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ELK MODELING AND ECOLOGY

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**COMPLETION REPORT
STATEWIDE WILDLIFE RESEARCH**

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ELK MODELING AND ECOLOGY

Abstract

STUDY I: Age determination for adult elk (*Cervus elaphus*) is routinely conducted using tooth wear or cementum annuli with a maximum accuracy of 3-4 months. Researchers studying neonatal elk find it difficult to use these techniques for accurate estimates of age. We developed a model for predicting age of an elk calf during the first 2 weeks of life using morphometric variables. Body measurements were collected from 83 captive elk calves used in a feeding experiment at Starkey Experimental Forest and Range Station, near LaGrande, Oregon. Linear, mixed effects models were used to evaluate the relationship between age and body measurements easily acquired in the field. Random effects were added to the models to accommodate the correlation due to nutritional, environmental, and genetic variation, and to broaden the applicability of these models to wild populations. The best models for predicting age included tooth length, mass, and a hoof measurement. From model validation, we calculated a 1.5 days average deviation between the true age and the predicted age. This mixed effects model will aid researchers exploring survival, recruitment, and birth patterns of young elk.

STUDY II: We studied the effect of habitat use, hunting season structure, and hunter density on mortality of bull elk during hunting season. Previous research has established road density, hiding cover, and topography as important proximate factors related to mortality. Although these previous studies have similar results, they are not directly comparable because different models were used, environmental factors were calculated in different ways, and factors were measured at varying scales. We determined whether relationships between environmental factors and mortality were similar for bull elk living in different habitat types and under various hunting management strategies. To explore this question, we related 8 variables to mortality rates using Cox's proportional hazards models. We examined factors at 2 spatial extents for 3 populations of elk from 4 different studies conducted between 1985 and 1994. Predictive capabilities of mortality models were explored with concordance (c) and Somers' D statistics. Relationships between mortality and hunting season structure and habitat use differed among study areas and between spatial extents. For example, increasingly rough terrain provided more protection for elk in 2 populations, while it was related to higher mortality rates for the third. Overall, our results demonstrated that elk exhibit a variable and flexible adaptive behavior to hunting pressure in each area. Although predictive capabilities of models were poor ($c < 0.5$), our results provide a better understanding about differences among elk vulnerability in different areas. Because our

models relate road density, habitat configuration, and hunting season structure to mortality in various ecosystems, they provide site-specific management tools to enhance coordination of elk hunting among multiple state and federal agencies in the inland Northwest.

STUDY I: AGE ESTIMATION & GROWTH OF ROCKY MOUNTAIN ELK CALVES

Background

Accurate estimation of age can impart important information about age-specific survival, fecundity, dispersal, recruitment, habitat use, and behavior of wild ungulates. Because of its importance, numerous methods have been developed to determine age of adult animals (Dimmick and Pelton 1996). Most of the techniques for cervidae are used to determine age within 1 to 1.5 years for adult animals. These methods include eye lens mass and bone structure development for animals already dead, whereas, techniques for live animals utilize tooth wear, teeth growth marks, and cementum annuli (Brown and Chapman 1991, Dimmick and Pelton 1996, Azorit et al. 2004). Daily and weekly estimates of age for live cervids cannot be determined using these techniques.

Although not as important for older age classes, daily and weekly age estimates for calves and fawns allow researchers to address questions related to neonatal mortality, age-specific survival, birth distributions, body growth, and recruitment. Obtaining weekly or daily estimates for newborn wild animals is especially challenging because young are often difficult to find and usually hard to capture during radio-collaring and tagging operations (Bartush and Garner 1979, Verme and Ullrey 1984). They also grow rapidly within the first few weeks of life and vital parental information is often unavailable. Additionally, calves and fawns spend the early part of life in hiding, making re-sighting and recapture difficult. All of these factors make capture events critical opportunities to obtain age information from easily measured characteristics.

Specifically for elk, there have been several approaches to aging newborns. First, Johnson (1951) presented a variety of qualitative methods for determining age of elk calves using various criteria, such as mass ranges, tooth length ranges, hair wetness, and condition of the umbilical cord. He developed age categories (0-1, 2-4, 5-7, 8+ days) for several characteristics of wild elk calves captured in the Gallatin River Basin of Montana. Another method was modified from quantitative techniques developed for white-tailed deer fawns (*Odocoileus virginianus*). Haugen and Speake (1958) developed the method, later modified by Sams et al. (1996), that related growth of the hoof to date of birth with regression models. Because hoof growth occurs from the leg hairline down, the distance between the hairline and a ridge on the hoof was used as the main predictor of age (Figure 1 [C]). A third approach estimated date of birth of elk calves using umbilicus condition, tooth eruption, and mass for newborn calves near Yellowstone (Smith et al. 1997). This method was developed from captured, wild neonates of unknown age. Although these techniques were adapted or developed for use in elk, they have never accounted for the full range of variation that one may encounter in elk calf development nor have any of these models been validated.

In this study, we expanded on methods of aging neonates by using mixed effects models and exploring the adequacy and fit of the selected model.

Objectives

Using data from captive animals, we had 4 objectives:

1. Develop a statistical model to predict age for Rocky Mountain elk calves (*C. e. nelsoni*) using morphological measurements that are non-lethal and easy to implement in the field.
2. Compare the statistical model to Johnson's (1951) aging criteria.
3. Determine if the captive calves were representative of elk calves from other experimental and wild populations.
4. Determine if individual variation in size could be explained by maternal nutrition.

Methods

Between 1996-1998, 83 Rocky Mountain elk calves were born from 63 captive cows at the Starkey Experimental Forest and Range Station (Starkey), near LaGrande, Oregon. Each mother had 1 calf per year, but some cows had a calf in consecutive years. During the first 2 weeks after birth, each calf was measured and evaluated 1 to 14 times ($n = 981$ total measurements). Day 0 was the calf's birthday and all calves were not measured every day. Three morphometric measurements were recorded: mass (kg), hoof length (cm), and length of outer edge of tooth (cm). More detailed descriptions of the measurements can be found in Figure 1 and Table 1.

Mothers, or dams, and calves were part of a summer-autumn and winter experimental feeding study designed to test the impact of nutrition on lactation, pregnancy, dam health, and survival of both mother and calf (Cook et al. 2004). Before the rut, in 1996, dams were randomized to 3 different summer-autumn nutritional feeding treatment groups (SAFG): high, medium, and low (Appendix A [Table 1]). These feeding groups restricted the mother's digestible energy intake. During winter of the first year, all cows were placed on a restricted winter diet (high diet) to initiate a 10% body mass loss (Appendix A [Table 2]). The next year of the study, dams were re-randomized to new SAFGs (Appendix A [Table 1]). Additionally, in 1998, non-lactating cows in the highest SAFG were randomized to 3 winter feeding levels: high, medium, and low (Appendix A [Table 2]). Eight yearling cows were also added to the study, but were given no dietary restrictions. For more details and descriptions of feeding levels, see Cook et al. (2004). Animals were handled in accordance with care and handling guidelines developed for Starkey (Wisdom et al. 1993).

To predict age between 0 and 14 days, we constructed regression equations using linear mixed effects models (Pinheiro and Bates 2000). Models were fit using the nlme package in R (Hornik 2005). Although data were collected in a longitudinal, repeated measures manner, under experimental conditions, we added random effect to allow the model more flexibility for 2 reasons. First, various aspects of an individual's growth may show some stochastic variation among calves. Some individuals may be intrinsically fast growers or slow growers (Diggle et al. 2002). Second, random effects allowed model inferences to apply to other animals, such as wild neonates sampled at random (Ott et al. 2000, Pinheiro and Bates 2000, Diggle et al. 2002). We

explored models containing fixed, main, higher order, and interaction terms and both random slopes and intercepts. A general form of the model containing both fixed and random slopes can be written as

$$Y = X\beta + Zb + \varepsilon \quad \text{Eq. 1.1}$$

$$b \sim N(0, D)$$

$$\varepsilon \sim N(0, \Sigma),$$

where Y was a vector of age measurements for each calf, X was a matrix of individual calf measurements for each age, β was a vector of mean intercept and slopes, Z was a subset of the individual calf measurements, b was a vector of random effects terms that represented random variation around the population means, D was composed of compound symmetric submatrices multiplied by a constant $\sigma_{s_i}^2$ for each intercept and slope measuring between-calf differences, and Σ was a within-calf error variance-covariance matrix (Pinheiro and Bates 2000). For example, one of the models explored can be written as

$$Y = (\beta_0 + b_0) + (\beta_1 + b_1) * Weight + (\beta_2 + b_2) * Tooth^2 + (\beta_3 + b_3) * Tooth + (B_4 + b_4) * Hoofline + (B_5 + b_5) * Sex + (D + \Sigma), \quad \text{Eq. 1.2}$$

where $\{\beta_0, \beta_1, \dots, \beta_6\}$ are the fixed slope for each variable, $\{b_0, b_1, \dots, b_6\}$ are the random slopes, $Weight$ was the weight of the calf measured at each age, $Tooth$ was the length of the outer edge of the first incisor, and $Hoofline$ was the distance between the hairline and indentation on the hoof measured at each age.

We made the assumptions that 1) the model was correctly specified; 2) the conditional residuals and residuals for each random effect were homogenous, homoscedastic, and normally distributed within and among groups; and 3) covariance structures D and Σ are independent. Model assumptions 1 and 2 were explored graphically (Pinheiro and Bates 2000).

We used Akaike's Information Criteria for small sample sizes (AICc) and likelihood ratio tests computed with restricted maximum likelihood (REML) estimates to compare nested models with different random effects (Pinheiro and Bates 2000, Burnham and Anderson 2002). AICc and likelihood ratio tests computed with maximum likelihood (ML) estimates were used to compare models with differing fixed effects. Model fit was examined by plotting predicted vs. observed values.

The within-calf error structure, Σ , could potentially result from auto-correlated, repeated measurements taken on the same calf. Autocorrelation, or serial correlation, might occur because an animal's growth may be the response of a time-varying, biochemical or physiological, stochastic process occurring within the animal (Diggle et al. 2002:82). The physical processes may make measurements taken close together in time more related than measurements taken farther apart. Various autocorrelation structures for the within-calf variation were added to the model. Models with different autocorrelation structures were assessed graphically with empirical

semi-variograms and models were compared using AICc computed with REML estimates (Pinheiro and Bates 2000).

Once the predictive model was parameterized, we explored the local sensitivity and elasticity of the model. Local sensitivity (S) attempts to give a measure of the relative change in the response based upon a percent increase in a parameter estimate with all other parameters held constant (Jorgenson and Bendoricchio 2001). S was calculated by [% change in age] / [% change in the parameter estimate]. To determine S for each fixed effect parameter estimate, we held the input, X , values constant and altered the parameter estimates 10-80%. Age was predicted with the altered models and percent change from the original age was evaluated for each percent change in a parameter estimate. We also determined the average elasticity (E) of the response variable with respect to each fixed effect. For a linear model, average elasticity was calculated by multiplying the *slope* by $[\bar{X} / \bar{Y}]$, where \bar{X} was an average body measurement and \bar{Y} was average age (Gujarati 1995). Average elasticity measures the average percent change in Y for a given percent change in X with all of the other variables held constant (Cooper et al. 2002). For example, an elasticity of 0.45 for mass implies a 1% increase in mass (kg) would lead to a 0.45 % increase in age, with all other variables held constant. Additionally, to address model sensitivity to feeding levels, we fit separate models for calves from each maternal SAFG and compared parameter estimates and prediction capabilities.

Models were validated using a 10-fold cross validation technique (Harrell 2001). Using this method, we randomly split the data into 10 groups. We removed 1 group of data, refit the model with the calibration subset (9 subsets) and predicted age of the calves for the removed validation subset (gregmisc package, R). This process was repeated 10 times. A prediction error, or loss value (D) was calculated for each validation subset, where $D = \sum (\hat{y}_i - y_i)^2$, or the sum of squared deviations between the i th ($i = 1, \dots, n$) prediction and known age (Geisser 1975, Browne 2000). If the predicted ages and true age of the calves matched, D would equal zero. The loss values were then averaged to obtain an average loss for all 10 repetitions (Geisser 1975, Browne 2000). Prediction errors were also calculated for each age. Loss values were also grouped by age to determine which age categories the models predict best.

An additional data set was also used for validation. This data set contained 48 mass, hoof, and tooth measurements from 32 elk calves at Moscow Mountain Elk Ranch (MMER), near Moscow, Idaho. These calves were hybrids of Rocky Mountain, Manitoban (*C. e. manitobensis*), and Roosevelt elk (*C. e. roosevelti*), and were raised in captivity for antler and meat production. Predicted ages were obtained using the full mixed effects model (see Eq. 1.2). A loss value (D) was calculated to determine prediction error between estimated and known age for the MMER elk calves.

Ages for both Starkey and MMER calves were estimated using Johnson's (1951) aging criteria. Measurements of the outer edge of the first incisor were compared to Johnson's dentition age categories (Johnson 1951:398). We first placed calves in an age category (0-1 days, 2-4 days, 5-7 days, and ≥ 8 days). Then, a more refined age was determined using the limits of the range for each category. For example, if an animal's tooth length was 0.8 mm, we would have placed it in the 0-1 days category and then assigned it an age of 0 because it was closer to the smallest value

in the range for the 0-1 days category reported by Johnson (1951). Model predicted ages and estimates obtained using Johnson's (1951) criteria (Johnson's ages) were compared graphically to known ages.

We also applied the model to a wild population of elk calves captured and radio-collared along the Lochsa and North Fork and South Fork of the Clearwater (Lochsa) rivers (P. Zager, Idaho Department of Fish and Game, unpublished data). We used our mixed effects model to predict age of wild newborns whose true ages were unknown. Age was also predicted using Johnson's (1951) aging criteria. The 2 methods were compared graphically.

The relationship between model predicted ages and ages from Johnson's criteria were explored using ANCOVA for the 3 groups of elk calves: Starkey, MMER, and Lochsa (Proc GLM, SAS 8.2). This relationship was explored because we hypothesized that if calf growth was similar in the 3 populations, the slope of the regression between model predictions and Johnson's (1951) age estimates should be the same.

For our third and fourth research objectives, differences in birth mass at 1-day-of-age, increase in mass over time, daily mass gain, tooth growth, and hoof growth were tested to determine if there were significant differences between sexes, years, and the 1996-1997 SAFGs. These factors were explored using ANOVAs and a repeated measures MANCOVA in SAS (Proc Mixed, SAS 8.2). We did not explore the 1997-1998 data for differences among SAFGs because we could not separate the effects of summer-autumn feeding treatments from winter feeding treatments. Finally, values for birth mass and daily mass gain were obtained from the literature to determine if elk calves from this study were comparable to elk calves from wild and other captive populations. Available means and standard errors were reported.

Results

Mixed Effects Model

Models to predict age were built using 4 independent variables collected on elk calves. Because not all measurements were taken at every period of observation, we only used measurements that contained complete records for sex, mass, hoof, and tooth. Models were built using 609 observations from 64 calves (62% of total measurements). For the predictive model, we explored all random effects and fixed effects combinations and interactions. The final model was chosen because it best met the assumptions of a linear mixed effects model, was the best model using likelihood ratio tests, and had a low AICc. Because prediction was the intention of the modeling exercise, the model with the lowest AICc was not chosen because it did not adequately meet assumptions. Seven models containing different fixed effects using maximum likelihood methods are compared in Table 2.

The final model contained a random intercept for each calf, random slopes for mass, hoof, tooth and tooth squared, a moving average autocorrelation structure with a step of 2, and all fixed effects (intercept, sex, mass, hoof, tooth and tooth squared). All terms in this model were significant at the 0.05 level (Table 3). Predicted values were very similar to observed ages

(Figure 2). The intercept and mass parameter estimates seemed to be the most sensitive, while the tooth and hoof values had the highest elasticities (Table 3).

For the 10-fold cross validation of the final model, we randomly subdivided the number of calves into 10 approximately equal subsets to be used for prediction. Because there were missing measurements for each calf, we were unable to get exactly equal subsets. Using each of these random subsets, we obtained predicted ages from the models and calculated a loss value and average loss value for the differences between observed and predicted ages. Average loss values ranged between 0.81 and 7.2 days² with a mean $D/n = 3.6$ days². For subsets with a low average loss value, such as subset 10 with $D/n = 0.95$ days², the predicted and observed values had a good 1-to-1 linear relationship (Figure 3). For subsets with a higher average D/n , there appeared to be 1 (subset 6, $D/n = 7.2$ days²) or more calves (subset 8, $D/n = 3.5$ days²) for which the model predicted very poorly. For the additional validation data set (MMER calves), the average loss value between predicted and observed ages was 10.4 days². The final model consistently predicted MMER calves to be older than their known ages (Figure 4). Models had the highest prediction errors at the youngest (day = 0) and oldest (day = 14) ages (Table 4). The youngest age had the worst predictions because it was the end of the range of ages examined and because so few complete observations were recorded at calves' birth dates ($n = 4$).

To ensure that models were not sensitive to calves from different mother's SAFGs, additional models were built and validated using a subset of calves from the highest summer-autumn and winter feeding groups and a subset from only the lower summer-autumn and winter feeding groups. Using these 2 restricted data sets, parameter estimates changed only slightly and predicted ages were within 0.5 days from the full model predictions. Because subsetting the data did not change the model, we decided that all of the data would better reflect variability found in a wild population.

Comparing with Johnson's (1951) Method

When model age estimates and Johnson's age estimates were compared to the true age of the animals, a very striking pattern emerged. The 2 methods predicted very different ages for the Starkey and MMER calves (Figures 2 and 4). For these known age animals, Johnson's age estimates under-predicted both Starkey and MMER ages, while model estimates accurately predicted ages for Starkey calves, and over-predicted ages of MMER calves. Additionally, we compared the relationship between model estimates and Johnson's age estimates for Starkey, MMER, and the wild, Lochsa elk calves graphically and with ANCOVA (Figure 5). Although the slopes appeared graphically similar, they are significantly different ($p = 0.04$) for each group. These results indicate that there was no consistent relationship between model predictions and Johnson's predictions, implying that elk calves for the 3 populations (Starkey, MMER, and Lochsa) grow at different rates.

Ranges for mass and tooth length were comparable to Johnson's (1951) reported values for each of his defined age groups (Table 5). Starkey calves had a higher mean mass for the first 2 age categories (0-1 days: 14.8 kg, 16.2 kg; 2-4 days: 16.4 kg, 17.8 kg for Johnson and Starkey, respectively), while the mean weights were exactly the same for the last 2 categories (5-7 days:

20.3 kg; ≥ 8 days: 24.2 kg). Johnson (1951) did not specify how the tooth length was measured on the I1 tooth, but we reported the length of the outside edge and middle of the tooth.

Birth Mass

Using ANOVA, we compared birth mass between gender, years, and their interaction (mass at age = 1 day). The overall model was significant ($p < 0.001$); birth masses were only different between sexes ($p = 0.003$). Neither differences between years ($p = 0.79$) nor the interaction term, sex*year ($p = 0.93$), were significant in the model. Males were almost always larger than females at birth (mean male mass = 17.09 kg [0.4], mean female mass = 15.52 kg [0.23]). We also explored differences between birth mass among SAFGs and sex for 1996-1997 elk calves. The overall model was significant ($p < 0.001$), but the main effect term and interaction terms for SAFGs were not significant. These results imply that there was a difference in mean birth mass between males and females, but no difference in mean birth mass for calves born from mothers in the high, medium, and low SAFGs. Additionally, mean birth masses were calculated for MMER elk calves. Although there was no statistically significant difference, average female birth mass (21.68 kg [1.4], $n = 7$) was slightly heavier than male birth mass (21.36 kg, $n = 1$).

Average birth masses were comparable to mean birth masses from other studies (Table 6). Most combined gender birth masses fell between 15.5 and 17.5 kg. Many of the other studies reported a higher birth mass for males than for females. Cook et al. (1996) reported the lowest combined mean birth mass (14 kg [0.0023]), while MMER had the highest average birth mass (21.52 kg [1.28]).

Growth Rates

We explored mass increase, tooth growth, and hoof growth for the 1996-1997 elk calves against time (age), between sexes, and among SAFGs. The interaction term for the overall MANCOVA was not significant (Wilke's lambda $p = 0.51$), while the main effects, sex, and SAFG were significant ($p = 0.0002$ and $p = 0.01$). We continued with separate ANCOVAs for tooth growth, hoof growth, and mass increase. For tooth growth, hoof growth, and mass increase, overall models were significant because animals grew over time ($p < 0.001$). Sex ($p = 0.009$), but not SAFG, was significant for mass regressed against time; for tooth and hoof growth regressed against time, only time ($p < 0.001$) was significant (Figures 6 and 7). These results imply that there were no differences in mean mass gained over time (slope) between males and females or calves born from mothers in the 3 feeding regimes. Only the average mass of males was greater than females' mass at all time points.

