Gratson and Zager 1999).

The South Fork has a relatively good elk recruitment history, good access, more recently disturbed habitats, and possibly lower predator densities than the Lochsa/North Fork (Gratson and Zager 2000). In 1997, calf:cow ratios were considered adequate (>30 calves:100 cows) in GMU 15 and had been generally stable since the early 1990s. Cow elk densities were approximately 0.4/km^2. Annual bear harvest was 39-86 (0.8-1.8 bears harvested/100 km^2) since the early 1990s in GMUs 14, 15, and 16. Annual mountain lion harvest was 21-51 (0.9-2.2 lion harvested/100 km^2) in GMU 15 (Gratson and Zager 1999). There was approximately 0.9 km of open road/km^2 on the South Fork study area, principally due to timber harvest (Gratson and Zager 1999).

Methods

Calf Capture, Tracking, and Necropsy

From 1997 to 2004, newborn calves were captured, radio-collared, and monitored to determine calf survival rates and cause-specific mortality. Each spring (approximately 25 May-15 Jun) we attempted to capture 30 newborn elk calves on each study area, except in 2002 and 2003 when we only attempted to capture calves on the South Fork study area. We located calves from helicopters by searching the area around solitary cows. Calves were captured by hand, blindfolded, and physically restrained or hobbled. We recorded calf sex, body mass, right hind leg length, chest girth, and overall condition. We also collected hair moisture and ear dampness, characteristics of the navel, incisor eruption pattern, hoof hardness and raggedness, presence of grass stains, "stature", and the hairline to hoof indentation measurement (Johnson 1951, Schlegel 1986, Sams et al. 1996). See Gratson and Zager (1999) for further details.

Each calf was ear-tagged and fitted with an expandable, drop-off, mortality-sensing radio collar. Calves were monitored from a fix-winged aircraft ≥3 days a week for the first 8-10 weeks after capture. We monitored calves weekly during August and September, and 1-3 times/week thereafter. Calf status (dead or alive) was determined during each flight. Calves were located on alternate flights during the first 4-5 months, then as often as possible thereafter. Locations were recorded using a GPS.

Mortalities were generally investigated within 30 hours. Personnel conducted necropsies in the field and thoroughly searched within 100 m of the calf remains for evidence that would help determine the proximate cause of death. Evidence could include trauma such as distance between paired canine punctures and location of bite marks, presence of subcutaneous hemorrhaging, sequence of consumption, and portions of calf consumed (Gratson and Zager 1998, 1999). Tracks, scat, and hair from predators were identified by field personnel when possible. Scat and hair samples were collected for later DNA analysis and identification of predators and/or scavengers at mortality sites (Onorato et al. in press). Dead calves that were essentially intact were taken to the Washington Animal Disease Diagnostic Laboratory at Washington State University for complete necropsy and evaluation.

Predator Manipulation

Beginning in autumn 1999, we attempted to manipulate black bear and mountain lion populations on a portion of each study area. We implemented a predator harvest increase "treatment" on the Lochsa River portion of the Lochsa study area. A bag limit of 2 bears and 2 lions per year was available per hunter within the 699 km^2 Lochsa treatment study area. To further effect this treatment, beginning with the spring 2001 bear season, IDFG offered non-resident hunters bear and mountain lion harvest tags at a significantly reduced cost valid in the Lochsa treatment unit. In contrast, the black bear and mountain lion bag limit and harvest regulations were unchanged on a 1,333 km^2 control area. However, the bag limits were increased to 2 bears and 2 lions per hunter per year in autumn 2003 (Figure 1).

Concurrently, the black bear and mountain lion harvest season was closed (treatment) on a 574 km^2 portion of the South Fork study area. The traditional bag limit of 1 bear and 1 lion per hunter per year was retained on the remaining 1,357 km^2 of the South Fork study area.

All harvested black bears and mountain lions must be registered at an IDFG office or an IDFG-designated business. Biological information and general location of the kill site were recorded. We used such information to monitor black bear and mountain lion harvest in the study areas. As an additional black bear population index, we recorded bear sightings as we searched for calves from a helicopter. We recorded bear location, group size, and color phase and age class of individuals. We then used bears sighted/hour of flying as a relative index of bear abundance in each study area. Additionally, at the start of this study, we attempted to monitor bear and lion population through a variety of indices, with variable success. Our methods are detailed primarily in Gratson and Zager (2000), Zager and Gratson (2001), Zager et al. (2002), and Zager and White (2003, 2004). Our results are primarily summarized in Zager and White (2004). We do not go into details regarding the bear and lion population indices and methods since we are reporting on the effects of a harvest manipulation, but we will refer to these findings when appropriate for supportive information.

Predictor Variables

We used Cox' proportional hazards model to investigate the effects of predator harvest, biological factors (e.g., gender, age at capture, mass at capture), spatial and temporal variation (e.g., study area, year), and landscape composition and configuration on elk calf survival.

Manipulation of Predator Harvest.—The variable "predator manipulation" referred to harvest levels of black bears and mountain lions. There were 3 levels of predator harvest: 1) "moderate harvest" represented control areas with a bag limit of 1 bear and 1 lion per hunter per year, 2) "high harvest" corresponded to the Lochsa treatment area where harvest was liberalized to allow harvest of 2 bears and 2 lions per hunter per year, and 3) "low harvest" described the South Fork treatment area where black bear and mountain lion harvest seasons were closed. Calves were assigned to one of these levels based on what harvest strategy was in place in the spatial unit within the study area the calf spent the majority of its time. In a few rare exceptions, calves may have spent equal time in spatial units with different harvest strategy; in these cases, the calves were assigned to the predator harvest strategy that they were exposed to for the first part of their life until 31 August.

Biological Factors.—We also included calf gender, age at capture, birth mass, and timing of birth in the modeling process. Where gender was not recorded in the field (*n* = 4), we used age and mass at capture and year of capture to estimate data (Proc Logistic; SAS 1999). Age at capture was determined using the aging criteria from Johnson (1951) and incorporating Sams et al. (1996) leg hairline to indentation on the hoof measurement Montgomery (2005).

Calf mass was measured (nearest 0.45 kg) at capture using a Pesola scale and birth mass was predicted using calf growth rates (Smith et al. 1997). In the 4 instances where gender was unknown, the growth rate value used was the average value between Smith et al. (1997) male and female growth rates. Where mass at capture was not recorded (*n* = 6), we used age at capture, gender, and birth year to estimate the missing values (Proc GLM; SAS 1999).

Date of birth was determined by subtracting the estimated age at capture from the capture date. Birth dates were then placed in sequential order from first to last. The calf(s) born the earliest received a 1 and calves born after that date were assigned a number corresponding to the number of days (+1) after the first birth(s). In this way, we developed a variable that represented timing of births.

Spatial and Temporal Variation.—We accounted for both temporal and spatial differences with 2 variables. The first was a year variable that had 8 levels, 1 level for each year of the study. Calves were assigned to whichever year cohort they belonged to. Spatially, calves were assigned to whichever study area (Lochsa or South Fork) that they were captured in. Inherently, both variations between years and between study areas could influence calf survival. However, neither one of these variables has enough finite detail (e.g., how does the study area alone tell us what causes survival differences?) to explain difference in calf survival in a way that would be both informative and manipulative (e.g., how do you change a year to result in higher survival?). Instead, year was treated as a stratification factor in our modeling and study area served coarsely as a measure of how well we are explaining biological factors found across our study areas. If study area is not found to be a significant factor in our models, then we believe we have measured biological factors that appear to measure calf survival variation on a more detailed level.

Landscape Structure Metrics.—To investigate the importance of habitat and landscape features on elk calf survival, we evaluated landscape composition and structure within a 500-m radius of calf radio locations. A 500-m buffer was chosen because it corresponded to our estimated telemetry error (485 m (CI = +/- 54 m). We subsequently buffered each calf radio location between birth and 31 August with a 500-m radius in ArcView™ (ESRI 1999*b*).

We derived land cover type from the Idaho GAP data (Scott et al. 2002). We classified the vegetation into 7 types: grassland, shrub fields, forest, water, riparian vegetation, barren, and other. We further divided the forest into 4 canopy cover categories: 1) <15% canopy cover, 2) 15-33% canopy cover, 3) 33-66% canopy cover, and 4) >66% canopy cover. We derived these forest canopy cover classes by overlaying a canopy cover layer obtained from the Landscape Dynamics Lab (University of Idaho, Moscow, Idaho; Idaho Canopy Cover, version 2.1; Scott et al. 2002) with the land cover type data and reclassifying the forest land cover data into the 4 forest categories. We used ArcView™ (ESRI 1999*b*) for most of the GIS analyses.

Spatial layers were projected into NAD27 IDTM (Idaho Transverse Mercator) using Toolbox in ArcGIS 8.2 (ESRI 1999*a*) and evaluated at the 30-m pixel scale.

Buffered calf locations were projected onto the reclassified land cover type data and land cover types were clipped to the 500-m radius. Those land cover types were then analyzed in the Patch Analyst (Grid) extension (Elkie et al. 1999) to obtain landscape metric values (McGarigal and Marks 1995). For each calf, the average landscape value (per metric) of all its locations was calculated to obtain a single landscape value per metric. All landscape metric percent data were transformed (arcsin) for further analysis, unless it was the relative variability about a mean.

We also calculated a topographic roughness or contour density index by first deriving 30 m contour lines from a 30 m USGS National Digital Elevation model (DEM) using Spatial Analyst version 1.1 in ArcView. Contour lines were clipped to each 500-m buffer and the length of the contour lines (m) was summed. We computed density by dividing total length of contour lines (m) by total buffer area (ha).

We selected 11 landscape metrics, (from a set of >40) as possible predictor variables for our survival models. Metrics were chosen a prior and excluded if they were highly correlated ($r \geq 0.70$) (PROC CORR; SAS 1999) with ≥1 other metric. Metric selection was also based on their perceived biological relevance to predicting elk calf survival.

The 12 landscape metric variables chosen for inclusion were contour density (Contour), patch size coefficient of variation (PSCV), contrast weighted edge density (CWED), mean patch fractal dimension (MPFD), mean nearest-neighbor distance (MNN), mean proximity index (MPI), Shannon's evenness index (SHEI), interspersion and juxtaposition index (IJI); and the percentage of the landscape composed of grassland (Grass), forest with 15-33% canopy cover (Forest 2), forest with 33-66% canopy cover (Forest 3), forest with >66% canopy cover (Forest 4; Table 1). To calculate the variable CWED, we defined edge contrast values between each potential pair of edge types based on our knowledge and field experience of structural differences and degree of gradient between land-cover types (McGarigal and Marks 1995).

Statistical Analysis

We focus on summer calf mortality because most (≥80%) of the annual mortality on our study areas occurs before 31 August. We included all calves captured and monitored during 1997-2004 unless it was abandoned or its fate was unclear. We used the calves estimated age at capture as the calves start dates in survival analysis and age as of 31 August as the cutoff point for censoring. Using the calf's age at capture essentially allowed us to treat the calves as cohorts by day-age groups. Calves had an event (mortality), were right-censor prior to 31 August due to collar loss or unknown fate, or were censored on 31 August.

Univariate Analysis.—We calculated calf survival rates for the summer period and annual periods using staggered-entry Kaplan-Meier estimates derived using the NCSS statistical software package (Hintze 2004). Annual survival for calves was calculated similar to survival until 31 August except that the last censoring occurred at 31 May of the following year for each year cohort. If a calf was known to have lived until the last tracking flight, completed sometime in May, they were considered to have been recruited into the adult population on 31 May. We examined several plot and correlation matrices of all the variables of interest. We also tested, using nonparametric test, each variable of interest for differences between those calves that died before 31 August and those calves that lived until 31 August or were right-censored. For each categorical variable we also generated and examined Nelson survivor function (negative empirical cumulative hazard estimate) curves for the different levels within the categorical variable (Proc Phreg; SAS 2002). For categorical variables with 2 levels, we tested for differences between the curves using a score test (Allison 1995). We tested for difference between dummy-variables representing >2 levels of a categorical variable (Allison 1995) using the TEST statement in Proc Phreg (SAS 2002).