Additionally, we explored the slope of mass against time, or daily mass gain per day, to see if there was any indication of compensatory growth or catch-up growth among SAFGs and between sexes. The overall model was not significant ($p = 0.62$). There were no differences in mean daily mass gain over time, among SAFGs, or between males and females. We calculated growth rates averaged for years, sexes, and feeding groups and compared this value to other mean daily mass gain in the literature (Table 7). Growth rates of elk calves from Starkey (0.77 kg/day [0.0004]) were comparable to calves in other studies. Mean daily mass gain for MMER calves (0.71 kg/day [0.15]) was similar to Starkey calves. Calves from Smith et al. (1997) had

the highest average daily mass gain (1.643 kg/day and 1.316 kg/day for males and females, respectively). Cook et al. (1996) had the lowest average mass gains (0.4 kg/day).

Discussion

Our model provides a method to objectively predict ages of elk calves ≤ 2 weeks old. We limited the predictive capabilities of our models to the first 2 weeks of life because that is when the majority of field-capture operations for radio-collaring and tagging neonatal elk calves occur. Predictions beyond that age are not advised because growth patterns do not remain linear throughout the course of development (Flook 1970).

We chose mass, tooth length, and hoof length for our models because they are relatively easy to measure during capture and can be collected without great measurement error or between-researcher measurement variation. Additionally, these 3 body measurements were not highly correlated (all were $r < 0.75$). Furthermore, we specifically chose length of the outer edge of the first incisor tooth because other studies have indicated that it is least affected by fetal and neonatal nutrition (Brown and Chapman 1991).

The inclusion of the individual calves as random effects allows the model to be used for elk calves from other populations. “A random effect is a reasonable description of [a] set of coefficients from a population of animals [that] can be thought of as a sample from a distribution” (Diggle et al. 2002:128). Although the model was created with a specific sample of calves, the original calf lineage was chosen at random from a wild population (Cook et al. 1996). Because of the random effects, inferences from this model may be extrapolated to other populations of similar calves. When making model-based predictions, random effects only come into play when calculating standard error for age estimates.

Although not modeled, variation imposed by feeding levels and elk calf mothers should be representative of variation in conditions that could be found in the wild. We did not consider these hierarchically-nested random effects because they were confounded. We had explored inclusion of mother as a random effect, because some mothers had 2 calves in different years, but inclusion of a mother random effect created unusual patterns in residuals.

Through cross validation with the Starkey data set, the final model appeared to predict calf age with low prediction error. Although the relationships between predicted and observed age had a small average loss value, there were several calves (≈ 10) for which the model predicted poorly. Such calves (e.g., calf 25 or calf 20) were born smaller and grew slower. These calves were not born to mothers in any particular summer-autumn or winter feeding group, nor did they die sooner than any of the others. We believe these calves simply demonstrated individual expression of genetic or environmental variation.

Validation with the MMER data set demonstrated lower prediction capabilities. The loss value was fairly high, implying that the model overestimated ages of these calves. We believe that the model performed poorly on average because MMER calves were heavier and larger than Starkey calves. The MMER were hybrids of Rocky Mountain, Manitoban, and Roosevelt elk. Roosevelt elk are thought to be the largest, existing subspecies and well-fed Manitoban elk are often

heavier than Rocky Mountain elk (O’Gara 2002). If these elk are larger as adults, they are likely also larger at birth. Additionally, these animals may have been larger at birth because they were being raised for meat and antler production. Like other husbandry operations, larger animals tend to be selected to maximize yield.

High sensitivity and elasticity would make predictions poorer if the model was applied to populations with different population parameters. The high sensitivity of the intercept and mass parameter estimates indicates that our model would not predict well for animals with different population growth rates and birth masses. The other parameter estimates seem fairly robust. The high elasticities of the tooth and hoof values indicate that outliers for these measurements would influence the model predictions.

Surprisingly, there was a large discrepancy between model predictions, Johnson’s age estimates, and the true ages of animals. We believe Johnson’s criteria underestimated ages for 4 reasons. First, Johnson never specified what part of the tooth he measured. Because of differences between the edge and middle of the tooth, our interpretation of his categories for dentition could have caused misclassifications. Second, he captured wild calves of unknown age. Potentially, he could have under-estimated age of older calves because only smaller, older calves were easy to catch. Third, calves born in the Gallatin River Basin may have less variation or be slightly larger at birth than elk calves in other populations. Fourth, we found that the relationships between Johnson’s age estimates and the model age estimates were different for the 3 populations. This may imply that there are different growth patterns or sizes at birth expressed in each population. Although Johnson’s (1951) work provides invaluable natural history and baseline information on growth and development of elk calves, age categories may not be accurate when applied to elk calves in all populations.

We recommend that the use of this mixed effects model be restricted to Rocky Mountain elk calves. Use on other subspecies is not advised because sizes at birth and rates of growth between subspecies are variable. For example, red deer’s (*C. e. elapahus*) birth mass and growth rates average around 8.5 kg and 0.35 kg/day, respectively (Haigh and Hudson 1993); Iberian red deer (*C. e. hispanicus*) have an average birth weight of 6.4 kg (Garcia et al. 1999); while Rocky Mountain elk calves have an average birth weight of 18 kg and an average growth rate of 0.825 kg/day (Haigh and Hudson 1993). Researchers should also use some caution when applying the mixed effects model to other populations of Rocky Mountain elk calves because of variation in average birth mass and growth rates due to maternal condition, genetics, and environmental factors.

Birth Mass

In our study, males were born heavier than females, mother’s SAFG did not influence birth mass, and mean birth masses of elk calves from this study were comparable to elk calves from other studies. Similarity of our findings to other studies suggests that calves from different regions may be of similar mass at birth and our models could be aptly applied to some populations of elk calves. We believe that when differences in birth size do occur, they are mainly a function of gender, physiological condition of the mother, and extreme environmental conditions.

Differences in male and female birth mass may be caused by longer gestation lengths for males (Jafar et al. 1950) or increased levels of growth-promoting hormones, such as androgen and testosterone, which begin being produced early in gestation (Holland and Odde 1992). In domestic cows (*Bos* sp.), androgen concentrations are much higher in the serum of male fetuses; and testosterone begins to be synthesized by the testes on day 45 of gestation (Challis et al. 1974). In other mammals, these higher levels of hormones found in males result in enhanced skeletal muscle development and increased muscle tissue growth (Challis et al. 1974, Michel and Baulieu 1980). Our findings are similar to the results of Smith et al. (1997), Wild et al. (1994), and Hudson et al. (1991), who reported that males were 0.7 to 2.0 kg heavier than females.

Our results suggest that maternal nutritional restrictions in early gestation have little effect on calf birth mass. We observed no significant differences between the birth masses of calves from mothers in different SAFGs. We hypothesize that nutritional restriction during early gestation does not greatly affect birth size because the embryo/fetus is not utilizing a large percentage of the mother's resources at that time. The fetus's demands are easily met by placental exchange of maternal nutrients (Hafez and Dyer 1969:54, Adam et al. 1988). In studies on domesticated cows, nutritional restriction during early gestation had little effect on birth mass, although it may have delayed or impaired early developing organs, such as the brain and heart, and may have potentially led to a reduced chance of survival (Hafez and Dyer 1969, Holland and Odde 1992). Unless severely deprived during middle and late gestation, most captive ungulate studies have shown that the fetus is not affected by early nutritional restriction (Holland and Odde 1992, Heasman et al. 1999).

Although we did not observe a correlation between birth size and early maternal nutrition, birth size may be affected by other changes in the intrauterine environment, including mother's metabolism, physiological condition, and extreme external environmental conditions (Price and White 1985). These other factors could explain the variation attributed to random effects in our aging models. Additionally, these sources of variation could potentially affect average elk calf birth size, thus directly impacting predictive abilities of the aging model for use in other populations.

We may have observed variation in birth mass because of differences in factors that directly relate to mother's metabolism and physiological conditions. These include maternal size, age, genotype, and previous lactational status (Holland and Odde 1992, Cook et al. 2004). The highly heritable factor, adult maternal size, quantified by body mass, is indicative of the "physiological capacity to support the fetus and fetal growth" (Holland and Odde 1992:774). Numerous studies have shown that larger dams produce larger newborns because of increased maternal capacity to supply the fetus with nutrients (Albon et al. 1980, Blaxter and Hamilton 1980, Holland and Odde 1992, Friedel and Hudson 1994, Schwartz and Hundertmark 1993). Maternal age influences birth mass because competition for nutrients between the growing, young mother and the developing fetus may result in a lower neonatal birth mass (Lasley et al. 1961, Holland and Odde 1992). For red deer, researchers reported no effect of dam age on birth mass that could not be explained by mother's pre-rut mass. Smaller, younger mothers produced smaller calves (Blaxter and Hamilton 1980). Genetics certainly influence the progression of fetal growth and development (Owens et

al. 1993), but for domestic cows and sheep, birth mass exhibited only low (10-20%) to medium (30-40%) levels of heritability (Hafez and Dyer 1969).

Even though “fetal growth proceeds along its course, protected by a resilient maternal buffer, attaining developmental horizons with a biological flexibility essential to survival” (Everitt 1967:132), we may have also seen variation in birth mass because of differing environmental conditions. Differences observed among individual or population birth mass could be attributed to external, environmental factors that include climate (Albon et al. 1980), population density (Albon et al. 1987, Andersen and Linnell 2000), altitude (Holland and Odde 1992), habitat characteristics, and major nutritional restrictions during late gestation. Although extremes in temperature or high elevation may affect birth size, these factors are rarely important for wild animals because the intrauterine environment greatly buffers the fetus (Bonsma 1949, Holland and Odde 1992, Cameron 2002). On the other hand, nutritional deprivation during late gestation has produced controversial results in captive studies. Thorne et al. (1976) reported that winter malnutrition affected birth mass of captive elk calves. Alternatively, Holland and Odde (1992:780) advocated that such effects on birth mass seem to be inconsistent and overall, relatively small. Effects may be small because of the mother’s ability to metabolize her own body reserves to meet the energy and nutrient requirements of the growing fetus. As long as chronic malnutrition does not occur, fetal compensatory growth may be possible if and when nutritional restrictions are decreased. Haigh and Hudson (1993:50) suggested that drastic maternal food restrictions rarely produced substantial changes in birth mass because there is often ample opportunity between spring green-up and calving for the dam to attain a higher nutritional plane and fetal catch-up growth to occur. By learning more about the effects of mother’s physiological condition and environmental factors on birth and growth rate, future research could further refine our elk calf-aging model and its widespread applicability.

Estimated birth masses from this study were similar to birth masses reported in other studies (Table 6). This resemblance supports applicability of our mixed effects aging model to other elk populations. Calves from the literature with the lowest birth mass developed various gastrointestinal illnesses ≤ 3 weeks after capture (Cook et al. 1996) and the 2 calves with the highest birth masses came from captive-raised, MMER calves (21.52 kg) and Robbins et al. (1981 [21.2 kg]). These high birth masses could be a function of many additive causes such as differences in the intrauterine environment, genetics, hybridization of subspecies, or captive rearing.

Although our mean birth masses are comparable to other ranch, captive, and wild studies, higher variation among other populations could cause the aging model to over- or under-predict calf age. In our study, birth mass had a relatively small standard error. Additionally, the parameter estimate for mass and intercept were the most sensitive parameters. Our study may not have captured the full range in birth mass that exists in free-ranging elk. To work with other populations, an intercept adjustment for size at birth should be considered or the model should be refit with additional data to account for genetic and environmental differences.

Growth Rates

We documented no difference between the daily rate of mass gain, or acceleration of mass gain over time, between males and females or among SAFGs. Similarly, we did not find differences in tooth or hoof growth between males and females or among SAFGs. Differences in daily rate of mass gain occurred because males and females were born at different masses and maintained that difference over the period of monitoring.

We believe that the SAFG did not affect neonatal growth rates because nutritional restriction did not continue throughout the rest of pregnancy or during lactation. The cows were given high quality forage beginning in March. This diminished any effects on late gestational fetal growth and milk quality and yield (Haigh and Hudson 1993). Everitt (1967) suggested that growth immediately after birth is simply an extension of intrauterine growth and postpartum maternal nutrition. As long as the calf acquires adequate milk and important antibodies from colostrum, calf growth will be similar to intrauterine growth (Schwartz and Hundertmark 1993, Cameron 2002). During the first 2 weeks post-partum, additional food sources, such as grass and forbs, are not important because the calf's 4 stomach chambers are still forming (Price and White 1985, Lyford 1988).

Rates of mass gain by elk calves during the first 2 weeks appear to be similar across populations (Table 7). The lowest daily mass gain reported in the literature was attributed to illness of calves (Cook et al. 1996). Also, this growth rate was measured during July when calves were 4-8 weeks old. By the second month, daily mass gain may have slowed (D. M. Montgomery, University of Idaho, unpublished data). Smith et al. (1997) reported the highest birth mass as well as high estimates of daily mass gains. He attributed high estimates to 1) the beneficial effects of winter supplementation at the Nation Elk Refuge, 2) bias in Johnson's (1951) study of wild calves, 3) superiority of free ranging dams' milk yields to captive animals because the mothers were allowed free choice in forage selection, and 4) incomparable results because rate of mass gain changes after the first week of life (Smith et al. 1997:35). Our findings were mixed with regard to Smith et al.'s (1997) explanations. If choice of good quality forage was the reason for fast growth, we expected ranch-born calves would have exhibited the same fast growth reported by Smith et al. (1997). On ranches, mothers are either offered high-quality forage or allowed free range to make individual choices. MMER and Friedel and Hudson (1994) calves were born on elk ranches where maximization of animal size was most likely a targeted objective, but these calves did not exhibit increased growth rates. As for incompatibility of results because of changes over time, we found no difference in average daily mass gain over the first 2 weeks. Based on our data, we believe that our results are comparable with those calculated for 1 week of growth (Smith et al. 1997). Our estimates for the 2-week period are even similar to rates of growth calculated for 1 month (Johnson 1951, Robins et al. 1981, Wild et al. 1994). On the contrary, relationships between Johnson's ages and model predicted ages were different among wild and captive populations, implying that wild calves grew differently than captive calves. Because of this mixed evidence, differences in mean daily mass gain between captive and wild animals should be explored further. If there is a difference between wild and captive elk growth, findings could significantly influence applicability of the slope parameter estimates in our aging model.

In the future, it would be useful to build models with additional data collected in a similar manner from other Rocky Mountain elk populations. By adding populations of calves that have other sources of variation, we could better model the random variations of growth and size at birth. Variation could be attributed to factors that affect birth size and growth rate, such as maternal size, parental age, genetic stock, metabolism, previous lactational status, climate, population density, elevation, habitat characteristics, and major nutritional restrictions during mid and late gestation. Until this is accomplished, researchers should be wary when using our calf-aging model. Researchers should consider recalibrating this model for other subspecies and for use in other regions of North America, where genetic stocks, habitat, and climate vary (Bridges et al. 2002).

Management Implications

Age may impart several important pieces of information about natural history and ecology of neonatal cervids. Accurate estimates of age could be used to calculate date of birth, thus providing insights about growth rates, fetal implantation, birth date distributions, neonatal survival, and their interrelationships. For example, researchers would be able to make better connections between date of birth and survival (Smith and Anderson 1996). Using age specific information, Albon et al. (1987) reported that early-born red deer calves had a 30% higher chance of summer survival (Blaxter and Hamilton 1980, Albon et al. 1987). Age information has also been used to impart information about herd condition. Squibb et al. (1986:1) documented bimodal conception dates caused by regularly scheduled hunting seasons. Using reproductive tracts from harvested females, they backdated date of conception, or age of the fetus, and speculated that hunting pressure interrupted normal breeding behavior (Squibb et al. 1986). Our models would make these relationships easier to explore.

With age information, researchers could refine their knowledge of neonatal ecology. Our mixed effects model provides precise age estimates for newborn elk. We selected morphometric measurements that were easy to measure during radio-collaring or tagging operations. By validating and testing our model, we have ensured that it will work with similar elk populations. Further enhancing applicability is that elk calves used in model construction have growth rates and birth weights that are similar to elk calves from other studies. We have also identified factors that may influence the model's predictive capabilities. These factors include natural variation in maternal conditions and environmental factors. Because this additional variation may not have been accounted for, we recommend adjusting parameter estimates for differing populations. Once calibrated for wild populations, our model could be a vital tool in monitoring and managing the youngest portion of elk populations.

STUDY 2: PROXIMATE FACTORS INFLUENCING HUNTING MORTALITY OF ELK IN IDAHO

Background

Over the past 10 years, vulnerability has become a focus in research and management of North American elk (*Cervus elapahus*). Vulnerability is the management of habitat security for elk during hunting season (Lonner 1991, Christensen et al. 1993). Animals that do not have access to

safe habitat would be more vulnerable or susceptible to mortality. With a higher risk of mortality, survival rates could be lower and overall population dynamics could be altered.

Managing vulnerability can be seen as a way to manage survival of elk during hunting season. By understanding vulnerability, wildlife managers could alter factors that reduce hunting pressure. Coupled with tag limits, season length, and timing, managers could more effectively sustain or enhance the vital role of elk in the ecosystem in the face of expanding human populations. This would ensure continuation of quality elk hunting opportunities and enjoyment by non-consumptive users (Lonner 1991, Duffield 1991).

Most studies that focused on vulnerability have documented changes in behavior, movement, and habitat selection during hunting season (Edge et al. 1984, Irwin and Peek 1983, Morgantini and Hudson 1985, Vieira et al. 2003). A few of these studies have linked individual changes in susceptibility to harvest with habitat selection or hunting management strategies (Bender and Miller 1999, Ballard et al. 2000, Hayes et al. 2002, McCorquodale et al. 2003, Unsworth 1993, Unsworth et al. 1993). Some researchers have focused on one particular topic related to vulnerability, such as human disturbance (Cole et al. 1997), hunting season strategies (Bender and Miller 1999), or topography (Lyon and Canfield 1991). Others have explored suites of proximate factors affecting elk vulnerability, such as road density or distance to roads, topography, and vegetation complexes (Canfield 1991, Unsworth et al. 1993, Hayes et al. 2002, McCorquodale et al. 2003, Hughbanks 1993).

Although understanding habitat selection, movement, and behavior is very important, linking individual habitat use and hunting season structure with mortality could provide further insight and enhance our ability to predict elk survival. More accurate models relating habitat to hunting mortality could aid in hunting season structure development and overall forest management. The models could provide more tools to aid managers who need to strike a balance between excessive vulnerability resulting in over-harvest and total security eliminating all hunting opportunities (Stalling et al. 2003). This would facilitate better understanding of population level responses that occur because of changes in survival rates (Garton et al. 2001).

Other studies have related elk mortality to hunting and environmental factors. Unsworth et al. (1993) and Gratson et al. (1997) examined elk vulnerability in the Lochsa-Clearwater River Basin of north-central Idaho. Their results indicated that probability of death was related to road density, complexity of terrain, and hunter density. The later study also found shrub density and elk age class to be important predictors. Using similar methods, Leptich and Zager (1994) and Hayes et al. (2002) determined that road density, interior hiding cover, and hunting season structure were the most important predictors of vulnerability for bull elk in northern Idaho, while Hughbanks (1993) found topography and hunter density were important for Sand Creek elk in southeastern Idaho. Several showed that risk of mortality increased with higher road densities, and decreased with higher topographic complexity studies (Unsworth et al. 1993, Hayes et al. 2002, Hughbanks 1993). These results are intuitive because elk using steeper areas would be less vulnerable to hunting mortality because of decreased hunter access. In south-central Washington, McCorquodale et al. (2003) observed the opposite results for topographic complexity; he reported that decreasing topographic complexity increased the probability of survival.

McCorquodale et al. (2003:255) attributed this difference among studies to “site-specific” qualities. In a Montana study using discriminant analysis, Weber et al. (2000) showed that road density, vegetation change, and hiding cover best discriminated between live and dead elk locations at 2 different spatial extents. Using a very broad spatial scale, Vales (1996) explained elk vulnerability with average slope, aspect contagion, percent of the landscape in security cover, and road density.

These previous studies are difficult to compare directly because different statistical models were used and predictors were constructed differently. McCorquodale et al. (2003), Unsworth et al. (1993), Gratson et al. (1997), and Hayes et al. (2002) used logistic regression models; Weber et al. (2000) used discriminant analysis; and Hughbanks (1993) used chi square tests. Predictors were constructed differently and measured in different ways, with different spatial layers and at varying spatial scales. For example, Gratson et al. (1997) measured hiding cover in terms of patch size and percent of 9 habitat classes, while Hayes et al. (2002) constructed several hiding cover variables using 8 vegetation types from combined soil and vegetation layers.

Spatial scale is a particularly significant characteristic because the relative importance of a particular variable or relationships between biological characteristics might change when different spatial or temporal scales are examined (Turner et al. 2001). Scale can be characterized by grain and extent. Grain can be defined as the resolution at which pixel characteristics are measured, while extent is the spatial size at which things are measured. Extents of the previous studies included hunting units or Game Management Units (Vales et al. 1998), home range (Unsworth et al. 1993, McCorquodale et al. 2003), and buffers of varying radii around points (Hughbanks 1993: 500 m-5,000 m; Gratson et al. 1997: 357 m, 1,000 m, and 16,000 m; Hayes et al. 2002: 357 m; Weber et al. 2002: 200 m and 700 m). Animals may use resources to avoid hunting mortality at several scales. Because of this, vulnerability of elk may be better understood by measuring influential factors simultaneously at various spatial scales.

Objectives

In this study, we attempted to evaluate complex relationships between hunting practices, environmental conditions, and elk vulnerability in 3 different study areas in Idaho. We addressed 4 main questions:

1. Do the same proximate factors influence bull elk vulnerability in different habitat types and under various hunting management strategies?
2. Can consistent, synoptic measurements of habitat structure be used to predict elk vulnerability?
3. Are the same proximate factors important at different scales?
4. What factors are important for females as opposed to males?

To address these questions, we standardized variables collected across 3 study areas, held grain size constant, and used 2 different spatial extents. Using survival models, we explored how proximate factors are related to mortality of elk during hunting season.

Study Areas and Data

The data used in this project originated from 4 different Idaho Department of Fish and Game (IDFG) studies. IDFG biologists collected data from radio-collared Rocky Mountain elk (*Cervus elaphus nelsoni*) between 1984 and 1994 in 3 areas of Idaho (Figure 8). Animals were captured by helicopter darting, net-gunning, or trapping for radio-collaring, and then relocated by aerial radio-telemetry ≥ 1 time a week during hunting season and 1 or more times a month during the rest of the year. Age class and sex were recorded at collaring. When animals were relocated, the coordinates of radio telemetry locations were usually recorded. Elk were relocated and inspected post-mortem to identify the cause of mortality.

The elk populations were located in 3 different geographic areas of Idaho: Coeur d'Alene River area, the Lochsa River and North Fork of the Clearwater River area, and Sand Creek area (Figure 8). The studies focused on male elk survival and, thus, radio-collared predominantly bulls. Because hunting season structure in the 3 areas was complex, we have included this information in Appendix B (Table 1).

The Coeur d'Alene River (CDA) study was conducted in Idaho Game Management Units (GMU) 3, 4, and 4A from 1988 to 1994. A small portion of relocations were in Montana Hunting District 121. This area is characterized by steep terrain with dense, cedar and conifer forests, open brush fields, and high road densities (Leptich and Zager 1994). Both a cow and bull general rifle and archery seasons were held annually. Only GMU 4 had a muzzleloader season. The Montana hunting district had a 7-day either-sex season and a 28-day bull-only season. The study area was mostly within the Idaho Panhandle National Forest. See Leptich and Zager (1994) and Hayes et al. (2002) for a more detailed description of the area and original studies.

The Lochsa River and North Fork of the Clearwater River (Lochsa) study occurred mostly in Idaho GMUs 10 and 12 between 1984 and 1994. Topography varied from steep slopes to flatter floodplains. Vegetation was highly mixed with open shrub fields and a mixture of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), Englemann spruce (*Picea engelmannii*), and sub-alpine fir (*Abies lasiocarpa*) forests (Unsworth et al. 1993). Portions of the area had both high and low density of roads (1.94 km/km^2 to 0.29 km/km^2 ; Unsworth et al. 1993) and some areas were unroaded and classified as wilderness. The population was exposed to rifle bull-only hunts. All GMUs, except 16, also had an archery season, and only GMUs 16 and 10A had muzzleloader seasons. Limited-permit cow and bull controlled hunts also were conducted. The study area was mostly within the Nez Perce and Clearwater National forests. See Unsworth et al. (1993) and Gratson et al. (1997) for more detailed descriptions of the area and original studies.

The Sand Creek study occurred primarily in Idaho GMUs 60, 60A, 61, 62, and 63A between 1984 and 1989. Some relocations were taken in Montana Hunting Districts 327 and 361 and Yellowstone National Park. The study area was mainly located on the Snake River Plain in

southeastern Idaho, southwestern Montana, and northwestern Wyoming. Targhee, Beaverhead, and Gallatin National forests, and Yellowstone National Park comprised much of the study area. These areas were characterized by moderate to steep slopes, plateaus, and low, flat areas (Brown 1985). The vegetation was heterogeneous, with a mixture of deciduous and conifer forests, active sand dunes, and high-desert sagebrush communities. In the 1970s and 1980s, mountain pine beetles infested much of the merchantable lodgepole in the area (Brown 1985). An increase of logging and road building ensued and much of the timber was salvaged (Pauley 1991). Animals of the Sand Creek population frequently crossed between Idaho, Wyoming, and Montana. GMUs 60A, 63A, Yellowstone National Park, and Harriman State Park had no hunting seasons. Also, GMUs 60A and 63A were frequently used as wintering grounds by many migrating elk. The remaining Idaho units had a 5-day bull-only rifle season. All units except GMU 60, 60A, and 63A, had an archery season and only GMU 61 had a muzzleloader season. There were also frequent bull and cow limited-permit, controlled hunts in all units. Montana Hunting Districts had a 35-day bull-only hunting season. See Brown (1985) and Pauley (1991) for a more detailed description.

Methods

We calculated crude estimates of average annual survival rates by treating uncensored data as a binomial process (Unsworth et al. 1993). We examined various annual survival rates from the literature for comparison. Annual survival was not explored further because it was addressed in other studies (Unsworth et al. 1993, Leptich and Zager 1991, Pauley 1991). Annual survival rates may differ from those previously reported because of censoring or addition of subsequent years of data to the published data sets.

For the vulnerability models, we examined the time period from 1 September to 30 November because all hunting-related deaths occurred during this time period and the start and end of most general rifle season hunts fell between these 2 dates. We related aerial radio telemetry locations collected between these 2 dates to several environmental variables. Information for habitat variables was collected for each radio telemetry point using the literature and a geographic information system (GIS). Environmental data were related to survival rates using Cox's proportional hazards models.

Habitat Data

Eight habitat variables were evaluated using several spatial layers: percent cool aspects, percent forested areas, contagion of vegetation, patch richness density, patch density, contour density (Beasom et al. 1983), road density (Unsworth et al. 1993, Hayes et al. 2002), and hunter density (Hayes et al. 2002). All of the spatial layers were projected into NAD1927 UTM11 using Toolbox in ARC 8.0.

For spatial scale, we explored all variables at 1 grain size and 2 spatial extents. We chose a fixed 30 m-pixel size for grain because it was the smallest grain available for our topography and vegetation layers that were consistent among all study areas (Johnson et al. 2000). For the 2 spatial extents, all data were collected within 2 different, contiguous buffers placed around each radio telemetry point. The first buffer was a 473 m fixed radius circle around each point (70.28

ha). This distance was chosen because it encompassed the largest known radio telemetry error of 473 m (Unsworth et al. 1993). Additionally, this area incorporated a core hiding area of 40 ha (Lyon and Canfield 1991) and/or the 2.5 ha of security area (Hillis et al. 1991, Thomas et al. 1979). For the large extent, the second buffer was a 2,077 m fixed-radius circle around each point (1352.22 ha), which distance was the median distance moved between consecutive points that were taken <8 weeks apart excluding migratory movements (Lyon and Canfield 1991, Boyce et al. 2003). We believe this large buffer size represented a pseudo-core area of the home range. In order to make consistent measurements among study areas, we wanted to choose a distance that was meaningful in all populations. The median was chosen because it was similar among all areas. Migration movements and consecutive distances more than 8 weeks apart were removed because we wanted to ensure that all locations represented movements within seasonal areas. Points were buffered using the Animal Movement extension or ArcGrid. The information collected for each buffer was then averaged for each animal for each year. Because extent was the only component of scale that we changed, we frequently interchange the terms scale and extent (Johnson et al. 2000).

Home range (Unsworth et al. 1993, McCorquodale et al. 2003) would have been a more meaningful extent to use, but we chose not to use home ranges because Sand Creek elk made long, migrational movements during hunting season, and we had very few locations for individual elk. Some elk even moved to traditional wintering grounds, back to their summer range, and then on to another location. They traveled large distances, with a maximum of 118 km between consecutive locations. We did not feel justified in determining a fall and winter home range based on 2 locations located 58 km or 118 km apart; yet, we did not want to completely eliminate these animals or locations because there were so few deaths, animals, and locations per animal (1-7 locations).

Percent of cool and warm aspects were estimated by first deriving aspect from a 30 m USGS National Digital Elevation model (DEM) using Spatial Analyst version 1.1 in Arcview 3.3. We reclassified aspect into cool (0° to 112.5° and 292.5° to 360°) and warm aspects (112.5° to 292.5°). Then, we used ARC Macro Language (AML) in ArcInfo to determine the number of pixels of warm and cool aspects for each buffered point. Percent cool aspects were calculated by dividing the number of pixels of cool aspects by the total number of pixels within each buffer, multiplied by 100. We chose to reclassify aspect into cool and warm aspects because northern, cool aspects frequently have more productive vegetation and denser, forested areas in this region. High-quality forage, greater biomass, and high levels of cover during autumn months are frequently found on these aspects (Running 1984, Skovlin et al. 2002). Cool aspects may provide a greater refuge from hunters while also meeting foraging needs during hunting seasons.

Percent forest was calculated by first reclassifying the 1992 30 m USGS National Land Cover Data (NLCD) into forested (including conifer, deciduous, and mixed conifer-deciduous forests with greater than 25% canopy cover) and non-forested (all other types). We used an AML to clip out buffers from the reclassified NLCD and recorded the number of pixels of forested and non-forested areas within each buffer. Percent forest was then calculated by dividing the number of forested pixels by the total number of pixels for each buffer. We used NLCD, rather than GAP because the elk point locations extended into Montana and Wyoming. Although NLCD provided

less detail, it provided a consistent coverage for all areas. This allowed us to test our hypothesis that surviving elk tended to use forested areas more because they provided more hiding cover.

Topographic roughness or contour density was calculated by first deriving 30 m contour lines from the DEM using Spatial Analyst in Arcview 3.3 for Windows. Using Xtools 3.0 extension in Arcview 3.0, contour lines were clipped to each buffer and the length of contours within each buffer was summed. We computed contour density by dividing total length of contour lines (m) by total buffer area (ha). Rather than using slope or elevation alone, contour density provided a single variable that described topographic roughness (Beasom et al. 1983). If topographic lines are longer within a buffer, slope and elevation increase for that area would be greater. Shorter and fewer topographic lines would indicate less change in elevation and less steep terrain. We predicted that elk that survived longer would use rougher terrain. Rougher terrain would provide more security because it would be less accessible by hunters (McCorquodale et al. 2003, Hayes et al. 2002).

Several road layers were used for road density. First, a 1:100,000 USGS Digital Line Graph (DLG) road layer (collected between 1974 and 1991) for the state of Idaho was merged with 2 other road layers from Wyoming and Montana. One road layer was developed by Montana Resource Information Services from 2000 Tiger Line Files at 1:100,000 scale. The other road layer was from the Northern Rockies Information Node, 1998 Tiger Line Files at 1:100,000 scale. Although the temporal scale of Montana and Wyoming road layers did not match the time of the study, we do not believe that the number of roads changed enough for there to be measurable difference. Primary, secondary, and tertiary roads, jeep trails, and 4-wheel trails were included in road layers. Foot trails were excluded. Using Xtools extension in Arcview 3.0, roads were clipped to each buffer and lengths of all roads within each buffer were summed. Due to time constraints, we did not differentiate between open and closed road densities. Road density was determined by dividing total length of roads (m) in each buffer by buffer area (ha). We predicted that elk would be more susceptible to hunting mortality in areas with high road densities because of greater vehicular disturbances and greater hunter access.

Patch density, patch richness density, and contagion of vegetation were calculated by first reclassifying the NLCD data into 5 different classes: open water, herbs and grasslands, shrubs, forests, and other. We then used an AML to clip out buffers for each elk location from the NLCD. Using the 8 cell rule, landscape and patch metrics were calculated from the raster buffers in Fragstats 3.3 (McGarigal et al. 2001). Patch richness equaled the number of classes of vegetation patches present within each elk buffer divided by total area of that buffer (ha). Patch density equaled the number of vegetation patches within each elk buffer divided by total area (ha). We predicted that high patch density would lead to lower survival because there would be fewer contiguous patches of hiding cover, but high path richness density would lead to higher survival because that area would better suit an elk's combined foraging and hiding needs. Contagion is expressed as a percent and represents both interspersed and composition of vegetation classes. When contagion is 0, every cell is a different vegetation type and is highly interspersed. When contagion equals 100, vegetation types are maximally aggregated (McGarigal et al. 2001). Although contagion of specific vegetation, such as shrubs, would be important, we used contagion of all vegetation because different types or combinations of

vegetation may be important in each study area. We hypothesized that areas of high contagion would result in higher survival because they would provide better hiding cover.

Hunter density was calculated as (number of hunter days x length of the general rifle season) / hectares (Hayes et al. 2002). The length of the season was obtained from Idaho Fish and Game and Montana Fish, Wildlife and Parks annual, big game hunting rules and regulations booklets. If hunter density was unknown for 1 year, the average over all years for that GMU was used. The number of total days hunted (hunter days) was obtained from IDFG and Montana Fish Wildlife and Parks annual telephone and mail surveys (Kuck and Rachael 1997; Candace Hinz, Montana Fish, Wildlife and Parks, personal communication). We reallocated hunter density according to probability of hunters' use of terrain. Using information from a study on radio telemetry of hunter habitat use, we weighted areas closer to roads (<1.0 km from roads) and with less steep slopes ($\leq 22\%$ slope) higher than areas farther from roads and with steeper slopes (>1.0 km from roads, >22% slope; Lyon and Burcham 1998, Broseth and Pedersen 2000). If a buffer overlapped more than 1 state and/or GMU, we created a weighted average of hunter density.

Two non-spatial variables, season structure and age class, were also explored as categorical variables. Season structure corresponds to the start of general rifle season in Idaho. Prior to 1991, general rifle season began during the peak of the rut. After 1991, the start of hunting season was delayed to begin after the rut (Hayes et al. 2002). Age class was divided into yearlings, 2.5-year-olds, and prime age adults (3.5-year-old or greater).

To explore weather, we summed snowfall 5 days before and 9 days after the start of general rifle season. For the Coeur d'Alene and Sand Creek study areas, we used the start of general rifle season for all Idaho GMUs. Annual start dates for GMU 12 was chosen for the Lochsa study area because most elk locations occurred in this unit. National Oceanic and Atmospheric Administrations (NOAA) daily data were used from weather stations that had complete records and were closest to elk locations (Cabinet Gorge for Coeur d'Alene; Fenn Ranger Station for Lochsa; and Ricks College in Rexburg, ID for Sand Creek).

Statistical Analysis

We combined all data using SAS data steps and conducted statistical analysis in both SAS software, Version 8.2 and R 1.9 (Hornik 2005). Animals for which age, sex, cause of death or date of death was unknown were excluded from our study. Additionally, animals that were not relocated between 1 September and 30 November were removed. Because we focused on the hunting season, we concentrated on deaths that were the result of hunting. These included deaths from general rifle, muzzleloader, special permit, or archery hunts, poaching, and rifle or archery wounding loss. Animals were right censored if they 1) died of another cause, 2) lived until 30 November, or 3) were of unknown fate due to collar failure or other unknown reasons.

We conducted separate analyses on male and female data sets because of expected differences in elk survival (Sauer and Boyce 1983). For both, we started by examining several plots and correlation matrices to understand relationships and interactions among variables and survival. Next, we estimated survival rates for each study area with Kaplan-Meier curves. Differences among curves were tested with log rank tests (Klein and Moeschberger 2003). We explored the

2 non-spatial variables (age class and season structure) using Kaplan-Meier curves because data were not available for certain study areas or had very unequal sample sizes. Confidence intervals for survival estimates were calculated using log transformations (Klein and Moeschberger 2003).

For males, we used proportional hazards models to relate habitat variables to the number of days the animal lived during hunting season each year. These models related the log of instantaneous mortality rate to categorical and continuous predictors. Log instantaneous mortality rate can be modeled with a parametric distribution or non-parametrically. Specifying a parametric distribution requires more stringent assumptions but makes the predictive power of the model much greater because a simple expression can be used for prediction. For males, we explored the appropriateness of the Weibull, exponential, log-logistic, and lognormal distributions with various transformations of time and Kaplan-Meier curves (Harrell 2001). If any of the transformations appeared linear for all 3 study areas, we planned to use that distribution to model the instantaneous mortality rate. Because none were deemed appropriate, we modeled the conditional mortality rate, or hazard rate, non-parametrically using Cox's proportional hazards model (Appendix B [Figure 1]).

Cox's proportional hazards model assumes no underlying distribution for the hazard rate. The general formula for a proportional hazard model is

$$h(t | B_1, B_2, \dots, B_k) = h_o(t) \exp(B_1 X_1 + B_2 X_2 + \dots + B_k X_k),$$

where $h_o(t)$ is the underlying baseline hazard rate and $\exp(B_1 X_1 + B_2 X_2 + \dots + B_k X_k)$ is a function of animal covariates. Only the non-parametric baseline hazard rate is a function of time. The cumulative baseline hazard rate is equal to

$$H_o(t) = \int_0^t h_o(u) du,$$

or the sum of the hazards until time t . Survival is related to the baseline hazard by $S_o(t) = e^{-H_o(t)}$. $S_o(t)$, the baseline survival rate, is the survival rate experienced by individuals whose X_i 's = 0. Thus, the survival function with covariates included is

$$S(t) = [S_o]^{e^{XB}},$$

where X is the matrix of data and B is a scalar of parameters (Klein and Moeschberger 2003).

Additionally, we stratified the model by study area because we believed that the underlying baseline mortality rate and survival curves were different for each study area, but relationships with each covariate would be similar (Therneau and Grambsch 2000). Because of this, we could not obtain estimates for study area effects, but we did explore interactions between strata and predictors. We explored interactions because we thought relationships between survival and

certain variables may differ among populations. We used the Efron approach to handle ties (Hosmer and Lemeshow 1999). Calculations were conducted with proc phreg in SAS software or coxph and cph in survival, Hmisc and Design packages of R.

Cox's proportional hazards model has 2 assumptions: 1) the relationship between predictors and hazard rate is linear and 2) relationships between predictors and hazard rates remain constant through time (proportional). These assumptions were explored using Martingale and Schoenfeld residual plots (Therneau and Grambsch 2000). Outliers were identified using plots of score or df beta residuals (Therneau and Grambsch 2000).

The proportional hazards assumption allows one to calculate a mortality or hazard ratio (HR) for each covariate. It is calculated by:

$$HR(t) = \frac{h_o(t) \exp(B_1 x_o)}{h_o(t) \exp(B_1 x_l)}$$

where x_o is the value experienced for 1 group and x_l is the realization for the other group. It can be interpreted as rate of dying of one group relative to another. For example, if $HR = 1.5$ when comparing males to females, we could say that males died at 1.5 times the rate of females.

We chose the best model from a suite of a-priori models using 3 criteria: 1) low Akaike information criterion (AIC), 2) meaningful confidence intervals for parameter estimates, and 3) assumptions of the models were adequately met. From the AICs, we calculated Δ AIC and AIC weights to aid in our decision making process (Burnham and Anderson 2002, Vierweig and Van Houwelingen 1993). We did not use AIC for small sample size (AIC_c) because the choice of sample size for the adjustment factor would have been arbitrary. Our set of 35 models was developed to explore specific hypotheses and test for interactions among populations. We limited our selection to models that were biologically reasonable.

To examine model fit, we plotted the observed Kaplan-Meier survival curves and compared them to predicted survival. Additionally, we calculated a Nagelkerke R^2 . This value does not give the proportion of variance of the dependent variable explained by independent variables as in linear regression. Instead, it provides a measure of how associated the predictors are with the response (Harrell 2001:247). We also calculated concordance at 3 fixed times. Concordance index (c) is "the proportion of pairs of animals whose survival time can be ordered such that the animal with the higher predicted survival is the one that survived longer" (Harrell 2001:493, Agresti 2002:229). If $c = 1$, the model is perfectly discriminating. If $c = 0.5$, the predictions are no better than random. Using concordance, we also calculated Somers' D (Dxy) rank correlation by $2*(c-0.5)$. It represents the difference in the probability that predictions are concordant with outcomes minus the probability they are discordant.

We validated the models by bootstrapping estimates 500 times. We refit the model with bootstrapped data and determined average R^2 , Dxy, and c over the 500 repetitions. Using these bootstrapped models, we made predictions with the original data and again calculated average

R^2 , Dxy, and c. By comparing bootstrapped estimates with original estimates, it provided a measure model overfitting and bias in the prediction capabilities of our models (Harrell 2001).

For females, we only modeled the CDA study area with the Cox model because the other 2 study areas had low sample sizes. Applying Harrell's (2001) rule of thumb for sample size (10-20 deaths for 1 predictor), we only explored univariate models for CDA females at the 2 different extents (Harrell 2001). We validated the models using the same methods described above.

Additionally, to gain understanding of habitat characteristics both within the complete study area and within buffers, we used correlation matrices, plots, and principle components analysis. We looked at relationships between spatial extents and vegetation types for variables within buffers. For overall habitat characteristics of each study area, we collected habitat variables within a buffered 100% minimum convex polygon (MCP) placed around all points. We buffered MCPs with 2,077 m buffers to include data collected on elk buffers at our largest extent.