Cox Proportional Hazard Models.—We used Cox's proportional hazards models to explore the relationship between instantaneous mortality rates and the categorical and continuous variables of interest. Survival in the Cox's proportional hazards is expressed in terms of the hazard function. We first conducted a model search using a macro (COX_ITER; available from C. T. Moore, University of Georgia, Athens, Georgia) written in SAS programming language (SAS 1999). The COX_ITER macro works in conjunction with several other macros (Model_Avg, and APLR available from C. T. Moore). Overall, the result is a procedure that used the corrected Akaike's Information Criterion (AICc) score to evaluate models based on a joint assessment of model bias and precision (Akaike 1973, Burnham and Anderson 1998). The program fit all possible Cox proportional hazards models up to size *k*, where *k* was user-specified, and it provided a set of estimated coefficients for a global prediction model, accounting for model-selection uncertainty (Burnham and Anderson 1998). The macro was further modified to always include the "predator manipulation" variable (3 levels represented by 2 dummy-variables) in all possible models. We do note in preliminary analysis, when not forcing the predator manipulation variable into the all possible models procedure, it was clear that other methods of generating a "best" model also resulted in the selection of the predator manipulation variable (C. White, Idaho Department of Fish and Game, unpublished data). Additionally, models were stratified by "Year" to account for between year variation, and believed the underlying survival curves graphically indicated some non-proportionality (Allison 1995, Therneau and Grambsch 2000).

Because the sample size is the number of deaths (Harrell 2001), we needed to limit the number of variables in any one model. We chose to model approximately 30 deaths for 1 parameter as a compromise between Harrell's (2001) suggestion of 10-20 deaths/parameter and the more rigorous criteria of 20 deaths/parameter or 50 deaths/parameter (Shtatland et al. 2005). Thus we limited our models to a maximum of 5 predictor variables. We strove for more precision by using a more conservative limit.

Accordingly, we entered all 4 biological predictor variables, 12 landscape metric predictor variables, and study area predictor variable into the COX_ITER procedure to fit all possible Cox proportional hazards models and selected $k = 6$ as the maximum size of any model. We choose the best model using 3 criteria: 1) low AICc score, 2) meaningful confidence intervals for hazard function, and 3) assumptions of the models were adequately fit (Montgomery 2005). We also examined the ΔAICs and AICs weights between the top models and report on all models within 2 AICc scores of the best (Burnham and Anderson 2002). Model assumption of proportionality was checked using Schoenfeld plots and examining the interaction of the individual covariates with time (Allison 1995). Influential points and outliers were identified using plots of deviance residuals (Allison 1995) and dfbeta statistics (Therneau and Grambsch 2000).

To examine the importance of each variable after accounting for uncertainty due to model selection, we estimated parameters of a global prediction model using model averaging (Burnham and Anderson 1998). Before doing this, we standardized variables so patterns of variable importance could be evaluated. We obtained standardized, model-averaged coefficients and 95% CIs for each variable. We used these quantities to make qualitative judgments about the strength and direction of association of each variable with calf survival: estimated coefficients with 95% CIs that did not overlap 0 were strongly associated with calf survival; coefficients with CIs that included 0 had less support (White et al. 2005).

Results

We captured and radio-collared 382 newborn elk calves between 1997 and 2004. Of the 355 calves included in the analysis, 166 calves died before 31 August. Over the same period of time, 208 calves died by 31 May of the following year in which they were captured. Of the 351 known genders, 183 were female calves and 168 were male calves. Seventy-four of the females and 78 of the males were captured on the Lochsa study area, and 110 females and 89 males were captured on the South Fork study area. The estimated mean mass at birth on the Lochsa study area was 15.29 kg (CI = 0.59; *n* = 150), and the estimated mean mass at birth on the South Fork study area was 15.72 kg (CI = 0.55; *n* = 195). The estimated mean mass for female calves (x = 15.54 kg, CI = 0.76, *n* = 108) was similar to the mean mass for male calves (x = 15.93 kg, CI = 0.81, *n* = 87) caught on the South Fork study area. However, the estimated mean mass at birth for female calves (x = 14.19 kg, CI = 0.72, *n* = 73) was significantly less ($P = 0.001$) then the estimated mean mass at birth for male calves (x = 16.24 kg, CI = 0.89, *n* = 77) caught on the Lochsa study area. Mean age of calves at capture was 4 days (range = 0-9 days). The median estimated birth date of captured calves was 2 June.

Survival and Cause-specific Mortality

Predators killed the majority (59.3%) of all calves marked annually (Table 2). The Lochsa study area experienced a 68.4% loss of all calves marked annually to predators. The South Fork study area experienced a 52.1% loss of all calves marked annually to predators. During the summer period, predators killed 45.6% of all the calves marked during this time period (Table 3). On the Lochsa study area, predators killed 54.6% of all calves marked during summer, and on the South Fork study area predators killed 38.7% of all calves marked during summer.

Predators have caused more than 85.6% of Clearwater elk calf proximate mortality. Predators on the Lochsa caused 90.1% of the calf mortality and predators on South Fork caused 81.3% of the mortality. Black bears (38.8%) and mountain lions (38.8%) were responsible for the majority of all proximate annual calf mortality. By study area, black bears accounted for 42.6% of calf mortality on the Lochsa and 34.6% on the South Fork. Mountain lions accounted for 41.6% of calf mortality on the Lochsa and 35.5% on the South Fork. When evaluating calf mortality until 31 August of each year, black bears were responsible for 47.6% of all proximate calf mortality and mountain lions were responsible for 33.7% of all proximate calf mortality. Up to 31 August, black bears accounted for 50.6% of calf mortality on the Lochsa and 44.6% on the South Fork.

Mountain lions accounted for 37.4% of calf mortality on the Lochsa and 30.1% on the South Fork (Table 4 and 5). Most calves (81%) killed by black bears were ≤28 days old and 91% of all calves killed by bears were ≤34 days old. Lions made 60% of their kills on calves ≤60 days old and 40% of their kills were >60 days old. The majority (78%) of all mortality occurred within 60 days of elk calf births.

In each study area, cause-specific mortality of calves shifted after the predator harvest levels were manipulated in a portion of each study area. In the Lochsa where a portion of the area received increased bag limits, black bear-caused mortality declined by ~20% after 1999 while mountain lion-caused mortality increased slightly (~6%). All other predator-caused mortality increased by ~10%. Diseases and other non-predatory causes of calf mortality in the Lochsa study area had a net increase of ~3% since the harvest levels were manipulated in 1999 (Figure 2). Conversely, in the South Fork where a portion of the area had all legal harvest removed, black bear-caused mortality increased ~5% after 1999 while mountain lion-caused mortality declined ~3%. All other predator-caused mortality increased by ~11% after 1999. Diseases and other non-predatory causes of calf mortality had a net decline of ~12% (Figure 3).

Predator Harvest

Long-term harvest data indicates that black bear harvest in the control portion of the Lochsa study area peaked (>130 bear/year) just prior and during the start of the predator harvest manipulation. Other than this high peak, it has fluctuated between 31-82 bears harvested per year. Long-term bear harvest on the increased treatment portion (i.e., increased harvest) of the Lochsa study area fluctuated between 6-30 bears harvested per year up to and including1999. Since implementation of the predator harvest manipulation, bear harvest has been ≥39 bears/year except for 2000. Harvest of bears in the treatment area since increased bag limits on bears has been as high as 64 bears/year (Figure 4).

South Fork study area long-term harvest data indicates that black bear harvest in the control portion was high (>20 bears/year) just before and during the early 1990s. Since then, bear harvest has been relatively stable and fluctuated between 9-18 bears/year with the exception of 22 bears in 2003. Long-term bear harvest on the decreased treatment portion (i.e., decreased harvest) of the South Fork study area grew steadily since the mid-1980s and peaked twice, 20 bears/year in 1992 and 16 bears/year in 1996. Bear harvest on the decreased treatment portion was almost non-existent since the implementation of the predator manipulation until fall 2004 when this area was once again legally open to bear harvest (Figure 5).

Number of bears observed per flying hour during calf capture declined steadily on the Lochsa study area since 1998 (Table 6). The decline coincided with increased black bear harvest on the control portion of the study area and continued as harvest substantially increased on the treatment area with implementation of increased bag limits in 1999. On the South Fork study area, the number of bears observed per flying hour has remained relatively stable between 0.05 - 0.13 bears/flying hour, with the exception of 0.24 bears/flying hour observed in 2000 (Table 6).

The 6-year average mountain lion harvest has declined by 30% on the Lochsa control area since 1999, whereas harvest increased by 33% on the treatment area during the same time period

(Table 7). The 6-year average mountain lion harvest declined by 45% on the South Fork control area, and declined by 92% on the treatment area.

Survival Rates and Univariate Analysis

Summer elk calf survival on the Lochsa study area varied between 0.17-0.68. Summer calf survival on the South Fork study area varied between 0.23-0.74 (Table 8). Annual survival on the Lochsa varied between 0.06-0.46. Annual survival on the South Fork varied between 0.18-0.57 (Table 9). On the Lochsa study area, summer survival and annual survival started low and increased as the study progressed. However, survival in both time periods had increased >0.20 in 2001 compared to 1999, 2 years after predator manipulation was implemented. Five years after implementation, survival had increased >0.30 than in 1999. Prior to this, survival was never <0.14 below the 1999 survival rate for either time period. Summer survival on the South Fork was >0.50 before predator manipulation, but was only above this mark 2 out of 5 years after 1999. Annual survival on the South Fork followed a similar trend; before predator manipulation, survival was >0.40 but after implementation survival was >0.40 once.

Univariate tests for differences between levels of categorical variables indicated that male calves survived somewhat better ($P = 0.060$) than females calves during summer. There was a significant difference ($P = 0.034$) in calf survival between predator manipulation levels during summer. Specifically, the treatment unit that had low predator harvest suffered a somewhat lower ($P = 0.062$) calf survival as compared to the control units (moderate harvest). Survival in the treatment unit that had high predator harvest was significantly higher ($P = 0.015$) than the survival in the treatment unit that had low predator harvest. We did not detect a significant increase ($P = 0.205$) in survival in the treatment unit that had high predator harvest versus moderate harvest. Not surprisingly, the South Fork study area had a significantly higher ($P = 0.039$) calf survival than did the Lochsa study area. Overall, summer calf survival was somewhat different ($P = 0.055$) between years. Calves born in 2004 survived significantly better than calves born in 1997 ($P = 0.014$), 1998 ($P = 0.010$), 2001 ($P = 0.001$), and 2002 ($P = 0.004$).

Cox Proportional Hazard Models

There were 4 competing models within 2 AICc scores. All 4 models appeared to meet the assumption of proportionality. There appeared to be outliers and influential points in the model data set, but further evaluation of these points revealed no apparent error in calculation or collection of these values. Removal of the most influential point did not change which variables were in the "best" model, and removal of all influential and outlier points did not remove any of the 4 models from being considered top models (within 2 AICc scores). As such, we choose to leave these points in the modeling data set as it is our view that they were collected, calculated, and recorded correctly and represent the natural variation that could occur in north-central Idaho.

All 4 competing models included the predator manipulation (selected a prior to be in each model), age at capture, and gender. Differences among models rested with the landscape variables. The best model included percentage of Forest 3 cover type and percentage of grass cover type. The remaining competing models included combinations of mean proximity index, percentage of Forest 4 cover type, and percentage of Forest 2 cover type (Table 10).

In all models, few variables had a hazard ratio >1. A hazard ratio >1 demonstrates a positive, increasing relationship between mortality and the predictor variable; or a decrease in survival as the predictor variable value increases. A hazard ratio <1 demonstrates a negative, decreasing relationship between mortality and the predictor variable; or an increase in survival as the predictor variable value increases. However if the 95% confidence interval around the hazard ratio includes 1, then it is difficult to interpret the relationship between the mortality rate and the predictor (Montgomery 2005).