Results

Females

Female annual survival rates were calculated for all 3 study areas. There were 61 females collared on the CDA, 21 on the Lochsa, and 26 on the Sand Creek study areas. Once an animal was collared, it was monitored for an average (SE) of 3.60 (0.19), 3.33 (0.40), and 2.15 (0.23) years for the CDA, Lochsa, and Sand Creek study areas, respectively. Average annual survival estimates (SE) were 0.89 (0.05) for CDA, 0.95 (0.03) for Lochsa, and 0.87 (0.09) for Sand Creek. Annual female survival was similar to other studies reported in the literature (Table 8). Tag recovery studies and translocated animals had the lowest survival (Peek et al. 1967, Kimball and Wolfe 1974). Sand Creek and CDA had survival rates comparable to other populations of resident females with controlled or general rifle seasons. Lochsa females had relatively high survival, but a small sample size of 21 females with only 1 death.

Survival was also examined during hunting season. Sample sizes were reduced during hunting season because not all animals remained in the study during hunting season. For the 3 study areas, 60 (CDA), 18 (Lochsa), and 26 (Sand Creek) elk were used in the survival analysis (Table 9). Because many females remained in the study for multiple years, 157, 42, and 57 elk-years were used in the analysis. There were 678, 342, and 193 radio telemetry locations used to gather habitat information. During hunting season, percentages of females that died due to hunting-related causes were 31%, 5%, and 27% for CDA, Lochsa, and Sand Creek, respectively (Figure 9). Most collared cows did not die during hunting season. Fifty-one percent, 55.6%, and 61.5% remained alive at the end of hunting season. The rest either were lost due to accidents, collar failure, or unknown reasons.

Female univariate analysis. -- We used Kaplan-Meier curves to examine survival differences between populations and explore the change in season structure for CDA females. Kaplan-Meier curves were not calculated for Lochsa females because they had only 1 hunting-related death. We found no significant difference between CDA and Sand Creek populations ($\chi^2 = 0$, d.f. = 1, $p = 0.86$) with only slight indication of earlier losses at CDA than Sand Creek (Figure 10 [A]).

Although a general rifle season was open in the CDA study area only, the Sand Creek and CDA groups had virtually equal Kaplan-Meier survival rates at the end of November (§, 95% CI: CDA: 0.89, 0.84-0.94; Sand Creek: 0.88, 0.76-0.95). The shape of the Kaplan-Meier curves was different because hunts started at different times. For CDA, we examined the difference between hunting-related deaths before and after the change in hunting season structure (pre- and post-1991). We found no difference between survival before and after 1991 ($\chi^2 = 0.40$, d.f. = 1, $p = 0.54$; Figure 10 [B]). The start of hunting season did not markedly change survival for female elk (Appendix B [Table 1]).

Female mortality models. -- Cox's proportional hazards models were used to explore the relationship between mortality and various predictors. We only examined univariate mortality models for CDA cows. Univariate models, rather than multivariate models, were examined because there were only 16 deaths. Using Harrell's (2001) rule of thumb, no models were explored for other study areas because there were only 6 deaths for Sand Creek and 1 death for Lochsa. To look at vulnerability, we fit models relating the natural log of the instantaneous mortality rate to mean habitat characteristics used by each elk for both the large extent and the small extent.

For the large extents, we explored 9 models containing 1 parameter. After examining plots of the Martingale residuals, we noticed a quadratic relationship existed for contour density and contagion of vegetation. Quadratic models for these 2 variables were also explored. The quadratic model for topographic roughness was the best model from the set of 11. After completing the analysis, we looked for outliers using the score residuals. Two elk were identified with very small values for contour density and large score residuals. These animals were removed from the analysis and only 7 models were refit. From residual plots, quadratic terms were no longer necessary. We reported all models using the reduced data set. Only 2 models were within 2 Δ AIC of the best model (Table 10). Of these 3, only the best model, or the model with the lowest AIC, had reasonable confidence intervals for the hazard rate. This model contained contour density with a hazard ratio of 0.997, 95% CI (0.95, 1.00). The hazard ratio implies that as topographic roughness increased, mortality decreased. This best model met the assumption of proportionality. The log likelihood ($\ln[L]$) of the best model ($\ln[L] = -77.1$) was not much better than the null log likelihood when no parameters were added ($\ln[L] = -79.58$). All models had very small R^2 values (Table 11).

For the small extent, we also explored 9, 1-parameter models using Cox's proportional hazards models. No transformations were necessary and no outliers were detected with residual plots. Using AIC, the best model contained percent contagion of vegetation (Table 10). The hazard rate was 0.98, 95%CI (0.95, 1.0). In other words, as vegetation types became less interspersed and more similar, mortality decreased. All of the models had low R^2 s and very similar Δ AICs (Table 11). When contagion of vegetation was related to percent forest and clumpiness of each vegetation type, it was most linearly related to percent of forest ($r = 0.92$). We did not find a strong relationship between contagion of vegetation at the small extent and topographic roughness at the large extent ($r = 0.27$).

Males

Annual survival was explored for males from the 3 populations. There were 94 males collared on the CDA, 215 on the Lochsa, and 79 on the Sand Creek study areas. Once an animal was collared, it was monitored for an average (SE) of 1.90 (0.08), 1.70 (0.04), and 1.50 (0.08) years for the CDA, Lochsa, and Sand Creek study areas, respectively. Average annual survival estimates (SE) were 0.62 (0.09) for CDA, 0.63 (0.09) for Lochsa, and 0.64 (0.1) for Sand Creek (Table 12).

Male survival was also examined during hunting season. Similar to females, not all males were monitored during hunting season. For the survival analysis, a total of 84, 193, and 57 males were used from the CDA, Lochsa, and Sand Creek study areas, respectively (Table 9). Because many of these elk remained in the study for multiple years, 154, 322, and 85 elk-years were used in the analysis. From these elk, we used 670, 3419, and 497 radio telemetry locations to gather habitat information. During hunting season, 70%, 69%, and 63% of animals died of hunting-related causes. Hunting-related mortalities that occurred between 1 September and 30 November included rifle mortality, rifle wounding, archery mortality, and poaching (Figure 9). Sixty percent, 53%, and 55% were specifically from the general rifle-hunting season, while 25%, 24%, and 29% of males remained alive. The length of general hunting season did not change much during the course of the study, but the start of the hunt changed from year to year prior to 1991. After 1991, the start of the hunt remained consistent for males (Appendix B [Table 2]).

Male univariate analysis. -- Kaplan Meier curves were used to explore survival in males among populations. Overall, there were no significant differences among the Kaplan-Meier survival curves for the 3 study areas ($\chi^2 = 2.8$, d.f. = 2, $p = 0.25$; Figure 11 [A]). However, shapes of the curves were different. Survival during hunting season for Lochsa was slightly lower than CDA males. The Sand Creek Kaplan-Meier curves crossed the other 2 curves (Figure 11 [A]). Crossing resulted from different start dates and durations of general rifle hunts. Sand Creek general rifle hunts began later and were much shorter in duration than CDA and Lochsa hunts (Appendix B [Table 2]).

At the end of November, estimated survival rates (\hat{s}) for males from each population were very similar (\hat{s} , 95% CI: CDA: 0.69, 0.61, 0.76; Lochsa: 0.63, 0.58, 0.68; Sand Creek: 0.59, 0.46, 0.69). The date at which 25% of all of the animals died occurred by the 2nd - 4th week of October in all 3 of the populations (time expressed in weeks from 1 September: CDA: 8 weeks; Lochsa: 7 weeks; Sand Creek: 6 weeks).

We compared pre-1991 Kaplan-Meier curves to post-1991 Kaplan-Meier curves to see if changing start dates of general rifle hunts altered survival (Figure 11 [B, C]). There was a large difference for CDA males ($\chi^2 = 7.6$, d.f. = 1, $p \leq 0.001$), but there was not as large a difference in the Lochsa study area ($\chi^2 = 0.3$, d.f. = 1, $p = 0.58$). Kaplan-Meier for each category curves crossed for the Lochsa elk because there was somewhat higher mortality after 1991, but the general rifle seasons started later.

When examined by age classes, we noticed a difference in male elk survival among populations (Figure 12). Sand Creek males in age class 1.5 appeared to have much lower survival than males

in the other study areas and age classes. These results are mainly due to the differences in sample size for each age class, year, and study design. For example, in 1985, 15 out of 17 Sand Creek males collared were in age class 1.5 due to the design of the original study.

Male, large-extent, mortality model. -- We explored 35 Cox's proportional models using data collected at the large extent. After models were fit, outliers were identified in the score residual plots. Five outliers were removed and the models were refit. Because the same model had the lowest AIC, parameter estimates did not change much; and assumptions were met better, we decided to omit those 5 outliers from further analysis. The 7 models with the lowest AIC are listed in Table 13. Four models were within 2 Δ AIC of the best model. Instead of choosing the best model or conducting model averaging, we selected the second best model with 8 terms because it was more parsimonious, made more biological sense, and parameter estimates were more interpretable. By choosing the 8-term model, we eliminated hunter density. In the 9-parameter model, the hunter density parameter estimate had an extremely large confidence interval and its parameter estimate did not make biological sense. The hunter density parameter estimate implied that an increase in hunter density corresponded to a decrease in mortality. The 8-factor model included road density, percent cool aspects, and interactions between study area and topographic roughness and contagion of vegetation (Table 14 and Figure 13). The hazard ratio (HR) suggested that mortality increased with road density because the $HR > 1$. Mortality decreased with increasing topographic roughness for Lochsa and CDA study areas ($HR < 1$). The opposite was true for Sand Creek males; with HR slightly above 1, topographic roughness had a positive relationship with mortality (Figure 13). Hazard ratios for percent of cool aspects and contagion of vegetation for Lochsa and Sand Creek implied an increase in those factors corresponded to a decrease in mortality. Contagion of vegetation was not important for the CDA study area because $HR = 1.00$. Contagion of vegetation was highly correlated with percent of area forested for the Lochsa and CDA elk ($r = 0.91, 0.83$, respectively), but not for Sand Creek ($r = 0.02$). Instead of forest, contagion of vegetation was most related to the percent of shrubs ($r = 0.20$) and clumpiness of forest patches ($r = 0.12$) at Sand Creek.

We conducted the analysis 3 additional ways to confirm our results: 1) standardizing the variables, 2) with and without outliers removed, and 3) all 3 populations explored separately. No matter which way we conducted the analysis; similar models were selected using our 3 criteria.

Fit statistics indicated poor fit for the selected model. The 9-parameter model had a low R^2 , Somers' Dxy, and concordance value (Table 15). For example, at week 13, the concordance value (c) equaled 0.638. This means that in 63.8% of pairs of live and dead observations, the x and y pairs were correctly ordered. We validated our best model by bootstrapping the data, fitting models to the new data, calculating fit statistics for each model and then averaging. Our estimated value with the original model did not change much when bootstrapped (Table 15). Corrected values differed from original models between 0.008-0.042 for Somers' Dxy.

Male, small-extent, mortality models. -- Again, 35 pre-specified models were fit using Cox's proportional hazards models with individual elk habitat variables collected at the small extent (70.28 ha). No outliers were identified in score residual plots. The 7 best models are listed in Table 16. Only 1 other model was within 2 Δ AIC of the best model. The 2 models with the

lowest AIC contained almost all variables and interaction terms. The interaction terms implied that there were different relationships between habitat and mortality for all study areas. The best model selected was the 15-parameter model (Table 17). Some relationships, such as road density, had similar slopes but varying magnitudes among study areas, while others had very different slopes. For example, topographic roughness was not important for CDA males and had the opposite relationship for Lochsa and Sand Creek males.

Because we wanted to understand study area differences further, we broke the analysis into 3 separate parts. We chose one of the best vulnerability models for each study area to explore further. Two models were within 2 Δ AIC of each other for Lochsa males at the small extent (Table 18). The best model for Lochsa males was chosen because it had the least number of parameters and smallest AIC (Table 19). For Lochsa males, this model included 4 predictors: topographic roughness, road density, percent cool aspect, and percent forest. Road density had a positive relationship with mortality ($HR > 1$), while topographic roughness, percent cool aspects and percent forested areas ($HR < 1$) had a decreasing relationship. The Lochsa model also had very low fit statistics (Table 20). For example, at time 7.5 weeks $R^2 = 0.105$, which indicated a poor relationship between the dependent and independent variables. The 2 best models for Coeur d'Alene males were the full models using Δ AIC values. We chose the model with the smallest AIC value that included road density, topographic roughness, hunter density, percent of cool aspects, and percent forest cover (Table 19). Mortality increased with increasing road density and topographic roughness. Similar to the other study areas, fit statistics were poor (Table 20). For example, at week 13 ($c = 0.340$), the chance of correct relationships being identified for pairs of x values was less than random chance alone. For Sand Creek males, we chose the best model using the AIC value (Table 18). This model included road density, topographic roughness, hunter density, percent of cool aspects, and contagion of vegetation (Table 19). Differing from the other 2 populations, topographic roughness at Sand Creek had an increasing relationship with mortality ($HR > 1$). Fit statistics were poor again, but R^2 values ($R^2 = 0.260$ at week 1) were slightly better than the other 2 study areas (Table 20).

To better understand study area differences, we gathered habitat information within buffered minimum convex polygons placed around all of the elk locations from each population. The summary characteristics can be found in Appendix B (Table 2).

Discussion

Elk vulnerability is the management of habitat security to decrease the risk of mortality for an individual elk during hunting season. By better understanding vulnerability, wildlife managers and biologists could alter factors to reduce hunting pressure and create a more secure environment. To investigate elk vulnerability, we explored male and female elk survival during hunting season at 3 different study areas: Coeur d'Alene, Lochsa and Sand Creek. We first compared crude estimates of annual survival to other studies. Then we conducted univariate analysis to explore differences among populations. Last, we related habitat characteristics to survival using regression models. Our main findings indicate that elk in various habitat types use environmental characteristics differently to enhance security during hunting season.

We made 5 assumptions in order to obtain unbiased estimates of elk survival for the 3 populations (Winterstein et al. 2001). First, we assumed that the data were a random representative sample of the population. Although this assumption was made, it may have been violated in various ways. For example, in 1985, a high number of 1.5-year-old males were included in the study. If this sample was not representative, the high number of yearlings could have biased survival estimates downward. Second, we assumed that the experimental units were independent. Again, this assumption may have been violated because radio-collared animals that congregate or forage together could have had a related or similar risk of mortality. This assumption may have also been violated because we used elk-years as our unit. Because many animals lived for more than 1 hunting season and we wanted to maximize data usage, we used elk-years as the unit of observation although the observations may have been correlated. To ameliorate the lack of independence, we averaged residuals over each animal when checking for outliers, but the estimates of standard error for parameter estimates may be incorrect. The third assumption was that researchers were in constant contact with radio-collared animals. We made this assumption in order to treat time as a continuous variable. We know that researchers did not check up on animals every day, but monitoring did occur at least 2 times a week (Unsworth et al. 1993, Hayes et al. 2002, Gratson et al. 1997, Pauley 1991). With this time interval, researchers could have pinpointed the exact date of death. The fourth assumption was censoring and deaths are unrelated or independent. Because poaching events were reported and almost every censoring event had an explanation, this assumption was most likely satisfied. The fifth assumption was radio-collars did not affect animal's risk of mortality. Based on other research findings, we do not believe that radio-collars affected elk survival (Unsworth et al. 1993, Hayes et al. 2002, Withey et al. 2001).

Females

Female annual survival estimates were similar to other hunted populations. Estimates from tag recovery studies were lower (Peek et al. 1967, Kimball and Wolfe 1974, Sauer and Boyce 1983), while most unhunted populations had higher estimated, annual survival rates (Ballard et al. 2000, Lubow et al. 2002). Estimates from tag return studies were probably lower because data are less accurate and harder to collect (Zager and Leptich 1991). As other researchers have found, most females did not die and remained in the studies for a long period of time (McCorquodale et al. 2003). Our annual survival estimates differed from estimates calculated in the original studies because we used different subsets for analysis. For example, Pauley (1991) used elk data from 1981-1989 and separated it into refuge and non-refuge estimates. We restricted the data set to 1984-1989 to fit into the time frame of analysis and meet our stringent requirements of sample size.

Female univariate analysis. -- Although hunting season structures were not the same, we found no difference between survival curves of CDA and Sand Creek cows. A 5-day antlerless hunting season was offered within the Coeur d'Alene, Idaho, GMUs, whereas various special permit hunts were offered in certain areas of the Sand Creek, Idaho, area. These special permit hunts varied in number of permits issued and length (i.e., 400 permits for a 10-day hunt to 50 permits for a 15-day hunt in 1985). The similarity of mortality rates suggests that short general seasons or special permit hunts are both effective ways of managing female harvest. Additionally, our results implied that the change in starting dates of general rifle hunts for Coeur d'Alene females

produced no difference. This change did not impact cow survival because the starting dates prior to 1991 varied annually and were not very different from the 1991 standard (Appendix B [Table 1]). Some start dates were close to 10 October while others were earlier, but in 1991, it was standardized to occur after the peak of the rut on 10 October (Hayes et al. 2002).

Although relationships seem reasonable, fit statistics indicated that our models did not predict precisely. None of the factors explored were very good predictors of mortality rates. The R^2 values for our models were very low and differences between the null log likelihood and the model log likelihood were not large. Our sample size of 57 females with 16 deaths was relatively small. In the future, larger sample sizes combined with other explanatory factors should be explored to identify more important factors influencing female vulnerability.

Males

Males had much higher mortality rates than females because they were the primary target harvested during hunting seasons. Bull hunting seasons were longer in duration and had more hunters participating. In most cases, deaths occurred during the first 2-3 weeks of the general rifle season (Pauley 1991, Smith et al. 1994, McCorquodale et al. 2003). Annual mortality from the 3 study areas was comparable to other populations. Unhunted animals had the highest survival (Lubow et al. 2002); males in Oregon and Washington had the lowest annual survival (Harper 1966, Smith et al. 1994).

Male univariate analysis. -- To explore survival during hunting season, we compared Kaplan-Meier curves among 3 populations, before and after the change in the hunting season structure, and among age classes. Survival rates during hunting season were not statistically different among the 3 study areas. Although no differences were detected, Sand Creek males had a lower average estimated survival rate and a different shaped Kaplan-Meier curve. Lower survival estimates may be due to a single year. In 1985, most Sand Creek males collared were yearlings and it was the only year for any study area in which it snowed during the first 2 weeks of hunting season. The combination of snow and a prevalence of yearling males in the sample may have precipitated a higher mortality estimate for Sand Creek, thereby driving the combined survival rate down. Shape of the Kaplan-Meier was different because the Sand Creek general rifle season was very short and intense, and the start date was also slightly later than the other 2 areas.

After 1991, the start of the general rifle season was postponed so that it would begin after the peak of breeding season. For CDA males, pre-1991 survival rates were lower than post 1991. Contrary to what we expected, we did not see this same difference for Lochsa males. Because we did not control for other factors in the analysis, it is hard to determine why we observed a difference in one group and not the other. Sand Creek males were not examined because adult bull rifle hunts were eliminated in 1991.

We hypothesized that a delayed start of general rifle season would increase survival in both populations because the hunt would start after the peak of breeding season. During rut, elk congregate in larger groups making their presence more apparent. Bulls form harems and actively defend and pursue females. During this time, bulls frequently respond to bugling from other males as well as from hunters imitating the call (Loftus 1991). After the rut, cow and bull

elk tend to disperse into smaller groups and increase alert behavior. “Elk ... go into seclusion after the rut...choosing terrain laden with obstacles for culling predators” (Geist 2002:404). By living in smaller groups during the hunt, bulls would be more effective at hiding from visual predators such as hunters (Picton 1991). Because of this change in behavior, we expected the delayed hunting season to have the same effect on both populations. By postponing the start, the hunt would have started after most of the harems had broken up, bulls would be more dispersed, be less responsive to hunters’ calls, and less vulnerable to harvest.

The observed difference may have occurred for 3 reasons. First, there may have been a difference in the timing of the rut at the 2 study areas. The hunt for CDA may have in fact interrupted the rut before 1991, while it did not interrupt breeding season for Lochsa males. Several studies have indicated breeding season variability both within and between populations. For example in Yellowstone, breeding has been reported to occur from 12 September to 14 October (Rush 1932), to end by 3 October (Knight 1970), or the average peak to be between 3 and 6 October (Morrison et al. 1959). In Canada, Flook (1970) reported most conceptions occurred between 18 and 28 September. Although we have no evidence, similar variation between populations may have occurred for Lochsa and CDA elk. The delay of general season could have only been beneficial to CDA males, while it never was or continued to be detrimental to Lochsa bulls because of variation in breeding periods. The lower survival observed for Lochsa males may have occurred because general rifle season began to interrupt the peak of rut after 1991. Males may not only be more susceptible during the rut, but an interrupted rut could prolong the breeding period. This could result in males that are less prepared for winter and more susceptible to future mortality (Freddy 1987, Stalling et al. 2003). Second, we did not control or account for other sources of variability such as differences in habitat use or population size. Because of this, annual variation in survival rates or differences in habitat management could have resulted in a change in mortality rates for CDA, but not Lochsa. For example, increased hunting pressure at the beginning of the season might have counteracted the later start date for the Lochsa population. Third, the method used to detect differences, the log rank test, may have failed to detect a difference because Lochsa curves crossed during the middle of hunting season. Log rank tests have relatively low power when the curves cross (Klein and Moeschberger 2003).

Average estimated survival rates appeared to vary among age classes in each of the 3 populations. The most drastic differences can mostly be explained by the structure of animals radio-collared, study area-specific weather events, and inconsistency in reporting of age among data sets. The best example is the Sand Creek yearlings. Survival for Sand Creek yearlings is biased low because of high numbers of yearlings monitored during a year in which it snowed during a short Idaho hunting season. Weather and other latent sources of variability may better explain differences observed among age classes.

Mortality models. -- We used Cox’s proportional hazards models to evaluate elk vulnerability at 3 study areas by relating habitat use to mortality rates at 2 different extents. We hypothesized that similar habitat characteristics would be important at all study areas and extents. Using the best and most parsimonious models, our findings indicated differences between the large and small extents among and between study areas (significant interactions). At the large scale, some habitat variables had similar relationships among study areas, while others differed. At the small

extent, almost all habitat characteristics from each population had different relationships with mortality rates.

Male, large-extent, mortality model. -- For the large extent, some factors were similar for all areas, and others were different at some of the study areas. The best large-scale model included road density, percent cool aspects, contagion of vegetation, and topographic roughness. Road density was positively related to mortality. Percent of cool aspects and contagion of vegetation were negatively related with mortality. Although overall relationships were similar, strength of relationships for contagion of vegetation differed among study areas. Relationships between topographic roughness and mortality differed for all areas.

In this model, elk that used areas with higher road density had a higher rate of mortality. Higher road densities made elk more susceptible to human disturbance and hunter pressure. Unsworth et al. (1993), Leptich and Zager (1991), Gratson et al. (1997), and Hayes et al. (2002) each found similar results using parts of the same data. Similarly, elk in south-central Washington had an increase in vulnerability with increased road access (McCorquodale et al. 2003). In Montana, 50% of all elk kills occurred ≤ 1 km from open roads (Weber et al. 2000). Many habitat selection studies have documented road avoidance, but they did not differentiate between elk that live or die, and they focused on summer habitat use. Those studies demonstrated that elk tend to select areas with lower road densities, farther from roads, and with less human disturbance in hunted environments (Basile and Lonner 1979, Rost and Bailey 1979, Irwin and Peek 1983, Witmer and deCalesta 1985, Lyon and Canfield 1991, Rowland et al. 2000). But in the absence of hunting, elk seem to be bothered little by human presence and disturbance (Schultz and Bailey 1978).

Mortality rates were also associated with cool aspects and contagion of vegetation. Both of these variables described the structure and composition of vegetation communities. For aspects, an increase in percent of cool aspects was related to a decrease in mortality rates. The same relationship existed for contagion of vegetation, but the type of relationship between contagion and mortality differed among study areas. Contagion of vegetation was most related to percent forest for CDA and Lochsa elk. Continuous, forested areas and more vegetated cool aspects provided more security for Lochsa and CDA males. Similarly, Marcum (1975), Weber et al. (2000), Edge et al. (1987), and Hurley and Sargeant (1991) reported that elk tended to select areas with higher cover during hunting season. Surviving elk tended to select less open areas during hunting season, while “elk that ventured or were pushed into areas with poor security appeared to have a higher probability of being killed” (Weber et al. 2000:92). Although forest types differed in the Lochsa and CDA areas, high cover may have provided similar protection in both areas. In Montana, elk selected lodgepole pine for security, but the author noted that other vegetative complexes, such as sub-alpine fir and Douglas fir, could provide similar security in other areas (Weber et al. 2000).

For these 2 areas, we documented a relationship between vegetation and mortality. It is more difficult to determine whether elk selected areas of higher cover to avoid hunters, they were pushed into forested areas or un hunted areas because of hunter pressure, or they used these areas as part of the normal cycle of behavior after breeding season. One study found that elk were pushed into timber and brush by hunters, interrupting their normal feeding patterns (Harper

1966:17), while others have implied habitat selection of higher cover increased before hunting season even opened (Lyon and Canfield 1991).

Large, contiguous tracts of forest may provide hiding cover for Lochsa and CDA elk, but Sand Creek elk had different relationships with vegetation. Contagion of vegetation was most related to shrubs and clumped patches of forest. In Sand Creek, much of the wintering grounds was characterized by large expanses of sagebrush. Elk may have sought refuge from hunting in their wintering grounds because those GMUs, 60A and 63A, did not have a general rifle season (Brown 1985). Additionally, we may have seen a different relationship because the available forest structure is much different in the Sand Creek area. Forests are thinner, drier, and patchier and they were hard hit by mountain beetle resulting in salvage logging.

We measured topographic roughness by using contour density, which captured changes in slope and elevation. For the Lochsa and CDA bulls, elk that used rougher terrain had a decreased rate of mortality. Using some of the same data, Hayes et al. (2002) and Unsworth et al. (1993) also found a decreased risk of mortality with an increase in topographic complexity. Areas with higher topographic complexity would have decreased hunter pressure because they would be less accessible by hunters and more hidden by topographic features. Sand Creek males had the opposite relationship. Elk that lived longer tended to use areas with less rough terrain. In heavily forested areas of the Garnett Mountains of Montana, some elk selected steeper topography during hunting season, but others tended to use “safety zones” or zones free from harvest (Edge and Marcum 1991). In an earlier study in a nearby area, cow elk selected areas closed to hunting because they provided security from hunting and plentiful forage (Edge et al. 1984). Although Sand Creek elk do not use steeper topography for security, they did use “safety zones” that are flatter and lower in elevation and have lower hunter pressure because they are mostly closed to hunting (Marcum et al. 1984). For example, GMU 60A is flatter, lower in elevation, has large sagebrush expanses, does not have a general rifle season, and is an area many elk move to during hunting season. Similar to Sand Creek elk, another study reported that surviving radio-collared elk used a flat, wet meadow complex at lower elevations to enhance security (McCorquodale et al. 2003).

Our results may differ from Hughbanks (1993) because we chose different spatial and temporal scales. For example, Hughbanks (1993) described Sand Creek non-migrating, yearling males selecting security habitat with steep terrain and high forest cover. We might not have observed this trend with our data because we did not measure topography and forest characteristics at the same scales and we did not separate males into migrating and non-migrating. Additionally, Sand Creek, Idaho, general rifle seasons were only 5 days long. Because our analysis included a much longer period before and after the hunt, we may not have detected short-term changes in behavior that may have occurred over those 5 days. Perhaps for 5 days, Sand Creek males were using areas with steeper terrain and higher canopy cover.

Although we tried to reconfigure hunter density, our results did not seem biologically reasonable. Similar to Hayes et al. (2002), we found elk mortality increased with decreasing hunter density. Although this is counter intuitive, relocations of collared animals by 1 researcher did not seem to be affected by hunter pressure (McLean 1972). He observed 1 elk that “spent the entire hunting

season within a quarter mile from an access road and 1 mile from a packer's camp" (McLean 1972:36). We believe the huge confidence interval for hunter density indicated that it is not very reliable and further studies should continue to search for a better predictor that describes hunter pressure.

Overall, at the large extent, elk that survived longer selected more secure areas or areas that were more inaccessible to hunters and experienced less human disturbance. Definitions of security for the large scale seem to be slightly different among study areas. Coeur d'Alene and Lochsa bulls tended to select forested areas, away from roads with steep terrain that were less accessible to hunters. Sand Creek bulls selected flatter areas away from human disturbance that provide a refugium from hunting. Although these patterns are biologically understandable, fit statistics indicate that these models would not provide precise predictions. Our values of c , R^2 , and Somers' Dxy all indicated that our models would predict about the same as if we simply assigned outcomes at random. Using some of the same data, Hayes et al. (2002) also had very low values for concordance. Poor fit could have occurred because we chose the selected predictors, models, or measurement methods that did not accurately capture relationships. Alternatively, animals' patterns of habitat use do not affect survival rates. Perhaps habitat use is only weakly associated with mortality. To further understand these relationships, further exploration of different variables and scales may be useful.

Male, small-extent, mortality models. -- Unlike the large-scale model, the best small extent model suggested that all relationships were different among study areas. For example, percent of cool aspects was not important for CDA or Sand Creek, while a decrease in aspect was related to a decrease in mortality rates for Lochsa bulls. Based on the hazard ratios, road density was positively related to mortality for all populations, but the relationship was much stronger for Sand Creek males. These differences between the large and small extents suggest that animals may have been selecting secure areas at different scales or under different orders of selection (Johnson 1980). The large extent represented a pseudo-home range, while our smaller extent described use of smaller areas analogous to selection within a home range. To lessen depredation risk, elk in all study areas may have selected areas more similarly at the home range level, or second order of selection. For areas within the home range (third order of selection), elk maximized unique characteristics of each study area differently to establish habitat security.

Because many different relationships existed at the small extent, we went on to determine the most important relationship for each study area. We modeled each study area separately and tried to identify the best and most parsimonious models describing mortality rates. Certain factors, such as hunter density, were not biologically interpretable in some of these models.

For Sand Creek, the best model included topographic roughness, road density, contagion of vegetation, percent of cool aspects and hunter density. Relationships between mortality and these factors once again related to the specific way that Sand Creek elk avoided hunting pressure. Surviving animals moved from their summer ranges to areas with lower road densities, less topographic roughness and higher contagion of vegetation to avoid hunting pressure. Like the large scale, these conditions describe traditional wintering grounds or the GMUs that are closed to general rifle seasons (Brown 1985) and the forest patterns found in that region. Our results

imply that surviving elk may have made migrations sooner to avoid hunting than elk that died. Other authors have found that elk increase their daily rate of movements, move to areas of lower hunting pressure (Hughbanks 1993, Pauley 1991, Brown 1985, Lyon and Canfield 1991) or shift their activity centers (Hurley and Sergeant 1991) during hunting season. In Colorado, elk on only 1 of 2 study areas shifted their movements due to a change in the opening date of archery season (Conner et al. 2001). The authors suggested that differences in movement among study areas may have been due to topographical differences between areas or differences in migrational patterns of each population (Conner et al. 2001). Sand Creek elk may have different relationships with security habitat because they migrate or simply have different “safety zones” available for use. Sand Creek males selected areas that met the trade-off between foraging and security within the available habitat.

The best models at the small extent were more similar for CDA and Lochsa males. Similar to Hayes et al.(2002), our model for CDA males demonstrated an increase in road density was associated with an increasing rate of mortality; while higher use of forested areas decreased mortality rates. Unlike Hayes et al. (2002), we did not compare closed roads with open roads because the acquisition of consistent data would have been very difficult for all 3 study areas. Our results confirm Hayes et al.’s (2002) recommendation that an overall reduction in road density (both open and closed) may decrease the risk of mortality. Although road closure may be useful, closed roads that are still intact may also continue to bring hunters on ATVs, bicycles, motorbikes, and foot traffic. In a study by Basile and Lonner (1979), closed roads actually increased hunter pressure because hunters considered these areas to be prime hunting spots. At the small scale, topographic roughness was an important predictor of mortality for CDA males. Elk that used areas with higher topographic complexity survived longer. Unlike Hayes et al. (2002), we did not include season structure in our model because it was not common to all 3 study areas. As we saw in the univariate analysis, this variable was important for CDA males, but season structure could have interacted with other habitat characteristics.

Similar to the large extent, the best model for Lochsa males included topographic roughness, road density, percent cool aspects, and percent of forested areas. Our findings characterize a mix of the best models found by Gratson et al. (1997) and Unsworth et al. (1993). Steeper areas with low road densities, more hiding cover, and denser vegetation on cool aspects provided more protection for elk in this area. Lochsa males selected site-specific characteristics that provided the best protection against hunter mortality in the Lochsa-Clearwater River Basin.

Differences between small and large extents and among populations make overall conclusions difficult. We were surprised that similar factors that provided security from hunting pressure were not important among areas and between extents. Animals used combinations of area-specific habitat to avoid hunting mortality. Our results imply that biologists and managers would have to weigh the unique combinations of hunting regulations, population characteristics, and habitat combinations in order to manage security of elk during hunting season.

In conclusion, our results indicate that elk in the 3 study areas have differing strategies to avoid hunting mortality. The 3 populations avoid hunting mortality by using different habitat features in diverse landscapes. Our results imply that elk are highly adaptable and may change their

habitat use in response to local hunting pressure by using the resources available to them. This adaptability has allowed elk to populate and presently re-colonize almost all of heterogeneous North America. Our somewhat conflicting results simply reaffirm the complex relationship that exists between populations, individual animals, and the environment they inhabit.

In the future, we would like to determine if we could develop better predictive models. All of our models had very poor fit and predictive capabilities. Different model structures or other, possibly more complex, variables may be necessary to better understand mortality during hunting season. We may also have excluded certain confounding factors, such as population density (Taper and Gogan 2002). Because data were not consistently available for all 3 populations, we may have missed certain factors that explained more of the observed variation. Obtaining more accurate layers, monitoring animals more frequently, exploring more temporal and spatial extents and resolutions may also aid in improving elk vulnerability models. Additionally, correlation among individuals needs to be better addressed because it may be skewing true relationships. A different model structure might even be useful. Since animals were not really monitored continuously, it may have been more appropriate to use a different model structure

Management Implications

Understanding the relationships between habitat and elk vulnerability to hunting provides powerful information to biologists and managers trying to provide sustainable, quality hunting opportunities. It allows biologists to not only manage hunting season structure and limits, but also habitat that will provide more or less protection from hunting mortality. Our study will add to the base of knowledge about relationships between habitat and elk survival rates. We demonstrated that elk vulnerability or security during hunting season is different under various environmental conditions and at different spatial scales. Managers will need to consider unique combinations of roads, topography, cover, and hunting season structures of each area at several spatial extents when deciding how to make management changes. For example, hiding cover and road density are 2 manageable components, but their importance for a particular elk population may be unique because of differences in available habitat and population characteristics. Managers should consider site-specific qualities when altering factors related to habitat security and monitor the changes in case relationships are altered. By using adaptive management strategies, we can ensure healthy elk populations and fair, quality hunts for many generations to come under changing environmental pressures.

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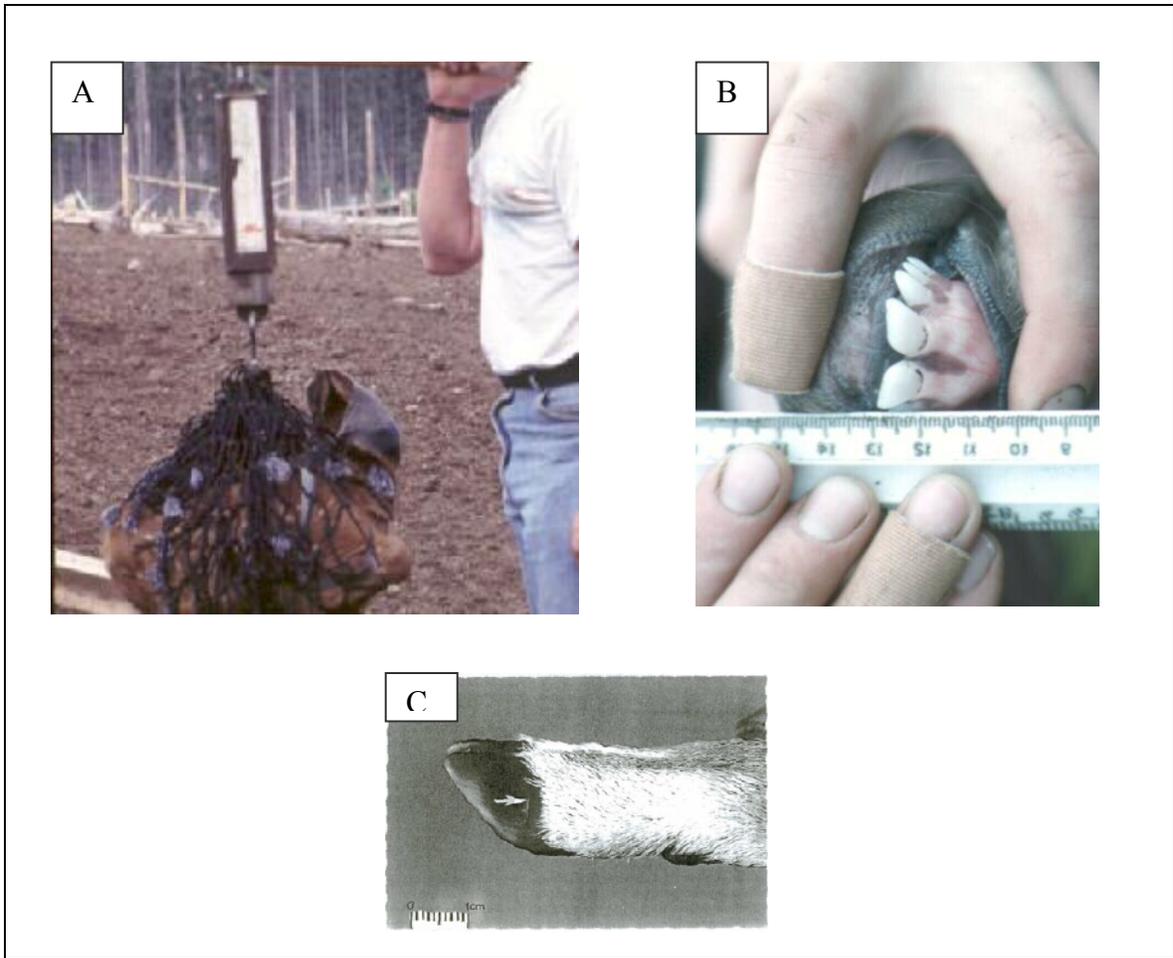


Figure 1. Techniques for measuring and predicting age of neonatal cervids. A = Spring scale used to measure elk calf mass. B = Measurement of outer edge of first incisor. C = hoof line of elk calf. Arrow points to indentation on the hoof. Haugen and Speake (1958) and Sams et al. (1996) used the distance between the leg hairline and the indentation to predict age of neonatal cervids.

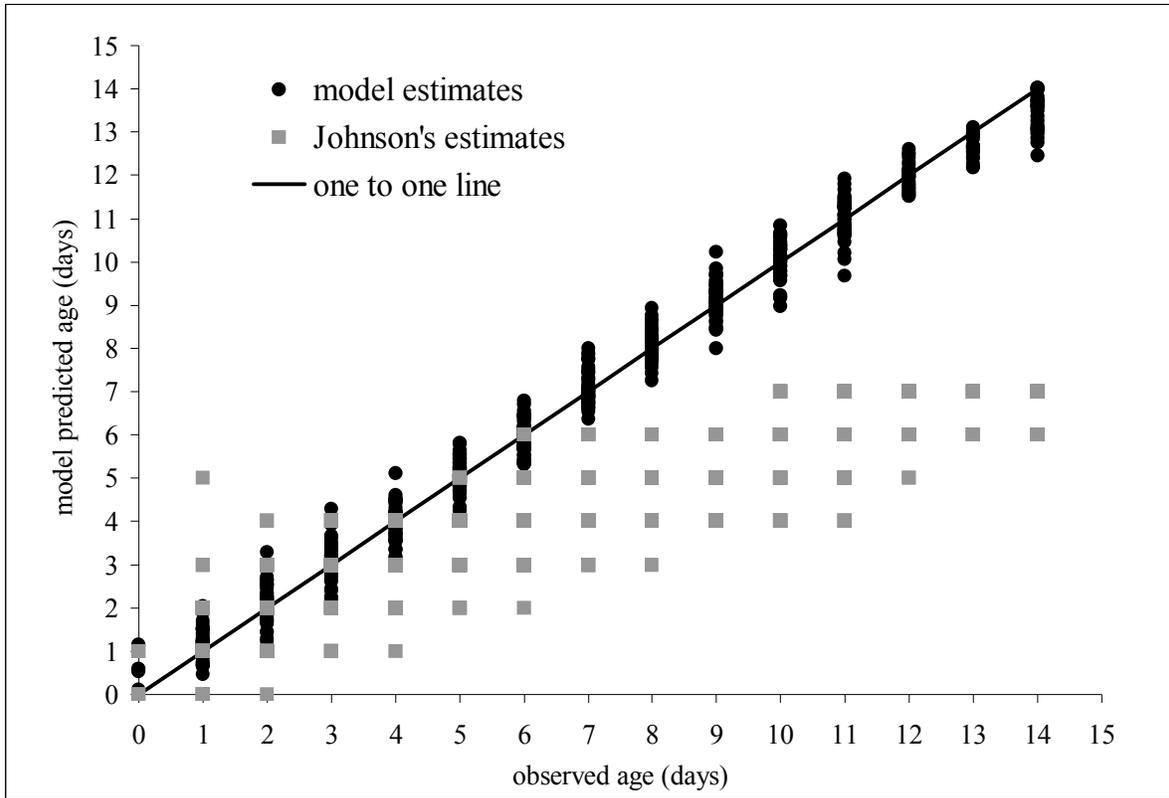


Figure 2. Ages predicted from morphometric mixed effects model and Johnson's (1951) aging categories compared to known ages of elk calves, 1-14 days after birth, at the Starkey Experimental Forest and Range Station, La Grande, Oregon, 1996-1998.