The decrease in predator harvest resulted in a hazard ratio >1 in all models, indicating that, as predator harvest was removed compared to the baseline control of moderate harvest (1 bear and 1 lion tag/person/year), calf survival declined. More specifically, when examining the best model, the hazard of mortality for those calves in the spatial unit with no predator harvest was 91% more than the hazard for those calves in the spatial unit with moderate harvest. Conversely, in the best model, an increase in predator or high harvest resulted in only 62% of the hazard of mortality for calves as compared to those calves in spatial units with moderate harvest. However, while an increase in predator harvest has a hazard ratio <1 in all models, the 95% confidence interval of the hazard ratio overlaps 1.0 in best and top 3 models, making interpretation difficult in these models (Table 11).

The other variable demonstrating a positive, increasing relationship with mortality was mean proximity index. Age at capture, percentage of Forest 3 cover-type, percentage of Forest 4 cover-type, percentage of Forest 2 cover-type, and percentage of grass cover all demonstrated a negative, decreasing relationship with mortality. In the models that gender appears in, male calves hazard rate was just 62-65% that of females (baseline).

Model-averaged coefficients and 95% CIs supported that a decrease in predator harvest, increase in calf's age, male gender, increase in percentage of Forest 3 cover, increase in percentage of grass cover, increase in percentage of Forest 4 cover, and decrease in mean proximity index resulted in better calf survival (Figure 6).

Discussion

Summer losses of elk calves, mostly by predation, were by far the greatest limit to calf recruitment. Black bears and mountain lions were responsible for the majority of all calf deaths. Majority of deaths in summer were attributed to black bears while mountain lions were responsible for most of the remaining summer calf deaths and most deaths after the summer period. Wolves (*Canis lupus*) were reintroduced into Idaho in 1995 and 1996, just prior to the beginning of this study. One of the earliest wolf packs was documented on part of the Lochsa study area; however, few calf mortalities in our study were attributed to wolves. Wolf densities were low at the beginning of this study and have increased steadily on both study areas. Wolf presence appears to have been widespread on both study areas by 2002-2003 (C. G. White, Idaho Department of Fish and Game, unpublished winter track data).

Raithel (2005:25-26) summarizes the summer mortality for a number of studies and reports that predators killed 10-22% of marked calves, with the exception of Schlegel's (1976) study which reports a summer mortality of 64%. The total summer predation rate on marked calves in our study (45%) is greater than most studies' reported summer mortality. Schlegel (1976), whose study area was in the Clearwater drainage and adjacent to our Lochsa study area, did a comparative calf recruitment study 24-31 years earlier. Schlegel (1976) reported a summer (by 7 July) calf mortality of 64%, somewhat higher than our summer mortality rate of 55% for the Lochsa study area. Raithel (2005:25-26) further summarizes that studies in Alaska report a high calf caribou (*Rangifer tarandus*) lost to predators (43-61%) and calf moose (*Alces alces*) lost to predators (41-63%) during a similar summer time period. Our summer predation rate would be within the lower range of mortality experienced by these other ungulate species who arguably exist in one of the most diverse large multi-predator systems, which includes predation by wolves and grizzly bears (*Ursus arctos*) (Singer et al. 1997).

The reported percent of annual cause-specific calf mortality attributable to black bear varied from 2-72% (Schlegel 1976, Myers et al. 1996, Smith and Anderson 1996, Singer et al. 1997, Raithel 2005, Rearden 2005). Singer et al. (1997) report black bear cause-specific calf mortality at 2%, but when factoring in all bear mortality (grizzly bear and unknown bear species), they report that bears comprise 23% of all cause-specific mortality. Schlegel (1976) reports the highest bear cause-specific mortality at 74%. A recent preliminary report on calf mortality in Yellowstone indicates that bears accounted for approximately 55-60% of all calf deaths (Barber et al. 2005). But most studies report a range of 2-36%. The cause-specific mortality we witnessed by black bear (39%) is high. We also saw some high individual year variations on individual study areas, including bear cause-specific mortality 4 out of 6 years on the Lochsa and a high bear-caused mortality of 71% in 2001 on the South Fork.

Annual cause-specific calf mortality attributable to mountain lions varied from 0-42% (Schlegel 1976, Myers et al. 1996, Smith and Anderson 1996, Singer et al. 1997, Rearden 2005). Raithel's (2005) study areas in Oregon witnessed a 1-year cause-specific mortality rate of 65% by mountain lions. Our cause-specific mortality rate by lions was 39%. Once again, this was the second highest cause-specific mortality witnessed. A unique thing about the bear and lion cause-specific mortality rates that we witnessed is that both were relatively high rates compared to other studies. Other studies either recorded a high bear mortality rate and low lion mortality rate or a high lion and low bear mortality rate on elk calves.

We found some success in manipulating harvest levels of black bears and mountain lions. Bear harvest on the control portion of the Lochsa, for the most part, remained within recent historical levels. There was a high harvest peak just prior to our implementation of the manipulation in 1999 that we attribute to anxious hunters desiring to reduce the bear population. Bear harvest increased and stayed above recent historical levels on the treatment portion of the Lochsa. Harvest level alone does not indicate bear population density. However, with such a reduction in bear numbers in the greater Lochsa area, you could expect that the overall net effect is fewer bears on the Lochsa study area. There were several reported indices of bear populations that support this statement. The number of bears observed per flying hour steadily declined at the start of the high harvest on bears in the control portion of the Lochsa in 1998 and continued as we harvested more bears in the treatment portion of the Lochsa. Further, data from black bear bait station surveys and a mark-recapture index (Zager et al. 2005) both indicate that bear populations declined on the treatment portion of the Lochsa where we increased harvest levels.

The bear harvest on the control portion of the South Fork study area also appears to have been similar to pre-manipulation harvest of bears, and bear harvest on the treatment portion of the South Fork was reduced or eliminated. Bait station surveys and mark-recapture indices (Zager et al. 2005) support an increase of bears in the treatment area to the point that it mirrors the bear population in the control portion of the South Fork. Overall, the number of bears observed per flying hour support a relatively stable bear population on the South Fork.

The harvest of mountain lions declined in both control areas after implementation of the predator harvest manipulation. It appears that there is a region-wide decline in mountain lion populations throughout the West. We expect that some of the decline in mountain lion harvest is an effect of fewer lions in the Lochsa and South Fork populations, potentially confounded by marginal weather in the last few years of the study to effectively hunt lions in. Nevertheless we were able to increase lion harvest on the Lochsa treatment by almost 33% after the start of the manipulation. If populations of lions had started to decline before manipulation, then the total effect of increased harvest may be several magnitudes higher than measured. On the South Fork treatment area, we removed virtually all known lion harvest which, along with a decline in harvest on the control, may have offset any net loss of lion population numbers due to other mortality causes.

In the end, what we recorded was low annual calf survival on the Lochsa (0.05-0.16) during the pre-manipulation period, a slight increase in survival (0.23) during the first year of increased predator harvest, and then a doubling in calf survival in the following years (0.41-0.46). Indices indicate that the bear population was declining in the treatment portion of the Lochsa in relation to the control portion of the Lochsa, and across the Lochsa, bear numbers declined. Lion harvest would appear to have had a substantially greater effect on lion populations in the treatment area versus the control area, and lion numbers declined across the study area.

Conversely, on the South Fork, annual calf survival rates were high (0.43-0.67). Survival declined during the first year of decreased predator harvest (0.31), declined sharply (0.18) by the second year, and remained relatively low (0.31-0.34) until 2004 (0.47). Indices indicated that bear populations increased on the treatment portion of the South Fork to numbers similar to the control area, and across the South Fork study area, the bear population was stable. Harvest of lions declined drastically in the treatment area while also declining in the control portion.

Our prediction held that calf survival was higher in areas with higher harvest levels of predators (presumably lowering predator densities) and calf survival was lower in areas with lower harvest levels of predators (presumably stable or increasing predator densities). This then begs the question of whether the calf mortality lost to predators (primarily bears and lions) is additive or compensatory. The primary mechanism of compensation is assumed to be density dependence relative to habitat potential (Caughley 1977). The fundamental assumption is that habitat, primarily forage, affects animal condition thus regulating population growth, yield, and density. The concepts of additive and compensatory mortality are implicit in this model and it is generally believed that as populations approach carrying capacity, all mortality due to predation is compensatory. In general, as populations approach the other extreme, far from carrying capacity, then mortality due to predation is additive (Macnab 1985, Ballard et al. 2003). When populations are somewhere between the high end and low end of carrying capacity, then mortality due to predation is likely a mixture of compensatory and additive (deVos et al. 2003). More simply, it has been suggested that bear mortality on ungulates would be compensatory if bears killed individuals in poor condition that were already predisposed to mortality from other causes (Boutin 1992, Singer et al. 1997).

We address the question of additive or compensatory mortality by examining cause-specific mortality data and 3 ancillary pieces of data recorded by IDFG during our study: calf:cow ratios (population growth potential), body condition of adult cow elk as a surrogate for habitat condition, and change in elk population (density). Mortality on the Lochsa does not appear to be largely compensatory but additive. After predator manipulation implementation on the Lochsa, we witnessed a decline in black bear mortality of 20%, an increase in lion mortality by 6%, and an increase in all other predator-caused mortality of 10%. Diseases and other non-predatory causes of calf mortality only increased by 3%. Clearly, calf mortality previously lost to black bear-caused mortality was replaced with more lion mortality and other predation losses, and not to starvation, diseases, or other factors that would indicate density dependence. However, that there was at lease some increase in disease and other non-predatory causes indicates that not all mortality by black bears was additive and, to a degree, mortality was compensatory. Further, it could even be argued that black bear mortality was compensatory to other types of predator mortality.

Other data also indicate that elk populations in the Lochsa study area are not likely limited by a density-dependent response to habitat. Recent summary of elk populations in and around the Lochsa study area indicate that elk density before and during our study drastically declined by as much as 39% over a relatively short time, and coupled with this was a 50% decline in recruitment. It has been reasoned that while the population may have been above carrying capacity, it is unlikely that habitat has declined at such a rapid rate (IDFG 2006). A more reasonable explanation is that inverse density dependence was evident and this explanation seems most plausible. Additionally, recent data on adult elk body condition in the Lochsa study area suggest that nutrition may not be limiting elk population performance (IDFG 2006). This, coupled with very little indication of deficiencies' in elk calves from blood work performed early in the study, would lend more credence that current and recent past habitat quantity is not limiting elk calf fitness at birth. Further, some have argued that maternal investment in male calves is an indication of greater maternal nutritional condition (Trivers and Willard 1973, Kohlmann 1999). It has also been reported in Yellowstone that male-biased calf elk sex ratios are associated with relatively lower elk densities (2.4/km^2) coupled with start of feeding and quality (Smith et al. 1996); another study recorded declining proportions of male red deer calves with increasing population densities and winter rainfall (Kruuk et al. 1999). The Lochsa sex ratio of radio-collared elk calves was 105 male:100 female (n = 152) and appears to support that maternal nutritional condition is not limiting.