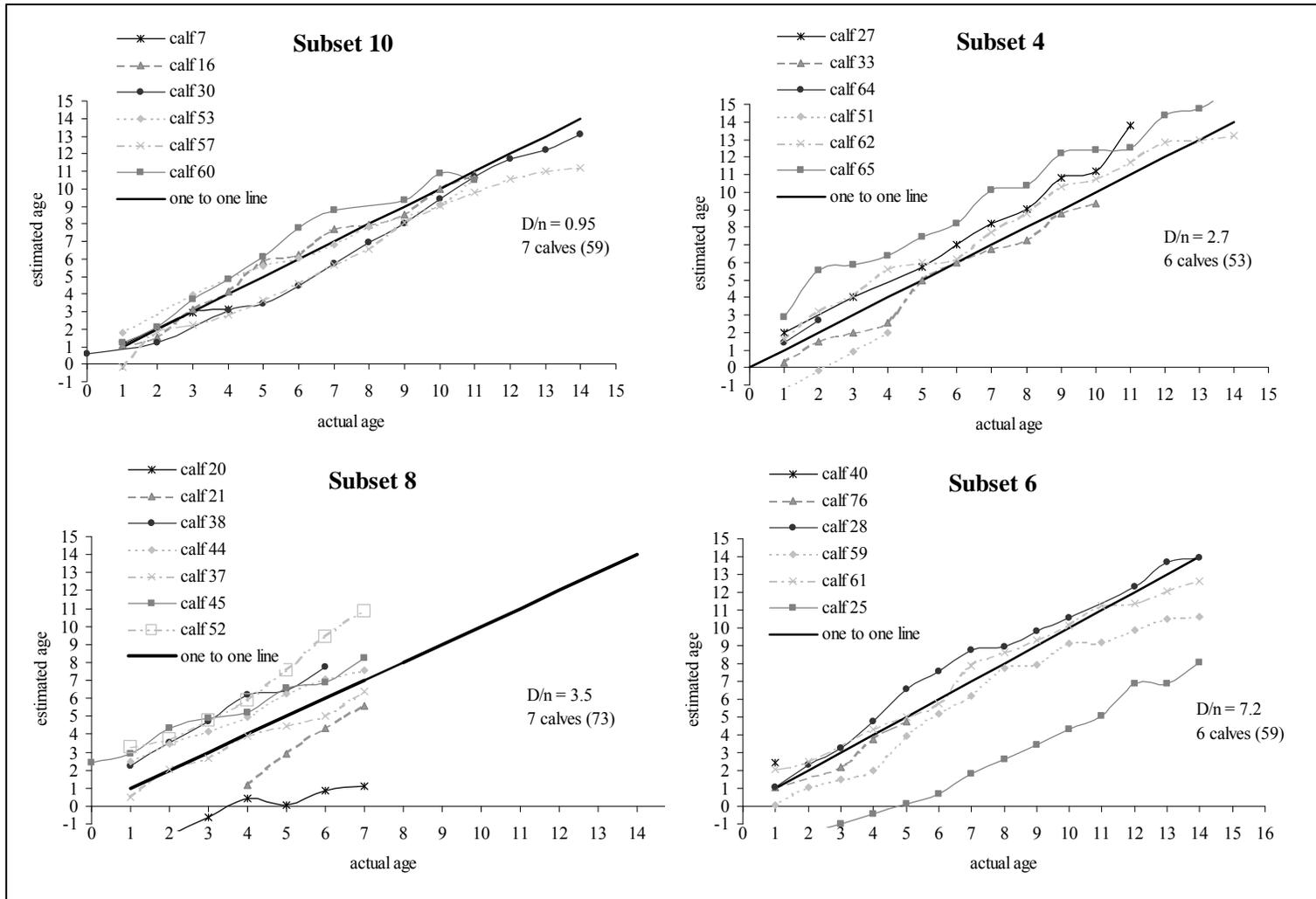


Figure 3. Relationship between known ages and predicted ages (days) of elk calves using the linear mixed effects model based on morphological measurements for 4 subsets used in 10-fold cross validation. D/n is a measure of prediction error (days²), for each group of n calves and their associated number of observations.

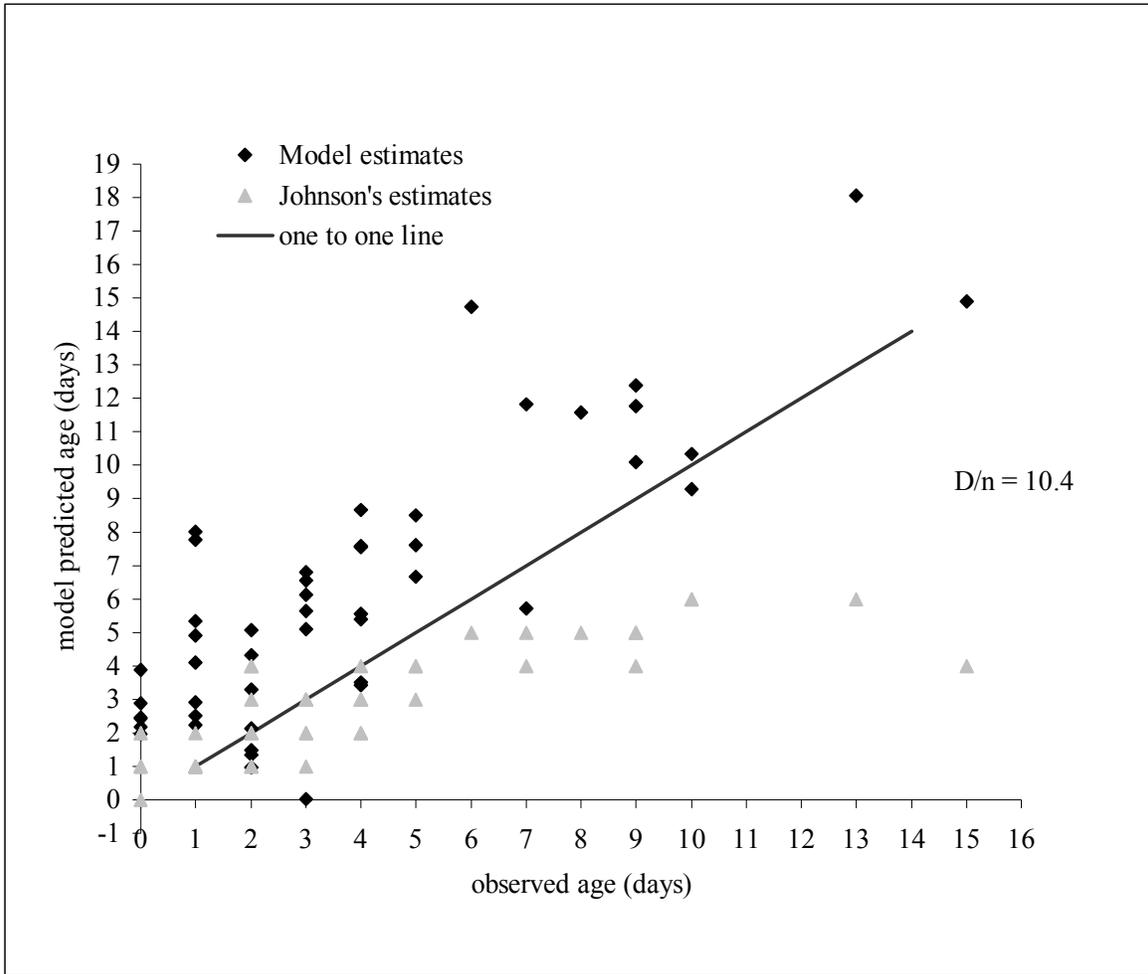


Figure 4. Ages predicted from morphometric mixed effects model and Johnson's (1951) aging categories compared to known ages, 1-14 days after birth, at the Moscow Mountain Elk Ranch, Moscow, Idaho (MMER) in 1999. Forty-eight measurements were taken on 32 calves.

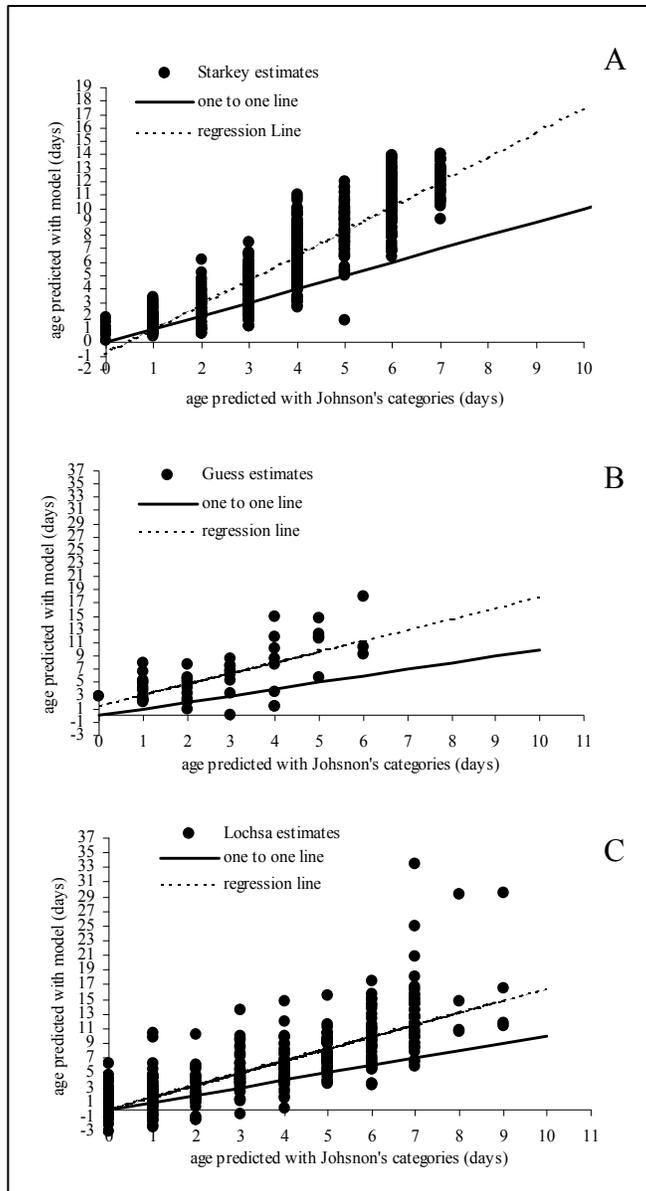


Figure 5. Age predicted using linear mixed effects model compared to age predicted with Johnson's (1951) aging criteria. A = captive calves, 1-14 days after birth, at the Starkey Experimental Forest and Range Station, La Grande, Oregon, 1996-1998 (Starkey). B = captive calves, 1-14 days after birth, at the Moscow Mountain Elk Ranch, Moscow, Idaho (MMER), 1999. C = wild neonate elk calves captured in the Lochsa and Clearwater River Basins, Idaho (Lochsa). Regression lines were: Model estimates = $1.62 + 1.63 \cdot (\text{Johnson estimates})$ for Guess; Model estimates = $0.14 + 1.64 \cdot (\text{Johnson estimates})$ for Lochsa; and Model estimates = $-0.84 + 1.83 \cdot (\text{Johnson estimates})$ for Starkey calves.

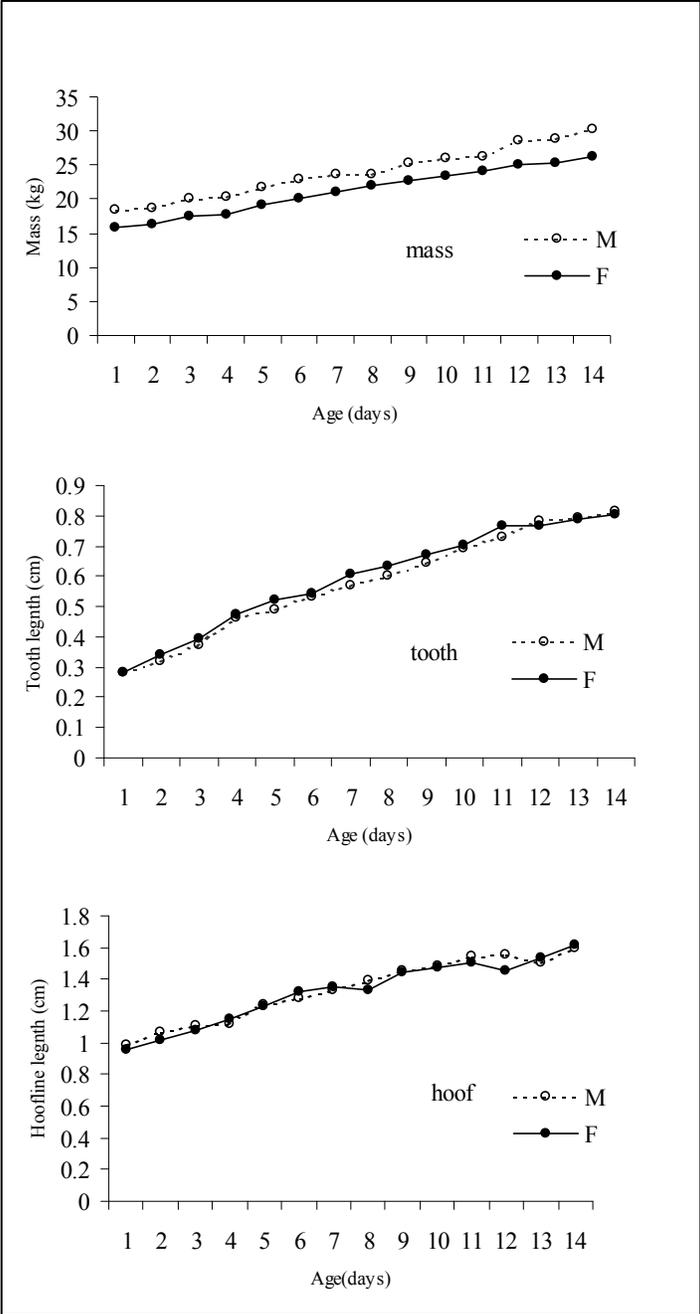


Figure 6. Mean mass (kg), tooth edge length (cm), and hoof line length (cm) of male (M) and female (F) Rocky Mountain elk calves at Starkey Experimental Forest and Range, Oregon, 1996-1998.

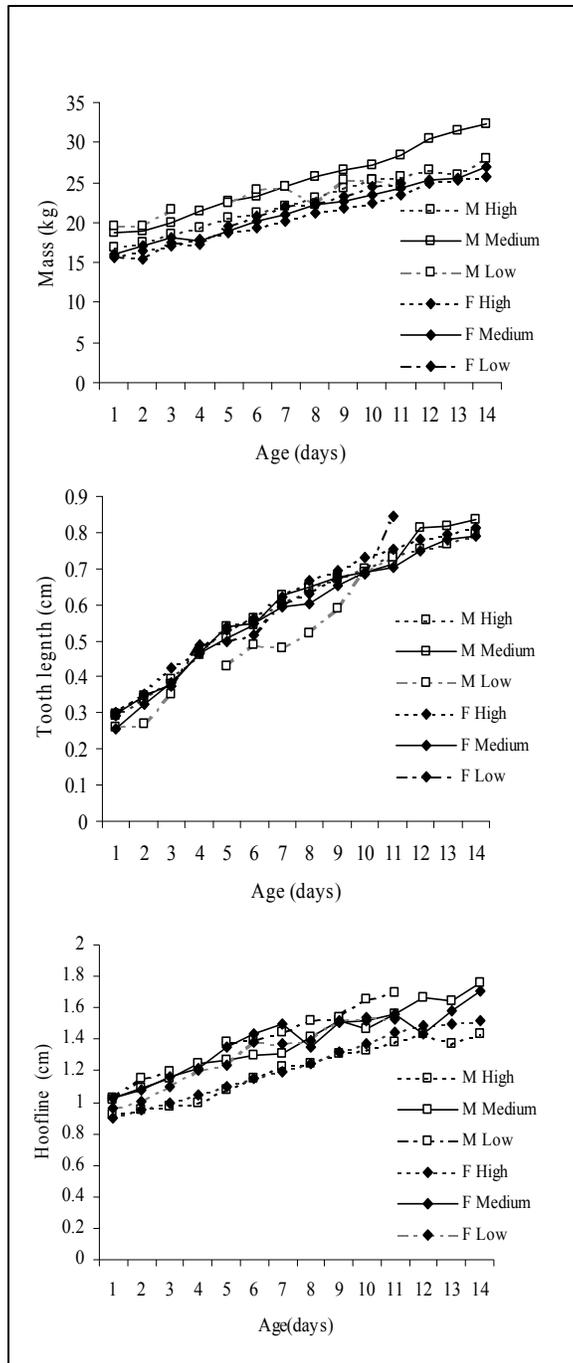


Figure 7. Mean mass (kg), tooth edge length (cm), and hoof line length (cm) for 3 maternal summer-autumn nutritional groups (High, Medium and Low) and sex (M = males and F = females) of elk calves at Starkey Experimental Forest and Range, Oregon, 1996-1997.

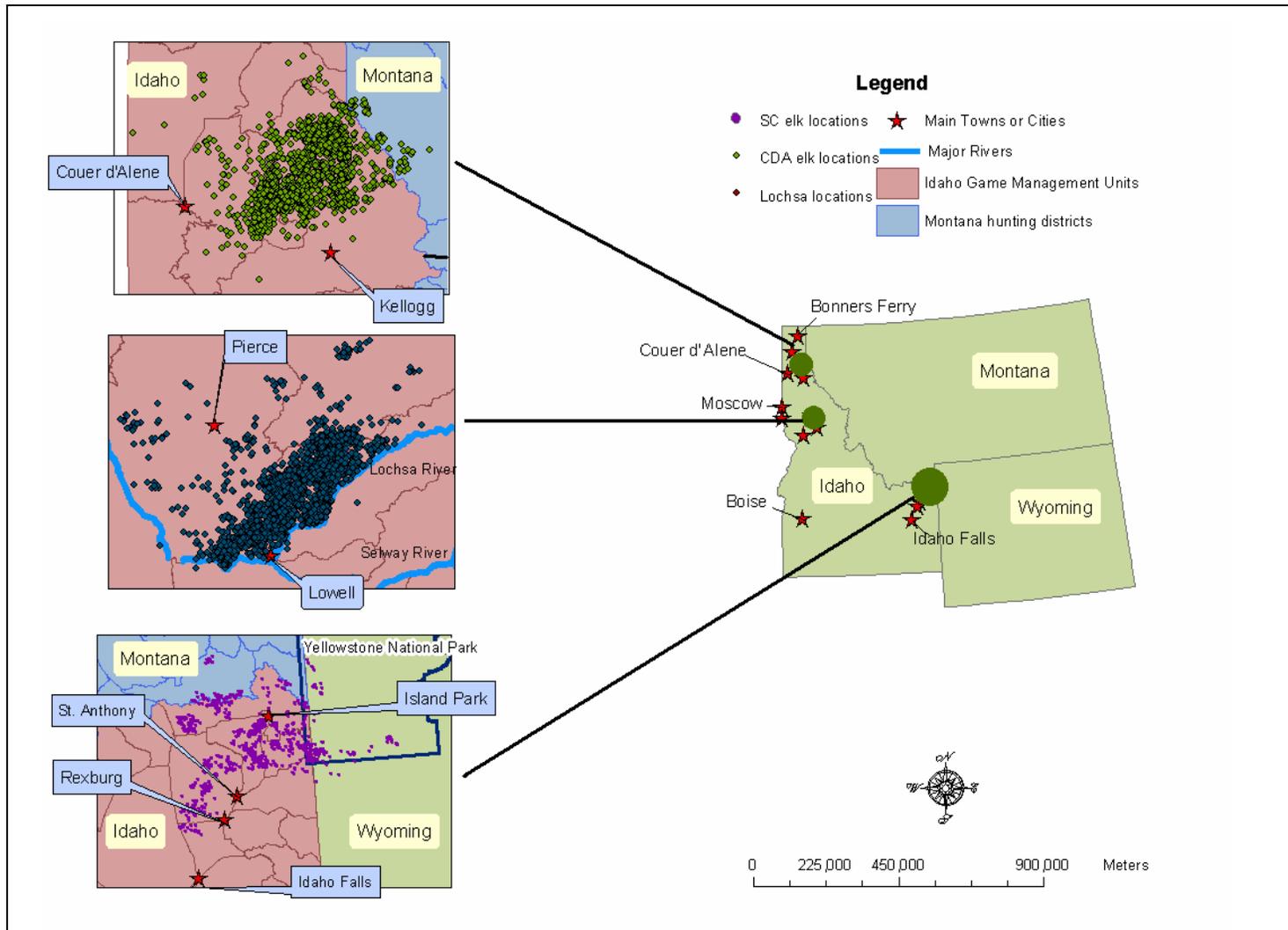


Figure 8. Locations of the 3 study areas, (Coeur d'Alene (CDA), Lochsa, and Sand Creek[SC], Idaho) used to explore the relationship between habitat selection, hunting season structure and mortality of radio-collared elk. Elk radio telemetry point locations are shown.

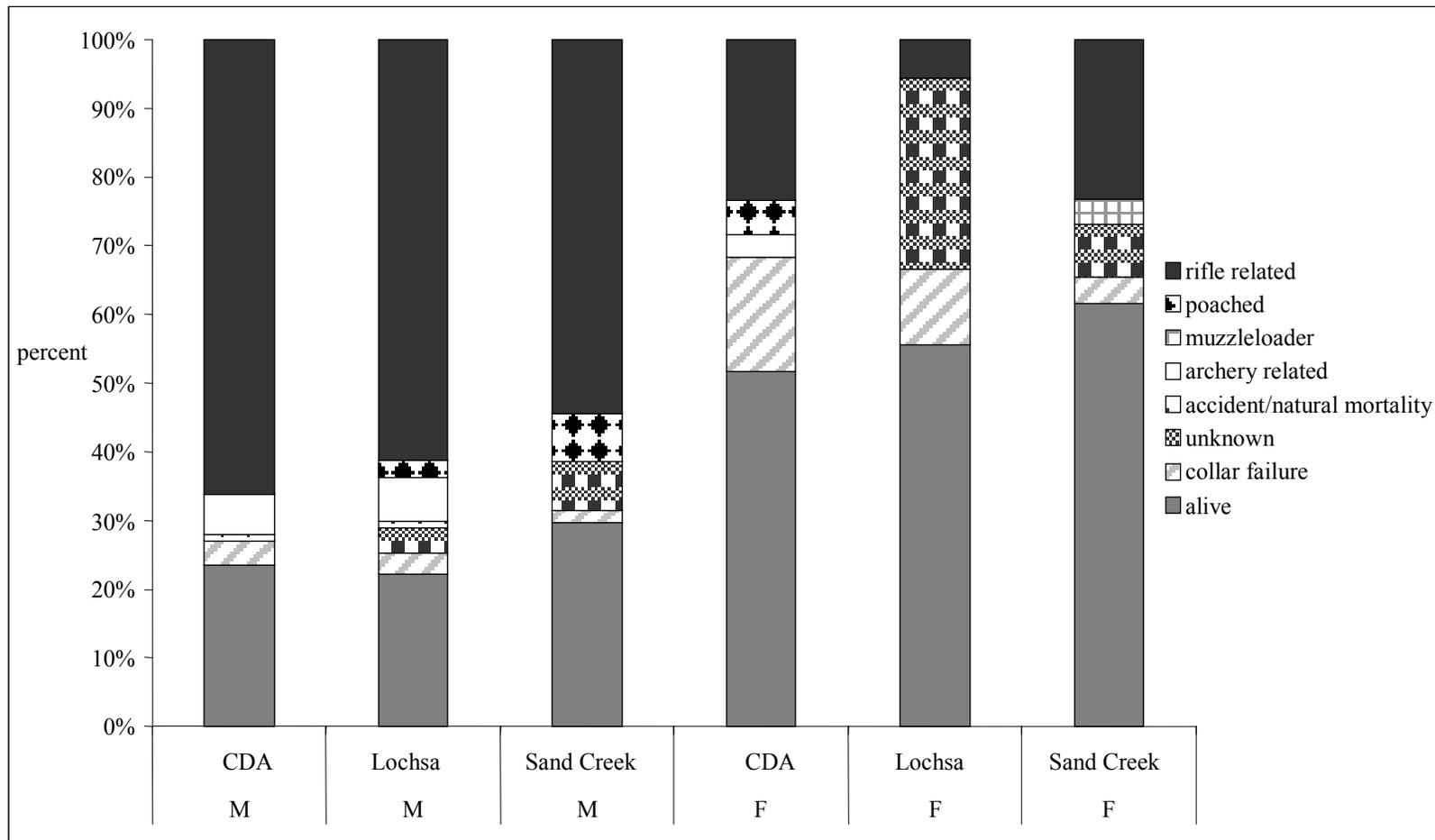


Figure 9. Causes of mortality for male (M) and female (F) radio-collared elk expressed as a percent for the 3 study areas (Coeur d'Alene (CDA), Lochsa, and Sand Creek, Idaho) between 1 September and 30 November, 1984-1994.

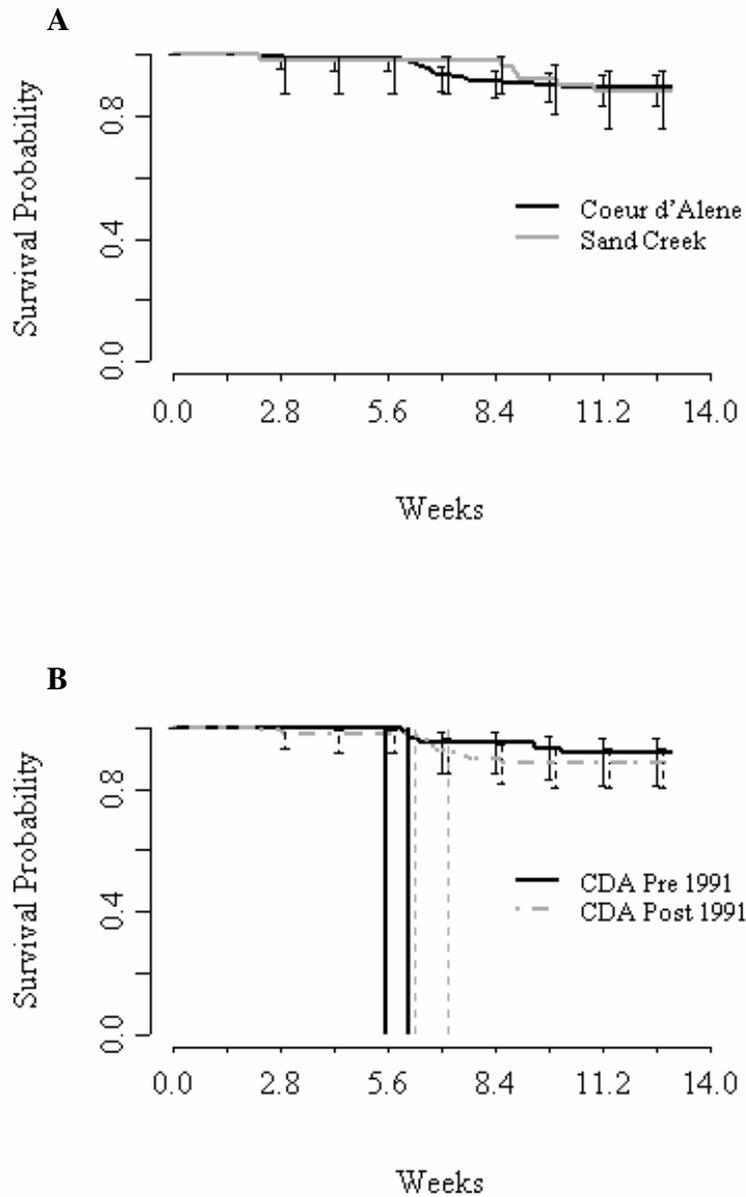


Figure 10. Kaplan-Meier survival curves of radio-collared cow elk. A = Coeur d'Alene and Sand Creek, Idaho, study areas monitored during hunting season from 1 September to 30 November pooled over 4-6 years. B = curves comparing differences in survival pre- and post-1991 (before and after the change in the general rifle-hunting season) for cow elk near Coeur d'Alene (CDA) between 1989-1994. The gray and black vertical lines indicate start and end dates of general rifle season in 1990 and 1991, respectively, in Idaho Game Management Unit 4.

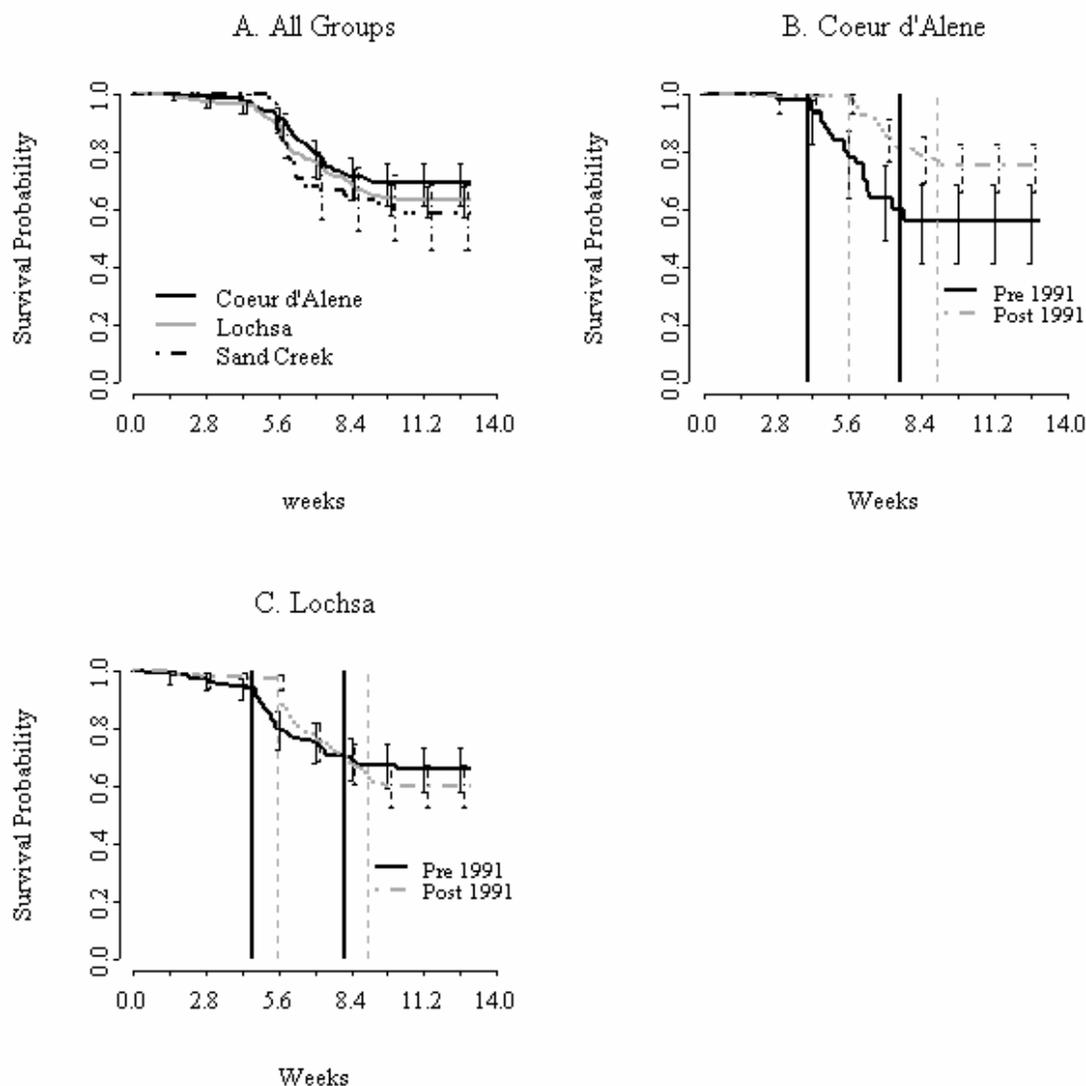


Figure 11. Kaplan-Meier survival curves for radio-collared bull elk. A = Coeur d'Alene, Lochsa, and Sand Creek, Idaho, study areas monitored during hunting season from 1 September to 30 November. 95% confidence bars were placed at equally spaced time steps. B and C = curves comparing differences in survival before and after the change in general rifle hunting season (pre and post 1991) for elk near Coeur d'Alene, Idaho, between 1989-1994 and for elk along the Clearwater and Lochsa River (Lochsa) between 1985-1994. 95% confidence bars are placed at evenly spaced time intervals. The black and gray vertical lines represent the start and end of general rifle hunts in 1990 and 1991, respectively, for Idaho Game Management Unit 4 for Coeur d'Alene and Idaho Game Management Unit 12 for Lochsa.

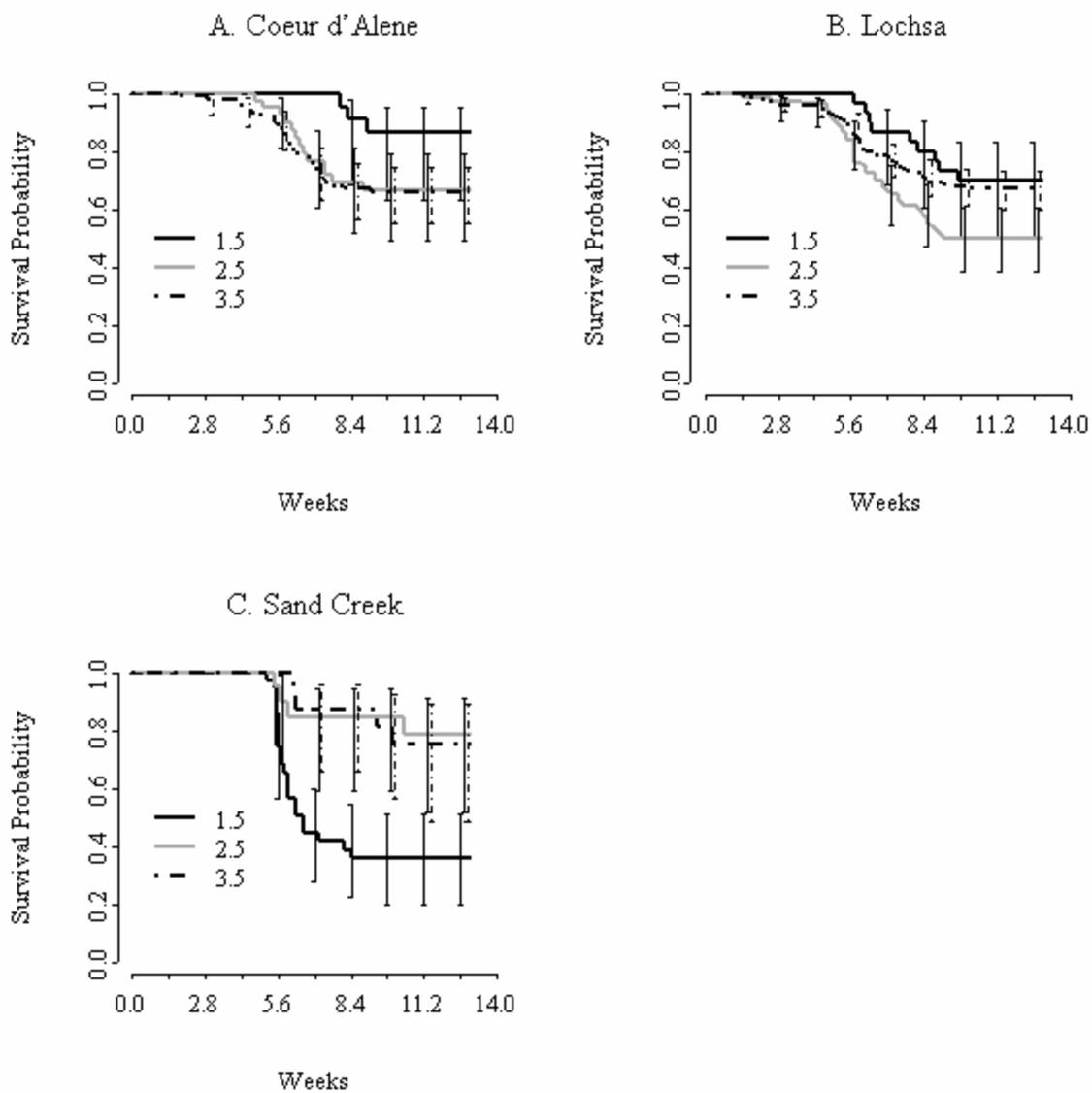


Figure 12. Kaplan-Meier curves comparing differences in survival among 3 age classes of males (1.5, 2.5, 3.5 years) during hunting season for elk from 3 different radio telemetry studies in Idaho. A = first study conducted near Coeur d'Alene (CDA), Idaho, between 1989-1994. B = second study conducted along the Lochsa River (Lochsa) between 1985-1994. C = last study conducted near Island Park (Sand Creek), Idaho, between 1985-1989.

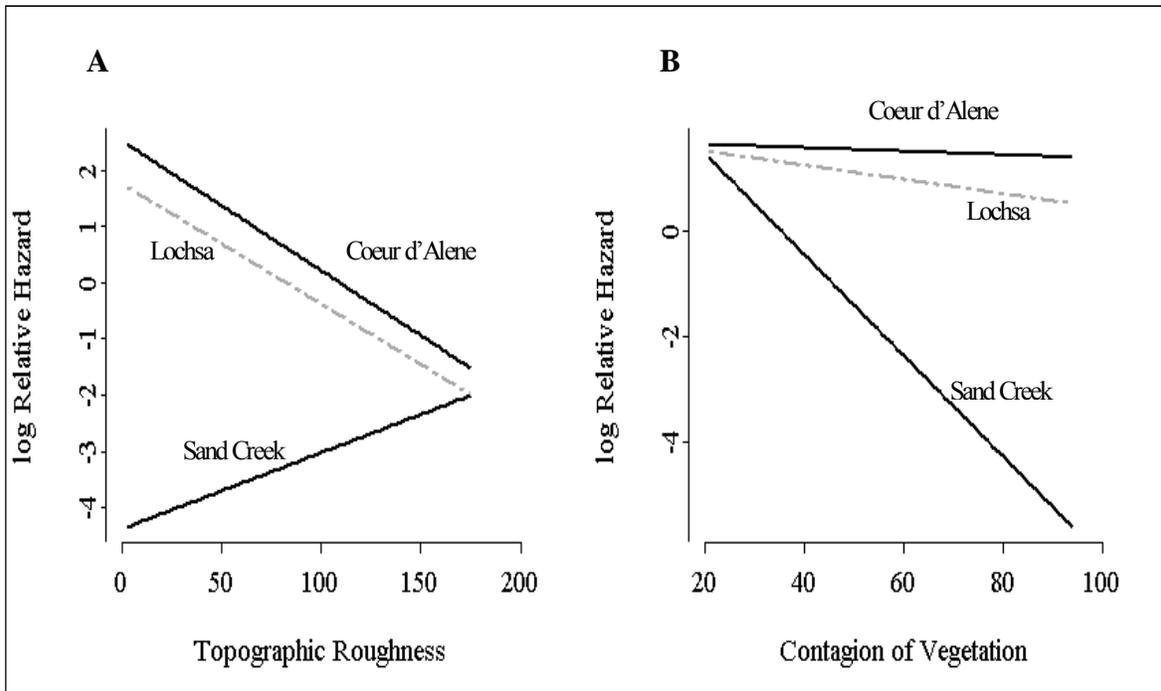


Figure 13. Relationship between log hazard rate for topographic roughness and contagion of vegetation for each of the 3 study areas at the large extent (1352.22 ha). All other variables were held constant at median values (for **A** median road density = 6.68 m/ha, proportion of cool aspect = 0.45, median contagion of vegetation = 88.9%; for **B** median road density = 6.7 m/ha, proportion cool aspect = 0.45, contour density = 46.2 m/ha).

Table 1. Morphological measurements and descriptive characteristics from captive Rocky Mountain elk calves recorded at Starkey Experimental Forest and Range Station, Oregon, 1997-1998.

Measurement	Description
Calf age	Age measured in days, 0 = birth day
Sex	Male or female
Mass	Mass of calf measured using spring scale (kg)
Hoofline	Distance from hairline to growth line on hoof (mm) using calipers (see Figure 1)
Tedger	Length of outer edge of I1 tooth taken from the bottom to gumline using calipers (mm)

Table 2. Seven models used in choosing the best fixed effects.

Model ^a	Intercept	Weight	Tooth edge	Tooth ²	Hoofline	Sex	MSE	AICc	BIC	<i>D/n</i>
Full model	-10.95	0.59	2.16	5.24	1.95	-0.84	0.51	1136.38	1241.76	3.75
Model 8	-10.51	0.67	2.60	5.65		-0.77	0.59	1185.79	1264.91	3.90
Model 7	-15.65	1.08				-1.07	0.86	1530.61	1570.22	8.99
Model 6	-0.12		1.93	15.66		-0.06	0.89	1598.68	1655.85	2.98
Model 5	3.18				2.54	0.21	2.76	2332.63	2372.24	9.82
Model 4	-15.70	0.88			3.47	-1.16	0.72	1418.80	1475.97	7.22
Model 3	-3.81		1.13	12.88	4.19	-0.05	0.75	1479.00	1558.12	3.58

^a The full model with 13 parameters was chosen to be the best model. It had the lowest MSE and AICc, but did not have the lowest average prediction error (*D/n*). Model estimates and fit statistics are computed using maximum likelihood methods, rather than restricted maximum likelihood. All models have the same moving average variance structure. Random effects were included for all slopes in each model.

Table 3. Final model for predicting age from morphometric measurements. Summary of SD (days) for mixed effects, parameter estimates (*B*) for fixed effects, and number of observations and groups used in the analysis. Also included are average parameter elasticity and parameter sensitivity for a +10% increase.