Conversely, on the South Fork, the distinction between additive or compensatory mortality is not as clear. After harvest removal of predators on a portion of the South Fork, we witnessed an increase in black bear mortality of 5%, a decrease in lion mortality by 3%, and an increase in all other predator-caused mortality of 11%. Diseases and other non-predatory causes of calf mortality had a net decline of 12%. The net result is that predators, including bears, were responsible for more calf mortality at roughly the rate that disease and other non-predatory causes declined. Calf:cow ratio's were estimated in 6 of the 12 years prior to and including the year of the predator manipulation in 1999 (Idaho Department of Fish and Game, Lewiston, Idaho, unpublished survey data). Calf:cow ratios were high 4 out of 6 years (above 32 calves:100 cows). Since predator manipulation, the calf:cow ratio has been below 30 calves:100 cows 2 out of 3 years that the survey has been conducted (Idaho Department of Fish and Game, Lewiston, Idaho, unpublished survey data). Population estimates have not been conducted since the predator manipulation was implemented, but prior to predator manipulation, the population had been increasing (Idaho Department of Fish and Game, Lewiston, Idaho, unpublished survey data). The South Fork sex ratio of radio-collared elk calves was 81 male:100 female (n = 199) and would not be a strong argument that maternal nutritional condition is not limiting. However, adult body condition scores on the South Fork have generally been higher than the Lochsa, and the primary wintering range is considered viable (Zager et al. 2005). This also, coupled with very little indication of deficiencies' in elk calves from blood work performed early in the study, would lend more credence that current and recent past habitat quantity is not limiting elk calf fitness at birth on the South Fork study area.

Hazard Modeling

The univariate test of predator manipulation treatment and Cox's proportional hazard modeling support that differing levels of predator harvest affected calf survival, which lends further support to the conclusion that mortality by predators was additive. We also found that other biological variables (i.e., sex and age at capture) and landscape structure predicted calf survival. In particular, our results demonstrated that the percentage of Forest 3 (forest with 33-66% canopy cover) cover type was a very strong predictor of elk calf survival as evidenced by both its frequency in all 4 of the top models and by the relative strength of the standardized, model-averaged coefficients and 95% CI. Since our investigation of landscape structure was observational in nature, we are limited as to what we can interpret from these results. But it is clear that calves with more of this forest cover type and other forest cover types within 500 m of their locations survive at a higher rate. Vegetation analysis conducted in similar forest types in Montana indicated that northwestern forest with moderate canopy cover may provide the structural cover for elk calves and forage nutrients for the cow (B. Gilbert, University of Idaho, personal communication). The top model may also express foraging needs of the lactating cow elk since percent of grassland also appears in this model. The grassland cover type's true representation on the ground is likely a mixture of grass, forb, and shrub since the original satellite imagery was captured 2-4 years before this study started and grassland succession will have progressed. The other vegetation cover types (Forest 4 and Forest 2) that made an appearance in 1 model each are variations of Forest 3. Since their appearance in the top models appears somewhat interchangeable, they may represent a gradient of the Forest 3 cover type in different succession stages and are a gradient between greater forage nutrients for the lactating cow, structural cover for the elk calf, and security for the elk population. Since the percent data was arcsine-transformed for our analysis, we caution against interpreting hazard ratios as 1 unit increase in percent data. Instead, it should be interpreted as 1 unit increase in arcsine-transformed percent data.

Although not considered for the final modeling analysis because of its high correlation with Forest 3, the percentage of shrub cover type within 500 m of calf locations had a negative effect on calf survival. This was demonstrated by both preliminary model analysis and in a univariate t-test ($P = 0.001$) which indicated that calves with less of this cover type within 500 m survived better than did calves with more percent cover type. During our own capture periods, we observed greater success at catching young calves that would "hang-up" or tire more quickly from trying to navigate older and thicker shrub fields. On the other hand, adult black bear appear to have the power and agility to "mow" through these fields. This is an important consideration since shrub fields are commonly believed to be one of the most important wintering habitat for elk in the Clearwater drainage (Leege 1969, Leege and Hickey 1977). These shrub fields were created from large catastrophic wild fires in the early twentieth century. Since there has been little fire of that magnitude on the landscape since the early twentieth century, it is a commonly held belief that the quantity and quality of shrub fields has declined. Thus, shrub field regeneration may be important not only for better quality and quantity of wintering range but also for lower structural and thinner shrub fields potentially making it more navigable for elk calves. We caution that while it is clear that calf recruitment has declined over much of this area, the relationship between habitat and recruitment on this range is still poorly understood. It is important to recognize that the relationships among habitat quality and quantity, elk density, and productivity and recruitment are complex (Mitchell and Crisp 1981, Albon et al. 1983, Van Horne 1983, Hobbs and Swift 1985, Clutton-Brock et al. 1987, Hobbs and Hanley 1990), and such relationships should more fully and properly be explored.

While most of the variables representing landscape structure were indicative of composition, there is also some indication that landscape configuration can play a role in elk calf survival. The third top model included MPI (mean proximity index) which is a measure of isolation and fragmentation on the landscape; as "MPI increases patches become less isolated from patches of the same type and patch types become less fragmented in distribution" (McGarigal and Marks 1995:117). In the model, MPI increased as calf survival decreased, or in other words, calf survival decreased as similar patch types became closer or more common in the 500 m landscape surrounding the calves. We believe this is an indication that fragmentation (or possibly diversity within the landscape) on a fine scale may be more beneficial to elk calves than a homogenous landscape directly around them (500 m). Considering the variety of needs and potentially conflicting needs (e.g., open forage versus security) a cow/calf pair would have, it perhaps is not surprising that a landscape fragmented with several different types of cover types would be more beneficial. It could provide foraging opportunity for the cow and cover for the calf in close proximity in different cover types.

The modeling also quantified, within the data range of age at capture that we collected, that the hazard of death for calves in our study decreased 12-13% for every day the calf survives. Our estimated ages at capture ranged from day of birth (0) to 9 days old. Considering that black bear predation rate in many study areas occurs by 28 days (Singer et al. 1997, Barber et al. 2005, Raithel 2005, Rearden 2005) and the majority of black bear-caused mortality in our study had also ended by 28 days, this came as no surprise. If lethal or non-lethal deterrents to black bear predation were attempted during elk calving, the effectiveness of it would be magnified by concentrating just before, during, and after the peak of elk calving, which in many western regions is considered approximately mid-May to mid-June (Rust 1946, Johnson 1951, Flook 1970, Schlegel 1976, Smith et al. 1997, Raithel 2005, Rearden 2005).

Our modeling also demonstrated that male calves survived at a higher rate than female calves. The variable appeared in all 4 models and hazard of death for male calves in our study was just 62-65% that of females. The sex ratio of all radio-marked calf elk was 91 male:100 female (*n* = 351). There was some disparity between study areas however. The Lochsa sex ratio was 105 male:100 female (*n* = 152), and the South Fork sex ratio was 81 male:100 female (*n* = 199). Estimated birth dates did not differ between study areas or between male and females on the Lochsa, but estimated birth dates did differ ($P = 0.024$) between males and females on the South Fork. However, since the sex ratio favored females on the South Fork, it is unlikely that this skewed sex ratios toward more females. Since all other estimated birth dates between study areas and Lochsa male and female calves did not differ, it is unlikely that capture efforts confounded timing. Male calves grow faster (Smith et al. 1997), so it is possible they would have been bigger and potentially harder to catch.

Better summer male survival contradicts the findings of Smith et al. (1996) and Smith and Anderson (1998). Potentially, survival favoring males will alter sex ratios, and changes in sex ratios or different sex ratios can significantly alter growth rates of ungulate populations (Medin and Anderson 1979, Smith and Anderson 1998). Over time, a bias towards higher male survival rate potentially will continue to slow or negatively impact the herd's growth since in the following years, there would be fewer females recruited into the population and subsequently fewer calves born. Conversely, hunter opportunity may increase for young bulls. Singer et al. (1997) did not find that gender affected calf survival, but did find that estimated birth mass did. We did not find a direct link between estimated birth mass and calf survival but hypothesize that birth mass of each sex may influence why male calves survived better in our study. Male calves weighed significantly more then female calves on the Lochsa and while male calves birth mass was not statistically significantly different from female birth mass on the South Fork, biologically it was lower. Thus, with male calves putting more mass on per day than female calves (Smith et al. 1997), the expectation would be that male calves grow bigger at a faster rate, and since each day in the calves lives added 12-13% increase in survival, the cumulative effect is that male calves survive better because they get bigger at a faster rate. Also, although we were not able to test it from our data, there could be greater maternal vigilance for male calves if cows consider males a greater investment (Trivers and Willard 1973, Kohlmann 1999).
We did not detect a survival difference due to timing of birth as some studies have (Singer et al. 1997, Smith and Anderson 1996, Smith and Anderson 1998, Rearden 2005). Our capture operation typically lasted ~14 days, and almost all calves captured had an estimated birth date between 23 May and 12 June. Our birth dates do not have the spread of potentially some studies (Singer et al. 1997, Raithel 2005, Rearden 2005, Barber et al. 2005), but they do appear comparable when examining survival of calves born during the mid-peak and late-peak birthing period.

Our results suggest strongly that predators, specifically black bears and mountain lions, limited calf survival (Figure 7, Table 11). These results support our predictions that calf survival is influenced by level of predator harvest. Further, calf survival was influenced by cover type composition and cover type arrangement within 500 m of the calves (Table 11). We demonstrate that both predator density and landscape structure influence calf survival, and that attempting to change only predator density through predator harvest or to manipulate only habitat will likely meet with limited long term success.

Management Implications

A continual criticism of ungulate-predation studies is lack of experimental manipulation (Hurlbert 1984, Boutin 1992). While we could not test the results of differing levels of predator harvest under all scenarios of prey and predator densities, we did manipulate predator harvest at 3 levels (high, moderate, low) in the Clearwater drainage which resulted in differing responses in calf survival. While predator removal has received widespread support among management agencies as a means of increasing low ungulate densities (Gasaway et al. 1983, Ballard and Larsen 1987), studies without experimental manipulations are difficult to interpret (e.g., Schlegel 1976). Our results indicate that over the short term, predator harvest manipulation can impact calf survival. Predation, mostly by black bears and mountain lions, limited calf recruitment; and predation was largely additive with some compensatory mortality at the population levels we tested. Our results also indicated that landscape influences calf survival. Since our investigation of cover types was observational, experimental manipulation of cover types are likely needed to more fully understand how the current landscape impacts calf survival.

Managers should also be aware that elk calves vulnerability was predicted to decrease on a daily basis. Any lethal or non-lethal deterrents to black bear predation may be most effective in the months before and, if possible, during the calving period. Female calf susceptibility to mortality may in the long term slow population growth or increase the population decline.

Continued high levels of predator harvest over the long term are doubtful, both due to economics and social issues. Although an increase in black bear harvest resulted in fewer calves predated by bears, the "slack" in cause-specific mortality was picked up by mountain lions and, a newcomer on the scene, wolves. Further, long-term benefits of high predator harvest would eventually be limited in the Clearwater drainage if the basic fundamental assumption that habitat, primarily forage, affects animal condition at higher density levels, thus regulating population growth, yield, and density. Finally, what we observed clearly reasons that approaches to management of calf recruitment is seldom an either/or proposition, and a diverse approach needs to be taken.

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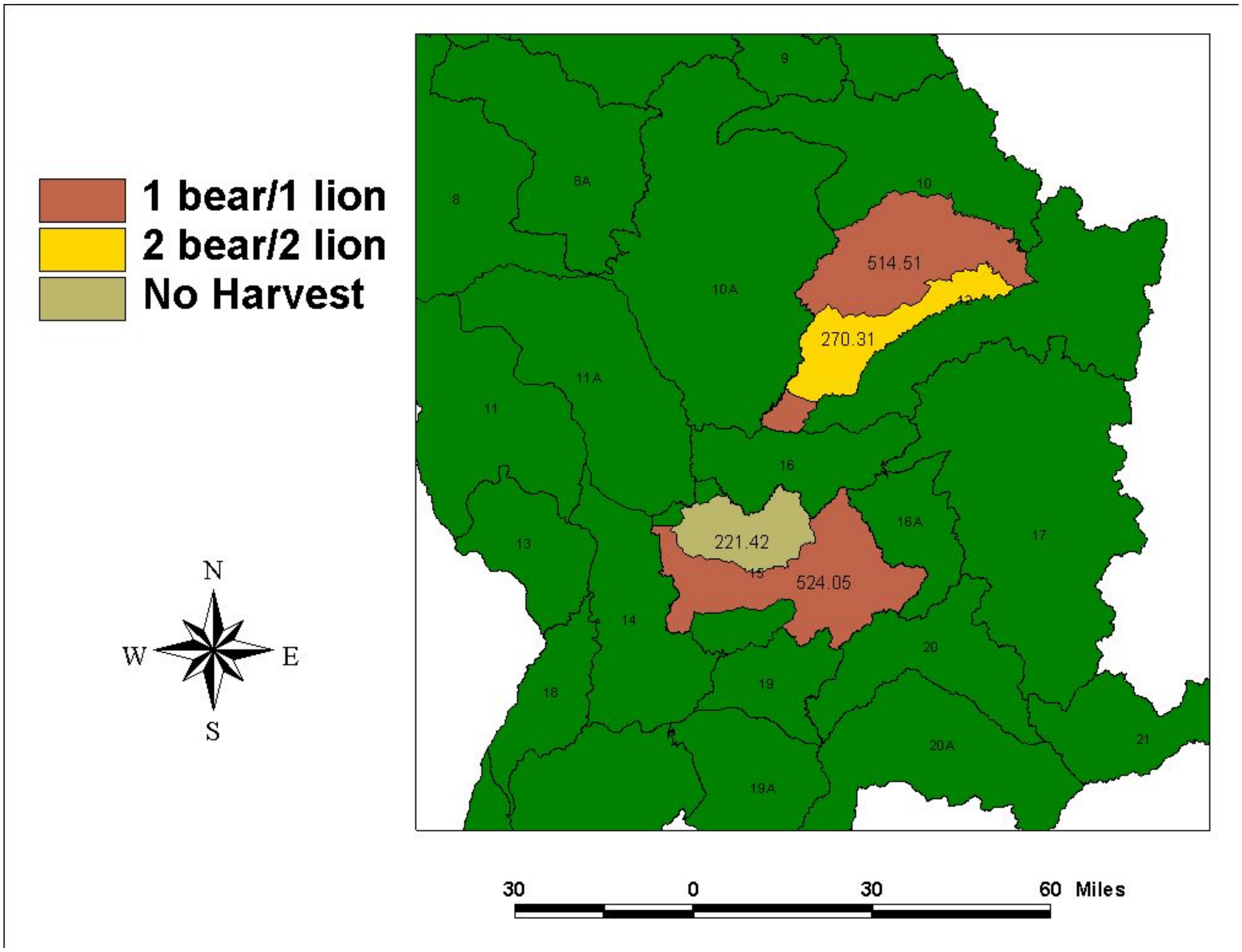

Figure 1. Lochsa and South Fork study areas in north-central Idaho, each subdivided into 2 spatial units to facilitate an experimental evaluation of the effects of black bear and mountain lion harvest on calf survival. The Lochsa study area was subdivided into a control area ("moderate harvest" at 1 bear and 1 lion tag/hunter/year) and a treatment area ("high harvest" at 2 bear and 2 lion tags/hunter/year). The South Fork study area was subdivided into a control area ("moderate harvest" at 1 bear and 1 lion tag/hunter/year) and a treatment area ("low harvest" where all legal harvest of bears and lions was eliminated).

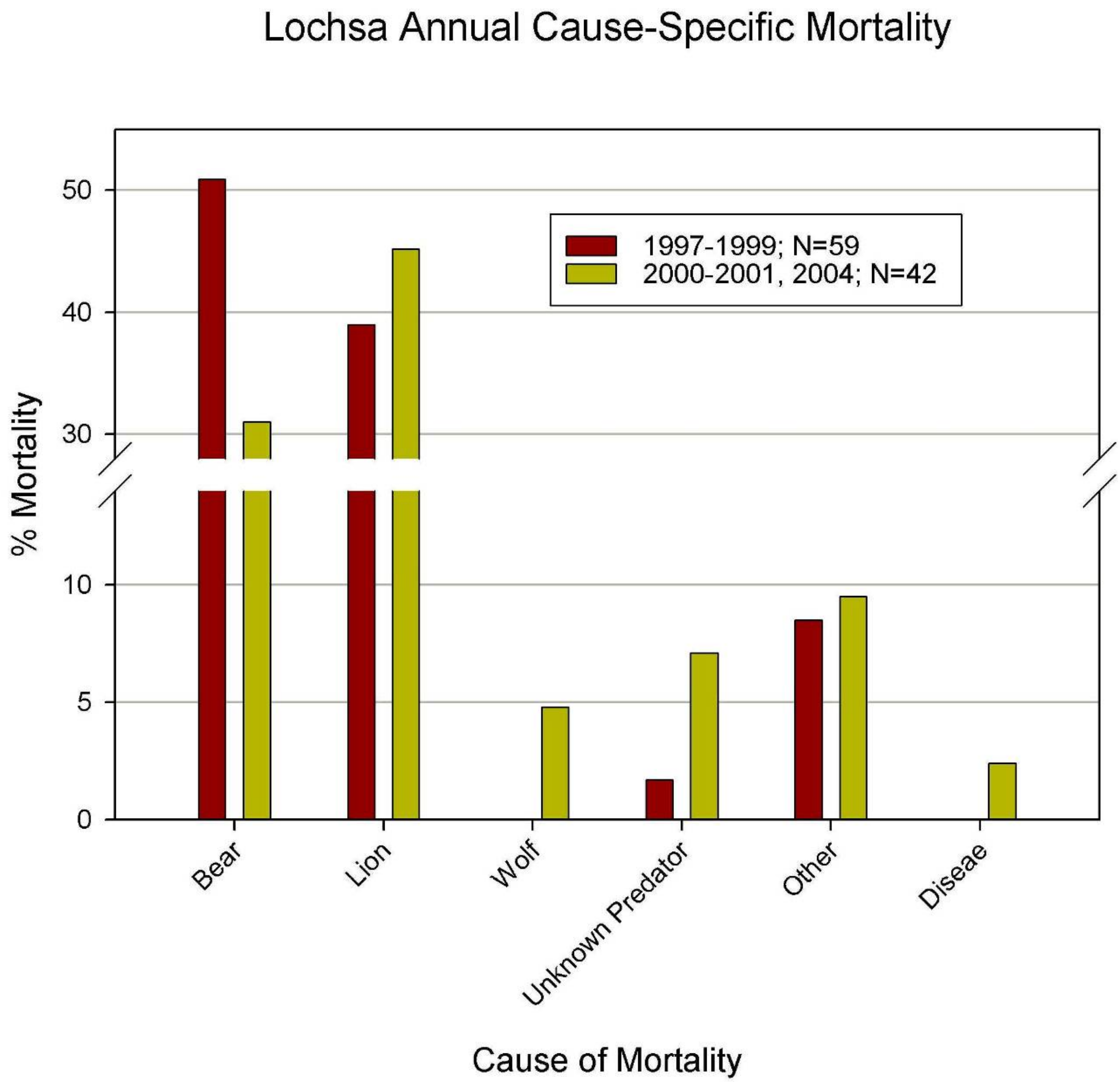

Figure 2. Annual cause-specific mortality on the Lochsa study area in north-central Idaho shifted after the black bear and mountain lion harvest levels where manipulated starting in fall 1999. Black bear caused calf deaths declined after the increase in bear harvest, while calf deaths from other predators increased.

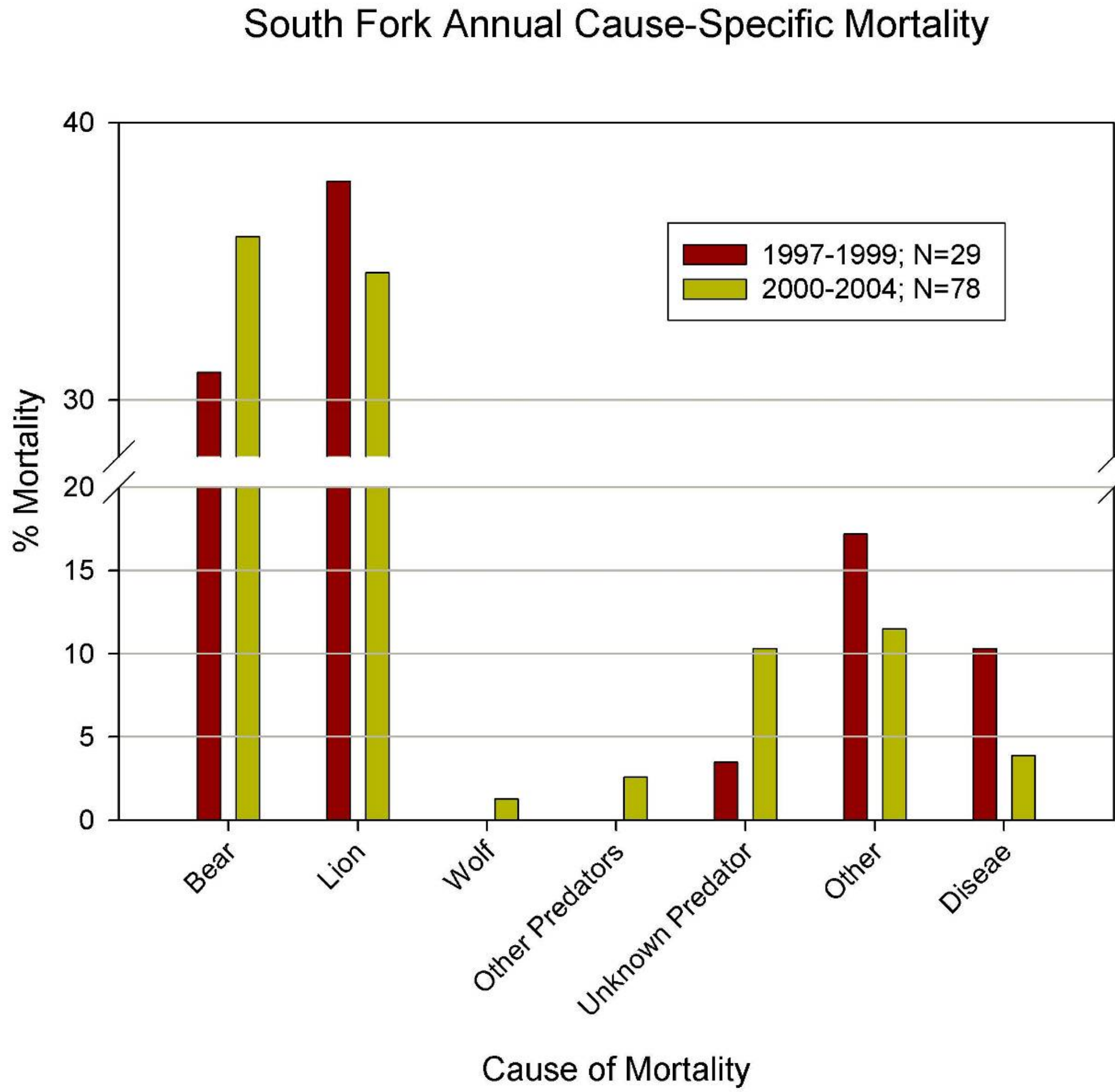

Figure 3. Annual cause-specific mortality on the South Fork study area in north-central Idaho shifted after the black bear and mountain lion harvest levels where manipulated starting in fall 1999. More elk calves were killed by black bears after the reduction in black bear and mountain lion harvest.

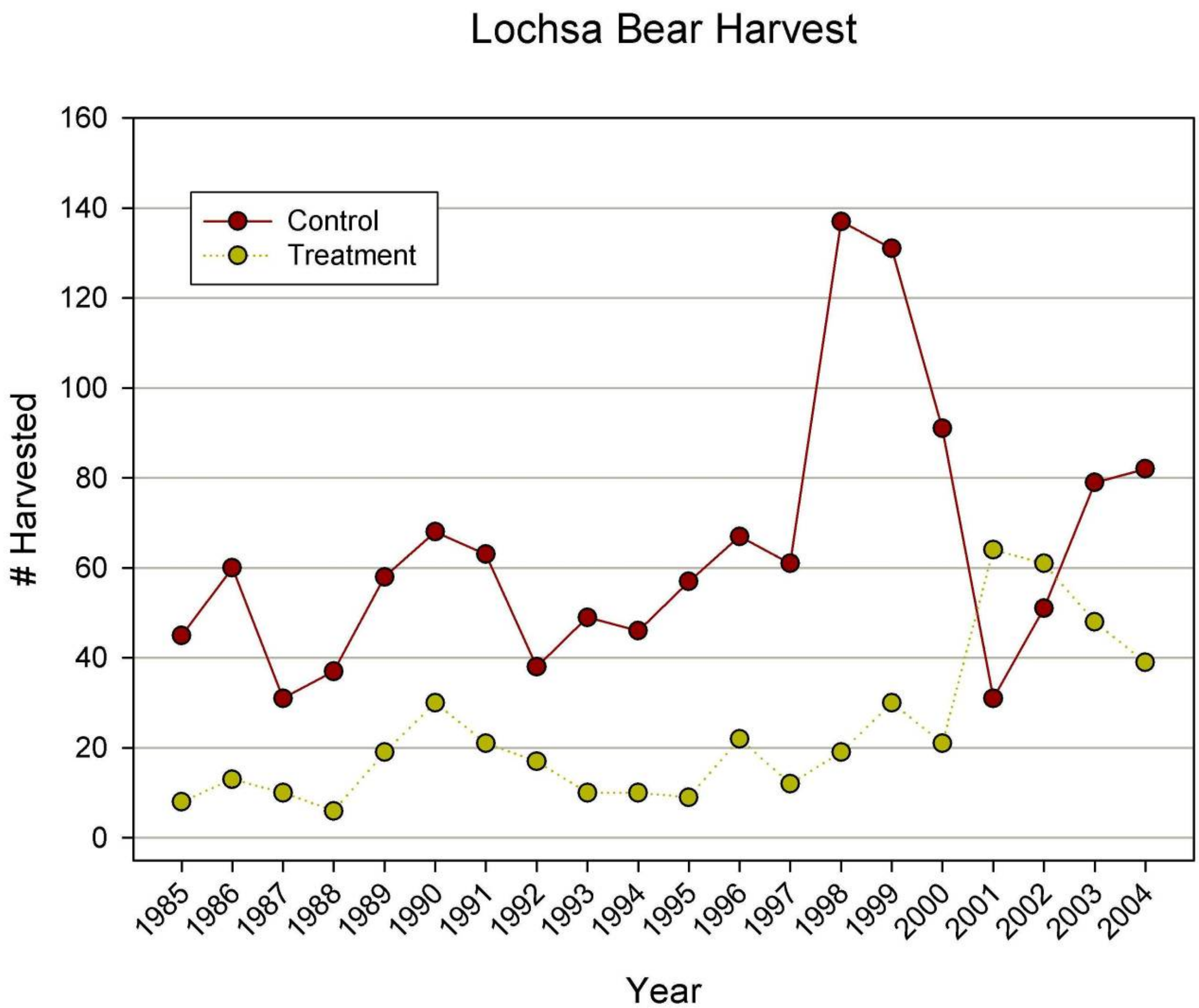

Figure 4. The black bear harvest level on the Lochsa study area in north-central Idaho was considered higher after harvest levels were manipulated starting in the fall of 1999.

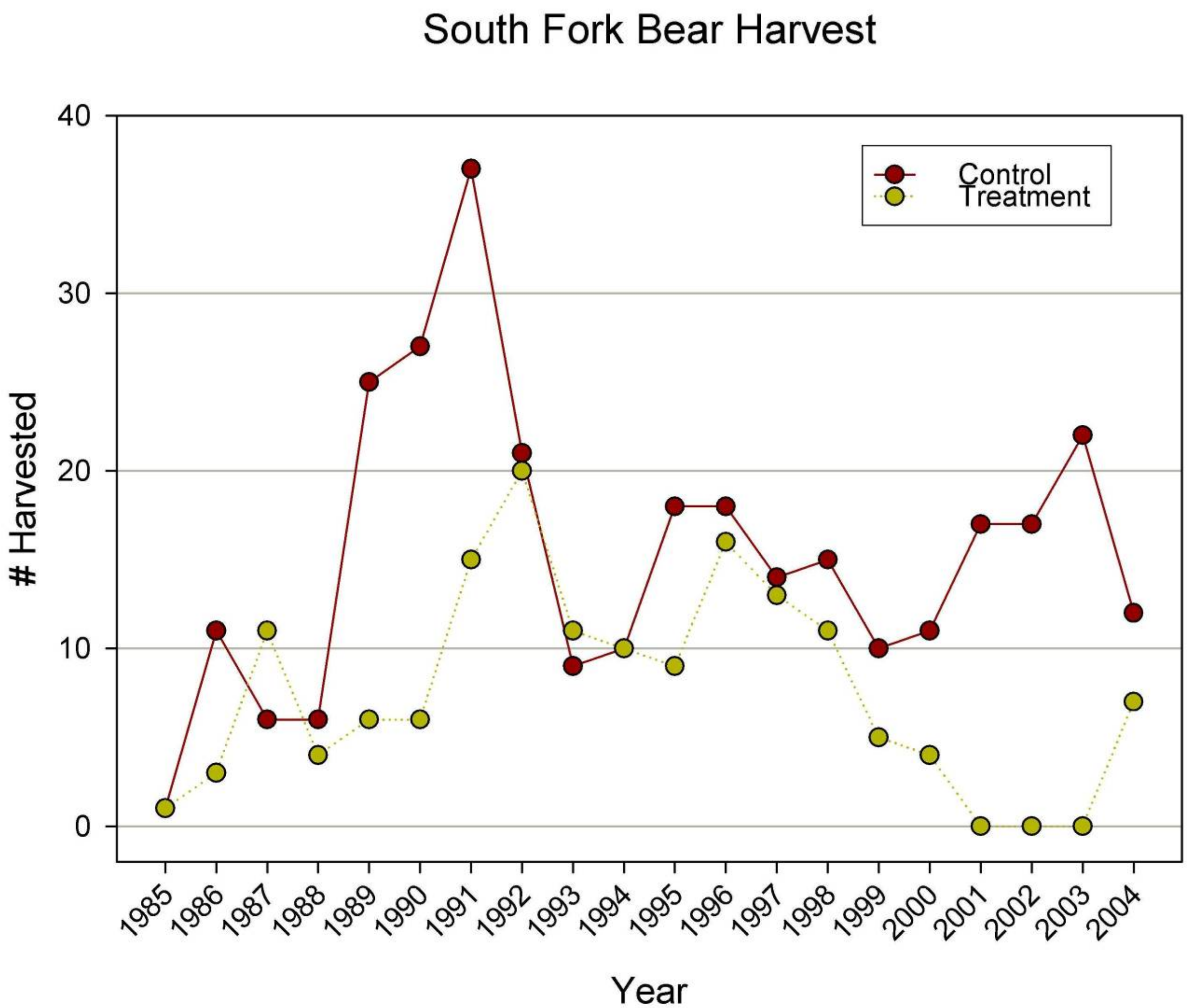

Figure 5. The black bear harvest level on the South Fork study area was considered moderate to low after harvest was removed on part of the study area as part of the predator manipulation treatment put into effect in the fall of 1999.

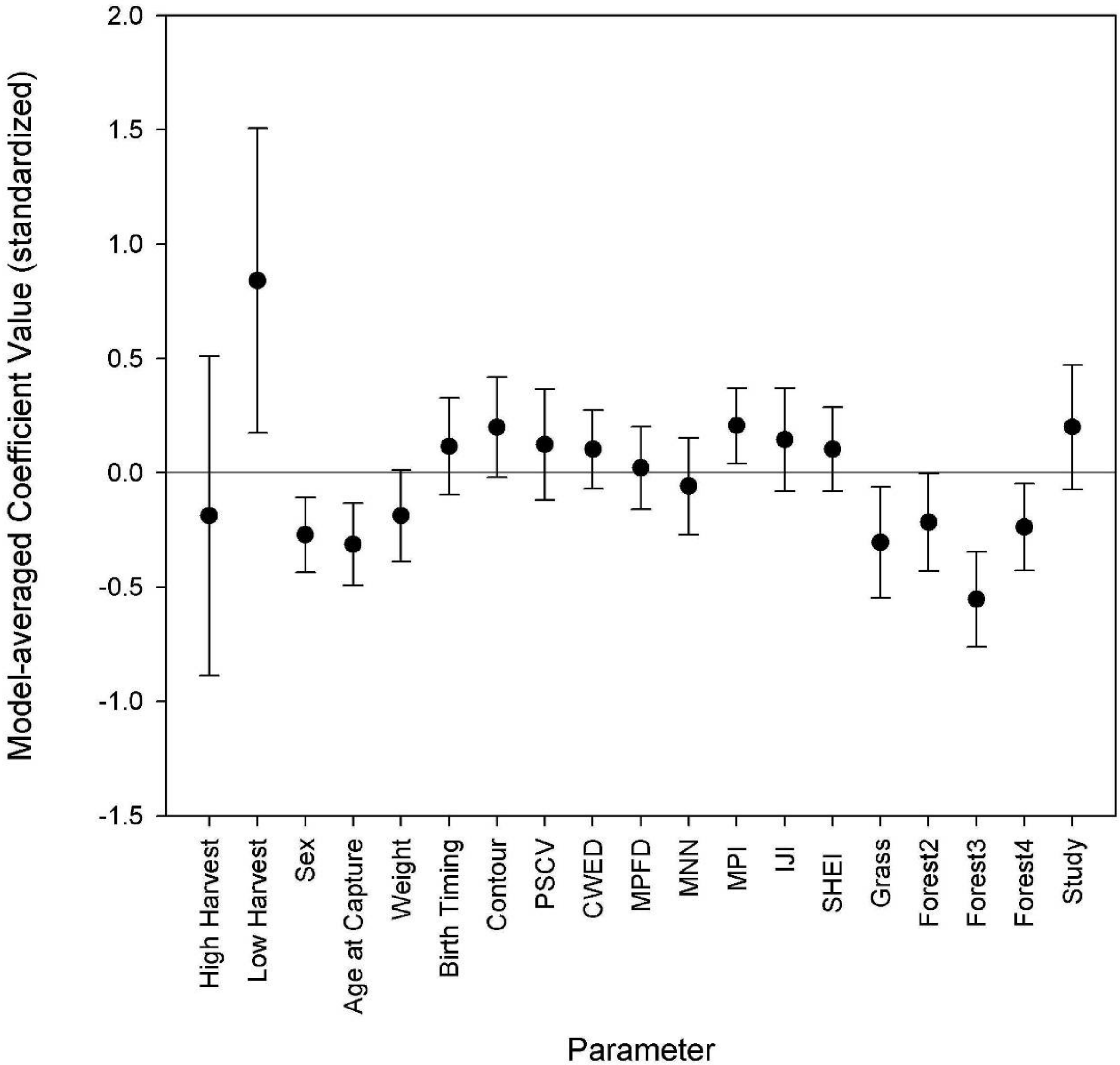

Figure 6. Model-averaged standardized coefficients and 95% CIs for predictor variables used in Cox's proportional hazard modeling to predict calf survival in north-central Idaho. Variables with 95% CIs that did not include 0 were considered to be strongly associated with relative prediction of calf survival.

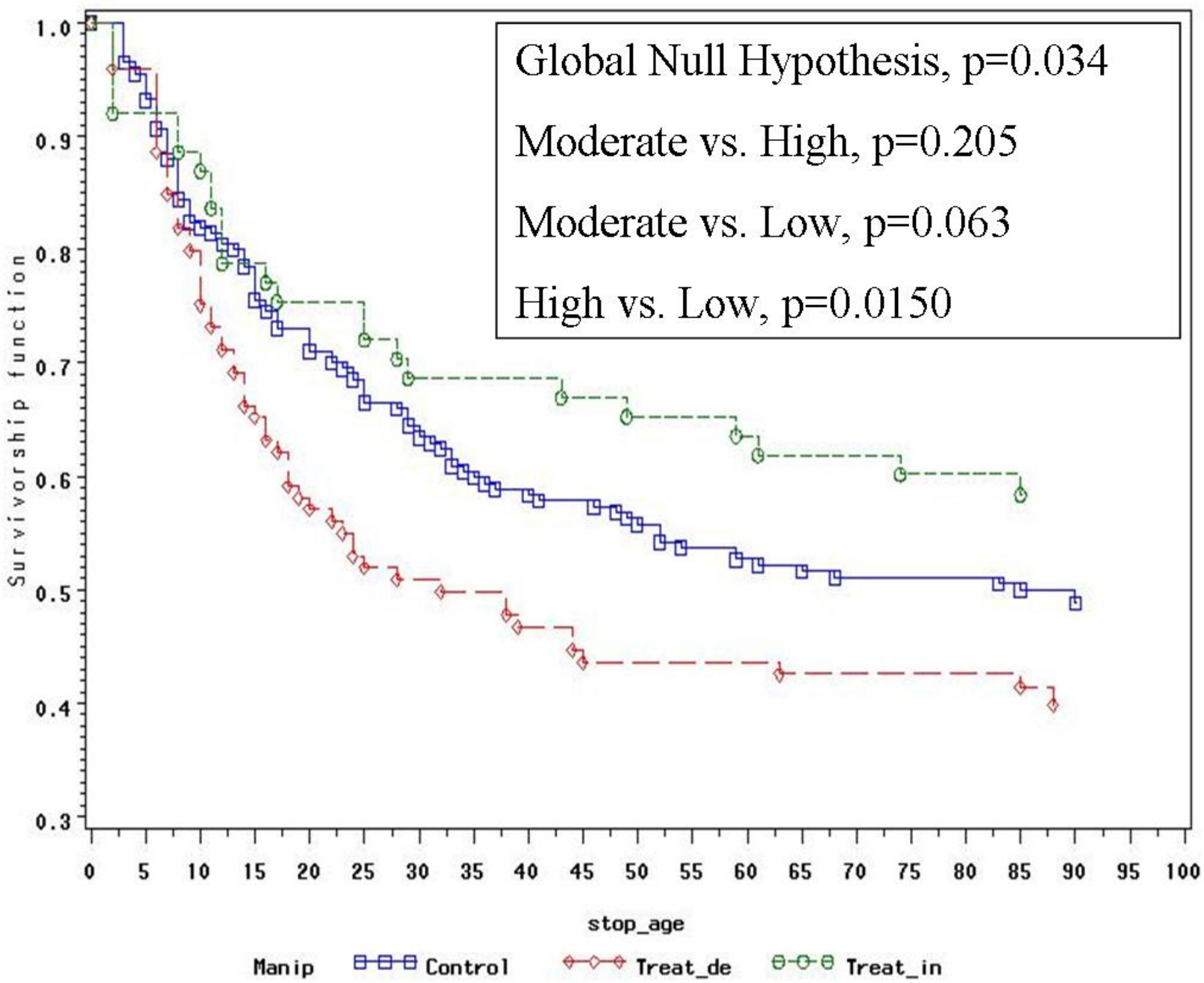

Figure 7. Elk calf survival curves for the summer period in north-central Idaho. Curves are depicting calf survival in relation to the 3 levels of black bear and mountain lion harvest (high, moderate, low). Also displayed are the statistical results from using the TEST statement in SAS (Allison 1995, SAS 2002) to test the hypotheses that the 3 harvest levels are similar.

Table 1. Description of landscape metrics used as predictor variables in development of Cox proportional hazard models for elk calf survival (1997-2004) in the Clearwater drainage of north-central Idaho.

Abbreviation	Units	Description[a]
Contour	m/ha	Contour density; computed by dividing total length of contour lines by total buffer area
PSCV	%	Patch size coefficient of variation
CWED	%	Contrast weighted edge density
MPFD	$1 \leq MPFD \leq 2$	Mean patch fractal dimension
MNN	m	Mean nearest-neighbor distance
MPI	$MPI \geq 0$	Mean proximity index
SHEI	$0 \leq SHEI \leq 1$	Shannon's evenness index
IJI	%	Interspersion and juxtaposition index
Grass	%	Percentage of landscape composed of grassland cover type
Forest 2	%	Percentage of landscape composed of forest cover type with 15-33% canopy cover
Forest 3	%	Percentage of landscape composed of forest cover type with 33-66% canopy cover
Forest 4	%	Percentage of landscape composed of forest cover type with >66% canopy cover

[a] See McGarigal and Marks (1995) for formulas and more detailed descriptions of habitat measures; excluding the Contour metric.

Table 2. Total number of deaths of radio-collared elk calves by cause from capture to 1 June of the following year, *n* = 355.

	Lochsa/North Fork							South Fork								
Cause of death[a]	1997	1998	1999	2000	2001	2004	Total	1997	1998	1999	2000	2001	2002	2003	2004	Total
Accident	2	0	0	0	0	1	3	0	1	0	0	0	0	0	0	1
Disease/starvation[b]	0	0	0	0	0	2	2	1	0	2	0	1	1	1	0	6
Unknown[c]	0	0	3	0	1	1	5	0	1	0	2	0	1	1	1	6
Predation																
Bear	10	7	13	5	7	1	43	5	3	1	2	15	5	4	2	37
Lion	8	7	8	13	2	4	42	4	5	2	5	4	6	8	4	38
Wolf	0	0	0	0	1	1	2	0	0	0	0	0	0	0	1	1
Bobcat	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Coyote	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Unknown[d]	0	0	1	1	0	2	4	1	0	0	0	1	4	1	2	9
Harvest[e]	0	0	0	0	0	0	0	1	2	0	2	0	0	1	1	7
N_m[f]	20	14	25	19	11	12	101	12	12	5	11	21	17	17	12	107
N_t[g]	21	16	29	22	17	28	133	19	20	17	16	25	23	24	23	167

[a] Tentative identification of causes of death; excludes deaths related to abandonment by cow presumably related to capture.
[b] Includes deformities.
[c] Cause of death unknown.
[d] Predation but unknown species.
[e] Including legal and illegal harvest.
[f] Total number of calf mortalities.
[g] Total number of calves vulnerable after subtracting abandonment by cow presumable related to capture, subtracting collars slipped before May of the following year, subtracting missing calves, and unknown fates.

Table 3. Total number of deaths of radio-collared elk calves by cause from capture to 31 August, *n* = 355.

	Lochsa/North Fork							South Fork								
Cause of death[a]	1997	1998	1999	2000	2001	2004	Total	1997	1998	1999	2000	2001	2002	2003	2004	Total
Accident	2	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1
Disease/starvation[b]	0	0	0	0	0	2	2	1	0	0	0	1	1	1	0	4
Unknown[c]	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	4
Predation																
Bear	10	7	13	5	7	0	42	5	3	1	2	15	5	4	2	37
Lion	6	5	6	11	1	2	31	1	5	2	1	3	5	6	2	25
Wolf	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0
Bobcat	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Coyote	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Unknown[d]	0	0	1	1	0	1	3	1	0	0	0	1	3	1	2	8
Harvest[e]	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2
N_m[f]	18	12	20	17	9	7	83	9	10	3	4	20	15	14	8	83
N_t[g]	22	17	29	26	19	30	143	29	21	18	17	25	25	28	23	186

[a] Tentative identification of causes of death; excludes deaths related to abandonment by cow presumably related to capture.
[b] Includes deformities.
[c] Cause of death unknown.
[d] Predation but unknown species.
[e] Including legal and illegal harvest.
[f] Total number of calf mortalities.
[g] Total number of calves vulnerable after subtracting abandonment by cow presumable related to capture, subtracting collars slipped before May of the following year, subtracting missing calves, and unknown fates.

Table 4. Proximate cause of death of radio-collared elk calves (%) from capture to 31 August, *n* = 355.

	Lochsa/North Fork							South Fork								
Cause of death[a]	1997	1998	1999	2000	2001	2004	Total	1997	1998	1999	2000	2001	2002	2003	2004	Total
Accident	11.1	0	0	0	0	0.0	2.4	0	10.0	0	0	0	0	0	0	1.2
Disease/starvation[b]	0	0	0	0	0	28.6	2.4	11.1	0	0	0	5.0	6.7	7.1	0	4.8
Unknown[c]	0	0	0.0	0.0	0.0	14.3	1.2	0.0	10.0	0.0	0	0	6.7	7.1	12.5	4.8
Predation																
Bear	55.6	58.3	65.0	29.4	77.8	0	50.6	55.6	30.0	33.3	50.0	75.0	33.3	28.6	25.0	44.6
Lion	33.3	41.7	30.0	64.7	11.1	28.6	37.4	11.1	50.0	66.7	25.0	15.0	33.3	42.9	25.0	30.1
Wolf	0	0	0	0	11.1	14.3	2.4	0	0	0	0	0	0	0	0	0
Bobcat	0	0	0	0	0	0	0	0	0	0	0	0	0	7.1	0	1.2
Coyote	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12.5	1.2
Unknown[d]	0	0	5.0	5.9	0	14.3	3.6	11.1	0	0	0	5.0	20.0	7.1	25.0	9.6
Harvest[e]	0	0	0	0	0	0	0	11.1	0	0	25.0	0	0	0	0	2.4
N_m[f]	18	12	20	17	9	7	83	9	10	3	4	20	15	14	8	83
N_t[g]	22	17	29	26	19	30	143	29	21	18	17	25	25	28	23	186

[a] Tentative identification of causes of death; excludes deaths related to abandonment by cow presumably related to capture.
[b] Includes deformities.
[c] Cause of death unknown.
[d] Predation but unknown species.
[e] Including legal and illegal harvest.
[f] Total number of calf mortalities.
[g] Total number of calves vulnerable after subtracting abandonment by cow presumable related to capture, subtracting collars slipped before May of the following year, subtracting missing calves, and unknown fates.

Table 5. Proximate cause of death of radio-collared elk calves (%) from capture to 1 June of the following year, *n* = 355.

	Lochsa/North Fork							South Fork								
Cause of death[a]	1997	1998	1999	2000	2001	2004	Total	1997	1998	1999	2000	2001	2002	2003	2004	Total
Accident	10.0	0	0	0	0	8.3	3.0	0	8.3	0	0	0	0	0	0	0.9
Disease/starvation[b]	0	0	0	0	0	16.7	2.0	8.3	0	40.0	0	4.8	5.9	5.9	0	5.6
Unknown[c]	0	0	12.0	0	9.1	8.3	5.0	0.0	8.3	0.0	18.2	0	5.9	5.9	8.3	5.6
Predation																
Bear	50.0	50.0	52.0	26.3	63.6	8.3	42.6	41.7	25.0	20.0	18.2	71.4	29.4	23.5	16.7	34.6
Lion	40.0	50.0	32.0	68.4	18.2	33.3	41.6	33.3	41.7	40.0	45.5	19.1	35.3	47.1	33.3	35.5
Wolf	0	0	0	0	9.1	8.3	2.0	0	0	0	0	0	0	0	8.3	0.9
Bobcat	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9	0	0.9
Coyote	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.3	0.9
Unknown[d]	0	0	4.0	5.3	0	16.7	4.0	8.3	0	0	0.0	4.8	23.5	5.9	16.7	8.4
Harvest[e]	0	0	0	0	0	0	0	8.3	16.7	0	18.2	0	0	5.9	8.3	6.5
N_m[f]	20	14	25	19	11	12	101	12	12	5	11	21	17	17	12	107
N_t[g]	21	16	29	22	17	28	133	19	20	17	16	25	23	24	23	167

[a] Tentative identification of causes of death; excludes deaths related to abandonment by cow presumably related to capture.
[b] Includes deformities.
[c] Cause of death unknown.
[d] Predation but unknown species.
[e] Including legal and illegal harvest.
[f] Total number of calf mortalities.
[g] Total number of calves vulnerable after subtracting abandonment by cow presumable related to capture, subtracting collars slipped before May of the following year, subtracting missing calves, and unknown fates.

Table 6. Black bear observations on Lochsa and South Fork study areas during aerial calf capture operations.

Year	Lochsa	South Fork
1997		
Bears/flying hour	1.68	0.09
Bear observations	94	7
1998		
Bears/flying hour	1.84	0.11
Bear observations	107	6
1999		
Bears/flying hour	1.15	0.12
Bear observations	60	7
2000		
Bears/flying hour	0.94	0.24
Bear observations	40	12
2001		
Bears/flying hour	0.85	0.09
Bear observations	46	4
2002		
Bears/flying hour	Not Flown	0.13
Bear observations		9
2003		
Bears/flying hour	Not Flown	0.05
Bear observations		3
2004		
Bears/flying hour	0.64	0.13
Bear observations	36	6

Table 7. Average harvest of mountain lions 6 years before and 6 years after the 1999 regulation change increasing the bag limit from 1 to 2 lions in the Lochsa treatment area; and eliminated harvest in the South Fork treatment area in north-central Idaho. Data presented corresponds to fall-winter lion seasons from 1993-2004 (e.g., fall 1993-winter 1994 season, fall 1994-winter 1995 season, fall 2004-winter 2005 season).

	South Fork		Lochsa	
Seasons averaged	Control	Treatment	Control	Treatment
1993-1998	22	13	10	6
1999-2004	12	1[a]	7[b]	8
Percent Change	-45	-92	-30	33

[a] Area was closed to harvest until the 2004-2005 lion season when 1 lion/hunter/year was allowed.
[b] Area changed to allow 2 lions harvested/hunter/year starting in 2003-2004.

Table 8. Survival rates (SE in parentheses) of radio-collared elk neonates from capture to 31 August using staggered KM procedure, *n* = 355.

	Survival rate[a]					
Year	Lochsa		South Fork		Combined	
1997	0.17	(0.08)	0.62	(0.10)	0.30	(0.13)
n[b]	27		31		58	
1998	0.27	(0.11)	0.53	(0.11)	0.42	(0.08)
n[b]	18		22		40	
1999	0.31	(0.09)	0.67	(0.20)	0.49	(0.07)
n[b]	31		19		50	
2000	0.32	(0.10)	0.74	(0.11)	0.44	(0.09)
n[b]	27		17		44	
2001	0.53	(0.11)	0.23	(0.08)	0.35	(0.07)
n[b]	20		29		49	
2002			0.40	(0.10)		
n[b]			28			
2003			0.43	(0.11)		
n[b]			30			
2004	0.68	(0.12)	0.64	(0.10)	0.64	(0.09)
n[b]	31		25		56	

[a] Excludes deaths associated with abandonment by cow presumably related to capture.
[b] Total number of radio-collared calves used in survival analysis.

Table 9. Annual survival rates (SE in parentheses) of radio-collared elk calves using staggered KM procedure, $n = 355$.

	Survival rate[a]					
Year	Lochsa		South Fork		Combined	
1997	0.06	(0.05)	0.51	(0.10)	0.26	(0.08)
n[b]	27		31		58	
1998	0.16	(0.09)	0.43	(0.11)	0.31	(0.07)
n[b]	18		22		40	
1999	0.14	(0.06)	0.57	(0.18)	0.34	(0.07)
n[b]	31		19		50	
2000	0.23	(0.09)	0.31	(0.12)	0.25	(0.07)
n[b]	27		17		44	
2001	0.41	(0.12)	0.18	(0.08)	0.28	(0.07)
n[b]	20		29		59	
2002			0.31	(0.09)		
n[b]			28			
2003			0.34	(0.10)		
n[b]			30			
2004	0.46	(0.15)	0.47	(0.10)	0.36	(0.16)
n[b]	31		25		56	

[a] Excludes deaths associated with abandonment by cow presumably related to capture.
[b] Total number of radio-collared calves used in survival analysis.

Table 10. Best[a] and top[b] models' corrected Akaike's Information Criteria (AICc), ΔAICc, and AICc weights from the Cox's Proportional Hazard Model regression analysis of elk calf locations in the Clearwater drainage, north-central Idaho, $n = 355$. Models were stratified by year which is almost like blocking by that variable. Model rank was simply done by assigning a 1 to the model with the lowest AICc score, a 2 to the model with the next lowest AICc score, and so on.

Model rank	Variable[c]	AICc	ΔAICc	AICc weights
1	Increase predator harvest, Decrease predator harvest, % Forest 3, Age, Gender, % Grass	1041.64	0.000	0.172
2	Increase predator harvest, Decrease predator harvest, % Forest 3, Age, Gender, MPI	1041.85	0.192	0.154
3	Increase predator harvest, Decrease predator harvest, % Forest 3, Age, Gender, % Forest 4	1042.36	0.720	0.120
4	Increase predator harvest, Decrease predator harvest, % Forest 3, Age, Gender, % Forest 2	1043.28	1.640	0.076

[a] The model with the lowest AICc score.
[b] The model(s) within 2 AICc scores of the best model.
[c] The predator manipulation variable had 3 levels (high harvest, moderate harvest, low harvest) and is represented by 2 dummy variables (high harvest, low harvest).

Table 11. Best[a] and top[b] models' coefficients (B) and standard errors (SE); and hazard ratio (HR) and 95% Confidence Interval (CI) from the Cox's Proportional Hazard Model regression analysis of elk calf locations in the Clearwater drainage, north-central Idaho, (*n* = 355). If HR is >1, there is a positive, increasing relationship between mortality and the predictor variable. If HR is <1, there is a negative, decreasing relationship between mortality and the predictor variable. If the CI of HR includes 1, then it is difficult to interpret the relationship between the mortality rate and the predictor (Montgomery 2005). Models were stratified by year. Model rank was simply done by assigning a 1 to the model with the lowest AICc score, a 2 to the model with the next lowest AICc score, and so on.

Model rank	Variable[c]	B	SE	HR	95% CI	
1	High harvest	-0.472	0.247	0.624	0.384	1.013
	Low harvest	0.645	0.195	1.905	1.299	2.794
	% Forest 3	-0.041	0.007	0.960	0.946	0.973
	Age	-0.133	0.036	0.876	0.816	0.939
	Gender	-0.472	0.160	0.624	0.456	0.853
	% Grass	-0.025	0.012	0.975	0.953	0.998
2	High harvest	-0.442	0.248	0.643	0.395	1.044
	Low harvest	0.567	0.182	1.763	1.234	2.517
	% Forest 3	-0.044	0.007	0.957	0.944	0.970
	Age	-0.139	0.036	0.870	0.811	0.934
	Gender	-0.479	0.160	0.619	0.453	0.848
	MPI	0.008	0.003	1.008	1.002	1.014
3	High harvest	-0.425	0.247	0.654	0.403	1.061
	Low harvest	0.524	0.177	1.689	1.195	2.388
	% Forest 3	-0.045	0.007	0.956	0.943	0.968
	Age	-0.136	0.036	0.872	0.813	0.936
	Gender	-0.443	0.160	0.642	0.469	0.879
	% Forest 4	-0.017	0.007	0.983	0.970	0.997
4	High harvest	-0.497	0.248	0.608	0.374	0.989
	Low harvest	0.614	0.188	1.847	1.276	2.675
	% Forest 3	-0.043	0.007	0.958	0.945	0.971
	Age	-0.134	0.036	0.874	0.815	0.938
	Gender	-0.467	0.160	0.627	0.459	0.857
	% Forest 2	-0.026	0.011	0.974	0.953	0.996

[a] The model with the lowest AICc score.
[b] The model(s) within 2 AICc scores of the best model.
[c] The predator manipulation variable had 3 levels (high harvest, moderate harvest, low harvest) and is represented by 2 dummy variables (high harvest, low harvest).

Submitted by:

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IDAHO DEPARTMENT OF FISH AND GAME

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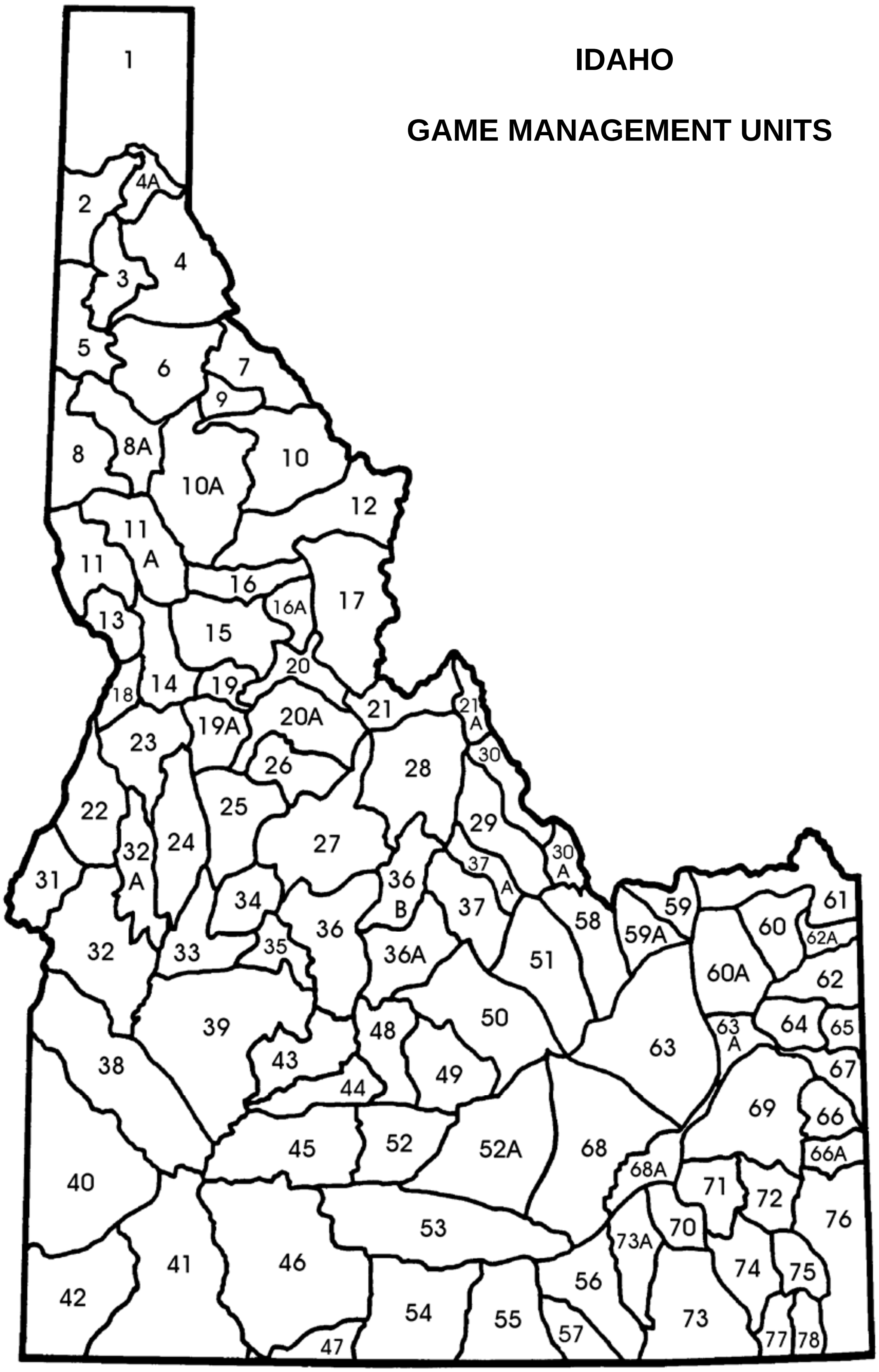
IDAHO

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.