Model information							
Model: AICc = 1120.96, <i>n</i> = 609 from 64 calves							
Autocorrelation structure: Autoregressive (2) theta 1: 0.53 theta 2: 0.384							
Random effects							SD
Variation attributed to calf intercept							2.77
Random slope for weight							0.21
Random slope for tooth							6.23
Random slope for tooth*tooth							6.34
Random slope for hoof line							2.19
Residual error							0.51
Fixed effects	<i>B</i>	SE	DF	t value	p value	Sensitivity	Elasticity
Intercept	-10.95	0.58	541	-18.73	<0.001	2.33	
Weight	0.59	0.04	541	15.40	<0.001	-2.84	1.91
Tooth	2.16	1.35	541	1.60	0.110	-0.50	0.06
Tooth*tooth	5.24	1.36	541	3.84	<0.001	-0.59	3.21
Hoof line	1.95	0.41	541	4.82	<0.001	-0.77	6.99
Sex (M)	-0.84	0.35	62	-2.37	0.021	0.20	

Table 4. Average prediction error (D/n) at each age for 7 fixed effects models found in Table 2.

Age	Frequency	Prediction error ^a						
		Full model	Model 8	Model 7	Model 6	Model 5	Model 4	Model 3
0	4.00	6.47	5.92	15.04	1.15		14.84	3.14
1	59.00	2.42	2.60	10.85	2.37	21.87	4.60	2.21
2	52.00	2.74	2.82	6.11	1.65	14.43	5.30	2.01
3	55.00	3.13	3.31	7.81	2.03	8.44	6.43	2.34
4	50.00	3.24	3.45	7.15	2.12	3.38	5.95	2.79
5	52.00	3.33	3.53	7.46	2.10	1.51	6.45	2.72
6	49.00	3.29	3.43	7.86	2.35	0.16	6.73	2.92
7	48.00	3.72	3.90	9.09	2.62	0.23	7.67	3.63
8	37.00	2.82	3.01	7.00	2.92	1.71	5.83	3.61
9	37.00	2.82	3.06	7.55	2.50	4.33	6.38	2.91
10	37.00	5.08	5.38	10.01	4.98	8.82	8.49	5.44
11	33.00	5.66	6.02	10.39	5.61	12.83	8.74	6.20
12	25.00	3.31	3.46	8.31	3.89	22.56	6.95	4.89
13	22.00	4.83	4.58	10.43	5.72	34.59	9.65	7.20
14	22.00	5.74	5.04	11.26	8.60	45.70	10.91	9.74

^a Prediction error was calculated by summing the squared prediction errors from each of the 10 subsets used in model cross validation. Age is measured in days; Frequency is number of observations recorded at each age. Model 5 was only validated 1 time because the model failed to converge for each of the other 9 subsets.

Table 5. Mass and tooth measurements for each age class, according to Johnson's age categories. Values from Johnson (1951) and measurements taken on captive calves at the Starkey Experimental Forest and Range (Starkey), 1996-1998.

Mass (kg)		Johnson (1951)			Starkey					
Age (days)	Mean	<i>n</i>	Range		Mean	SE	Animals	<i>n</i>	Range	
0-1	14.8	23	8.6	20.5	16.2	0.23	81	87	11.4	22.1
2-4	16.4	48	9.5	21.8	17.8	0.17	82	206	11.8	20.9
5-7	20.3	47	15.5	26.8	20.3	0.20	79	206	12.5	27.7
8+	24.2	22	18.2	36.0	24.2	0.19	68	341	13.6	34.1

Tooth (mm) Johnson (1951)			
Age (days)	Mean	<i>n</i>	Range
0-1			0.00 3.18
2-4			3.18 6.35
5-7			6.35 9.50
8+			9.53 15.9

Tooth (mm) Starkey ^a										
Mean (E)	Mean (M)	SE (E)	SE (M)	Animals	<i>n</i> (E)	<i>n</i> (M)	Range (E)		Range (M)	
2.87	1.85	0.10	0.21	82	64	65	1.4	6.7	0.0	6.7
4.07	4.60	0.04	0.15	65	160	161	2.0	6.8	0.0	7.9
5.65	7.04	0.07	0.08	56	153	152	3.5	7.6	4.3	9.7
7.50	8.60	0.05	0.05	47	247	247	4.5	9.2	6.7	10.3

^a Because Johnson (1951) did not describe how the tooth was measured, the measurement for both outer edge (E) and middle (M) of first incisor have been included, respectively, for Starkey animals. Animals correspond to total number of animals measured; *n* was the total number of measurements taken.

Table 6. Birth masses of known age elk calves from both wild populations and experimental studies reported in the literature.

Author	Location	Parental care	Type of study	Sex	Age of calf	Mean (kg)	SE (kg)	<i>n</i>
Model building set (Starkey)	Oregon	Captive mother	Experiment	Combined	1 day	16.15	0.230	81
Validation set (MMER)	Idaho	Captive mother	Ranch	Combined	1 day	21.52	1.280	8
Cook et al. 1996	Starkey ERF	Bottle fed	Experiment	Combined	Birth	14.00	0.023 ^a	67
Thorne et al. 1976	W Wyoming	Captive mother	Experiment	Combined	Birth	14.70 ^b	0.097 ^a	36
Johnson 1951	SW Montana	Wild mother	Field study	Combined	0-1 day	14.77	0.128 ^a	23
Smith et al. 1997	National elk refuge	Captive mother	Experiment	Combined	Birth	15.70 ^c	0.300	86
Smith et al. 1997	NW Wyoming	Wild mother	Field study	Combined	<24 hours	15.90 ^c	0.200 ^c	165
Hudson et al. 1991	Alberta, Canada	Captive mother	Experiment	Combined	Birth	15.50 ^b	0.650 ^b	116
Rush 1932	Montana	Wild mother	Field study	Combined		16.81	2.49 ^d	
Friedel and Hudson 1994	Alberta, Canada	Captive mother	Ranch	Combined	Birth	17.70	0.300	1084
Hudson et al. 1991	Alberta, Canada	Captive mother	Experiment	Combined	Birth	17.85 ^b	0.570	12
Robins et al. 1981	Washington	Captive mother	Experiment	Combined	12 hours	21.20	2.200	7
Model building set (Starkey)	Oregon	Captive mother	Experiment	Female	1 day	15.52	0.230	49
Validation set (MMER)	Idaho	Captive mother	Ranch	Female	1 day	21.68	1.400	7
Smith et al. 1997	NW Wyoming	Wild mother	Field study	Female	<24 hours	15.50 ^c	0.250	75
Wild et al. 1994	Colorado	Captive mother	Experiment	Female	<48 hours	15.50		1
Wild et al. 1994	Colorado	Bottle fed	Experiment	Female	<48 hours	16.60	1.200	5
Hudson et al. 1991	Alberta, Canada	Captive mother	Experiment	Female	Birth	16.80	0.300	43
Model building set (Starkey)	Oregon	Captive mother	Experiment	Male	1 day	17.09	0.400	32
Validation set (MMER)	Idaho	Captive mother	Ranch	Male	1 day	21.36		1
Smith et al. 1997	NW Wyoming	Wild mother	Field study	Male	<24 hours	16.20 ^c	0.260	90
Wild et al. 1994	Colorado	Captive mother	Experiment	Male	<48 hours	17.50		1
Hudson et al. 1991	Alberta, Canada	Captive mother	Experiment	Male	Birth	19.20	0.400	46

^a SE approximated from range (Ott et al. 2000:91).

^b Averaged over all feeding levels or age classes.

^c Birth weight calculated from adjusted means. See (Smith et al. 1997) for description.

^d SD reported because *n* is unknown.

Table 7. Daily mass increase (kg/day) of known-age elk calves from both wild populations and experimental studies reported in the literature.

Author	Method	Length of time	Sex	Growth rate	SE	<i>n</i>
Model building set (Starkey)	Captive mother	2 weeks	Both	0.770	4E-04	81
Validation set (MMER)	Captive mother	2 weeks	Both	0.710	0.15	7
Cook et al. 1996	Captive mother	1 month (July)	Both	0.440		
Johnson 1951	Bottle fed	1 month		0.450	0.31	1
Wild et al. 1994	Bottle fed	1 month	Both	0.630		
Friedel and Hudson 1994	Captive mother		Both	0.720	0.01	1084
Hudson et al. 1991	Captive mother		Female	0.737		95
Wild et al. 1994	Captive mother	1 month	Both	0.782		
Robins et al. 1981	Captive mother	1 month	Both	0.790	0.30	7
Hudson et al. 1991	Captive mother		Male	0.821		95
Johnson 1951	Wild mother	2 weeks	Both	0.900		16
Smith et al. 1997	Wild mother	1 week	Female	1.316		
Smith et al. 1997	Wild mother	1 week	Male	1.643		

Table 8. Annual survival rates for cow elk from literature compared to annual survival rates for radio-collared cow elk from 3 study areas (Coeur d'Alene, Lochsa, and Sand Creek, Idaho).

Author	Location ^a	Survival ^b	SE	<i>n</i>	Technique ^c	Status ^d	Type of hunt ^e
Ballard et al. 2000	Northern Arizona	0.975	0.001	175	Radio telemetry	R	None
Howell et al. 2002	Coastal California	0.965	0.044	38	Radio telemetry	R	Very limited and discouraged
Cole et al. 1997	Oregon	0.957	0.056	29	Radio telemetry	R	General-post road removal
Lochsa	North-central Idaho	0.956	0.020	21	Radio telemetry	R	Controlled
Hurley and Sargeant 1991	Western Montana	0.930		37	Radio telemetry	R	Controlled
Lubow et al. 2002	Rocky Mtn National Park, CO	0.929	0.230	44	Radio telemetry	R	None
Eberhardt et al. 1996	Washington	0.927 ^f		503	Aerial surveys	R	Private land only
Stussy et al. 1994	Oregon Cascades	0.920	0.050	184	Radio telemetry	R	General
Nickelson et al. 2003	Olympic Peninsula, WA	0.910	0.020	131	Radio telemetry	R	Limited or none
Larkin et al. 2003	Kentucky	0.900	0.020	327	Radio telemetry	T	None
Ballard et al. 2000	Northern Arizona	0.897	0.001	18	Radio telemetry	R	General
Cole et al. 1997	Oregon	0.891	0.040	21	Radio telemetry	R	General-pre road removal
Coeur d'Alene	Northern Idaho	0.890	0.050	61	Radio telemetry	R	General
Unsworth et al. 1993	Northern Idaho	0.886	0.094		Radio telemetry	R	Controlled
Leptich and Zager 1991	North-central Idaho	0.880		66	Radio telemetry	R	General
Sand Creek	Southeastern Idaho	0.870	0.086	53	Radio telemetry	R	Controlled
Smith et al. 1994	Washington	0.848 ^g	0.040	217	Radio telemetry	R	Controlled
Vore 1998	Montana	0.845	0.145	107	Radio telemetry	R	Controlled
McCorquodale et al. 2003	South-central Washington	0.830	0.052	27	Radio telemetry	R	General
Smith and Anderson 1998	Grand Teton National Park, WY	0.826 ^h	0.001	122	Radio telemetry	R	Reduction
Pauley 1991	Southeastern Idaho	0.795	0.046	53	Radio telemetry	R	Controlled
Freddy 1987	Colorado	0.780		58	Radio telemetry	R	General
Stussy et al. 1994	Oregon Cascades	0.770	0.080	35	Radio telemetry	T	General
Peek et al. 1967	Southwestern Montana	0.730 ^f		522	Tag recoveries	R	General
Kimball and Wolfe 1974	Northern Utah	0.726	0.024	573	Tag recoveries	R	General
Nickelson et al. 2003	Olympic Peninsula, WA	0.700 ^f	0.050	25	Radio telemetry	T	None
Sauer and Boyce 1983	Northwestern Wyoming	0.630 ^f	0.050	1376	Tag recoveries	R	General and special permit

^a General location of the study.

^b Estimated annual survival rate.

^c Method used to monitor animals.

^d Whether animals were newly translocated (T) or resident (R) animals.

^e Brief description of the type of rifle hunt offered in the area.

^f Estimate averaged over several years.

^g Estimate averaged over several study areas.

^h Estimate calculated for combination of males and females.

Table 9. Number of radio-collared cow and bull elk studied in Idaho.

Year	Study area					
	Coeur d'Alene		Lochsa		Sand Creek	
	Cows	Bulls	Cows	Bulls	Cows	Bulls
1984					26	1
1985					17	17
1986			6	30	8	20
1987			7	38	4	32
1988	10	11	9	45	2	20
1989	23	20	9	36		
1990	26	20	13	41		
1991	25	25	6	47		
1992	26	27	3	54		
1993	26	27	1	68		
1994	21	30	1	31		
Total ^a	157	160	55	390	57	90
Animals ^b	60	89	18	193	26	57

^a Total number of elk-year combinations.

^b Number of individual animals collared during the entire study.

Table 10. Models relating instantaneous mortality rate and habitat for radio-collared cow elk near Coeur d'Alene, Idaho, between 1 September and 30 November, 1988-1994, at the large (1352.22 ha) and small (70.28 ha) extent.

Scale	Model ^a	Variables	B ^b	SE (B) ^c	p value	Hazard ratio	95% confidence intervals ^d	R square	AIC	AIC weights	
Large											
	1.1	Topographic roughness	-0.003	0.001	0.019	0.997	0.995	1	0.032	158.200	0.381
	1.2	Patch density	20.500	10.500	0.052	7.830E+08	0.872	7.03E+17	0.024	159.481	0.201
	1.3	Percent forest	-6.970	3.990	0.080	9.380E-04	3.790E-07	2.32	0.019	160.239	0.138
	1.4	Patch richness density	741.000	584.000	0.200	Infinity	7.4E-176	Infinity	0.009	161.766	0.064
	1.5	Road density	0.002	0.002	0.240	1.000	0.999	1.01	0.008	161.991	0.057
	1.6	Percent contagion	-0.210	0.022	0.340	0.980	0.939	1.02	0.006	162.317	0.049
	1.7	Season structure	0.350	0.540	0.510	1.420	0.494	4.09	0.003	162.732	0.040
	1.8	Percent cool aspect	2.170	3.920	0.580	8.760	0.004	19159	0.002	162.875	0.037
	1.9	Hunter density	5.490	19.200	0.780	242.000	0.000	5.75E+18	0.001	163.092	0.033
Small											
	2.1	Percent contagion	-0.025	0.016	0.110	0.975	0.946	1.010	0.015	161.172	0.247
	2.2	Percent forest	-3.130	2.310	0.180	0.044	0.000	4.060	0.010	162.020	0.162
	2.3	Percent cool aspect	1.510	1.590	0.340	4.510	0.201	101.000	0.006	162.717	0.114
	2.4	Season structure	0.330	0.540	0.540	1.390	0.483	4.000	0.002	163.227	0.089
	2.5	Road density	0.016	0.025	0.540	1.020	0.967	1.070	0.002	163.262	0.087
	2.6	Patch richness density	-10.900	30.300	0.720	0.000	0.000	1.080E+21	0.001	163.481	0.078
	2.7	Patch density	1.060	3.330	0.750	2.900	0.004	1970.000	0.001	163.514	0.077
	2.8	Hunter density	-0.890	16.100	0.960	0.410	0.000	2.260E+13	0.000	163.610	0.073
	2.9	Topographic roughness	0.000	0.013	0.990	1.000	0.975	1.030	0.000	163.613	0.073

^a One parameter per model.

^b Parameter estimates

^c SE(B) standard error for parameter estimates

^d 95% confidence intervals are reported for the hazard ratios.

Table 11. Fit statistics for best vulnerability models at large (1352.22 ha) and small (70.28 ha) scales for cow elk near Coeur d'Alene, Idaho, at 3 different times during hunting season (week).

Scale	Week	Statistics	Full model fit ^a	BSTRP model fit
Large	1	Somers' Dxy	-0.279	-0.264
	1	R square	0.049	0.049
	1	Concordance	0.361	0.368
	7.5	Somers' Dxy	-0.279	-0.267
	7.5	R square	0.049	0.049
	7.5	Concordance	0.361	0.367
	13	Somers' Dxy	-0.279	-0.265
	13	R square	0.049	0.049
	13	Concordance	0.361	0.367
Small	1	Somers' Dxy	-0.211	-0.171
	1	R square	0.024	0.024
	1	Concordance	0.394	0.415
	7.5	Somers' Dxy	-0.211	-0.178
	7.5	R square	0.024	0.024
	7.5	Concordance	0.394	0.411
	13	Somers' Dxy	-0.211	-0.183
	13	R square	0.024	0.024
	13	Concordance	0.394	0.409

^a Full model fit statistics were calculated using the full data set. They include Somers' Dxy, a modified R square value, and a concordance index. Data were then bootstrapped 500 times and models were refit for each group. Fit statistics were calculated for each group and then averaged over the 500 replications to obtain bootstrapped (BSTRP) model fit statistics.

Table 12. Annual survival rates for bull elk from literature compared to annual survival rates for radio-collared bull elk from 3 study areas (Coeur d'Alene, Lochsa and Sand Creek, Idaho).

Author	Location ^a	Survival ^b	SE	<i>n</i>	Technique ^c	Status ^d	Type of hunt ^e
Lubow et al. 2002	Rocky Mtn National Park, CO	0.929	0.230	44	Radio telemetry	R	None
Petersburg et al. 2000	Colorado	0.890	0.050	36	Radio telemetry	R	Lottery
Eberhardt et al. 1996	Eastern Washington	0.765		200	Composition counts		Private land
Smith and Anderson 1998	Grand Teton National Park, WY	0.729	0.004		Radio telemetry	R	Reduction
Peek et al. 1967	Southwestern Montana	0.69 ^f		513	Tag recoveries	R	General
Pauley 1991	Southeastern Idaho	0.667 ^g	0.083	66	Radio telemetry	R	General
Sand Creek	Southeastern Idaho	0.640	0.100	57	Radio telemetry	R	General
McCorquodale et al. 2003	South-central Washington	0.633	0.510	51	Radio telemetry	R	Multiple hunting strategies
Lochsa	North-central Idaho	0.630	0.090	215	Radio telemetry	R	General
Vore 1998	Northwestern Montana	0.629	0.220	20	Radio telemetry	R	General
Coeur d'Alene	Northern Idaho	0.615	0.090	100	Radio telemetry	R	General
Unsworth et al. 1993	Northern Idaho	0.6 ^f	0.070		Radio telemetry	R	General
Hurley and Sargeant 1991	Western Montana	0.600		20	Radio telemetry	R	General
Kimball and Wolfe 1974	Northern Utah	0.580	0.243	418	Tag recoveries	R	General
Bender and Miller 1999	Southwest Washington	0.49 ^h	0.063		Composition counts	R	Multiple hunting strategies
Leptich and Zager 1991	North-central Idaho	0.480		57	Radio telemetry	R	General
Sauer and Boyce 1983	Northwestern Wyoming	0.4569 ^f	0.073	350	Tag recoveries	R	General and special permits
Unsworth 1993	Lochsa, Idaho	0.425	0.793		Radio telemetry	R	General
Harper 1966	Southwestern Oregon	0.41 ^f		44	Check station	R	General
Smith et al. 1994	Washington	0.354 ^g		118	Radio telemetry	R	General

^a General location of the study.

^b Estimated annual survival rate.

^c Method used to monitor animals.

^d Whether animals were newly translocated (T) or resident (R) animals.

^e Brief description of the type of rifle hunt offered in the area.

^f Estimate averaged over several years.

^g Estimate averaged over several study areas.

^h Estimate averaged over several treatment groups.

Table 13. Seven best models from large-scale (1352.22 ha) analysis relating mortality rate to habitat for bull elk at all 3 study areas: Lochsa, Coeur d’Alene (CDA), and Sand Creek (SC), Idaho, monitored between 1 September and 30 November, 1984-1994.

Scale	Model	P ^a Variables	p value ^b	R square	AIC	Delta AIC	AIC weights
Large	3.1	9 Road density, percent cool aspect, hunter density, topographic roughness, contagion of vegetation, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek)	<0.001	0.10	1956.05	0.00	0.18
	3.2	8 Road density, percent cool aspect, topographic roughness, contagion of vegetation, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek)	<0.001	0.10	1957.16	1.12	0.10
	3.3	15 Road density, topographic roughness, percent cool aspect, percent forest, hunter density, road density*strata (Lochsa), road density*strata (Sand Creek), topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), percent cool aspect*strata (Lochsa), percent cool aspect*strata (Sand Creek), percent forest*strata (Lochsa), percent forest*strata (Sand Creek), hunter density*strata (Lochsa), hunter density*strata (Sand Creek)	<0.001	0.12	1957.52	1.47	0.09
	3.4	15 Road density, topographic roughness, percent cool aspect, contagion of vegetation, hunter density, road density*strata (Lochsa), road density*strata (Sand Creek), topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), percent cool aspect*strata (Lochsa), percent cool aspect*strata (Sand Creek), contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek), hunter density*strata (Lochsa), hunter density*strata (Sand Creek)	<0.001	0.12	1957.74	1.70	0.08
	3.5	9 Road density, percent cool aspect, hunter density, topographic roughness, percent forest, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), percent forest*strata (Lochsa), percent forest*strata (Sand Creek)	<0.001	0.09	1965.68	9.64	0.00
	3.6	4 Road density, contagion of vegetation, contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek),	<0.001	0.07	1967.24	11.20	0.00
	3.7	5 Road density, percent cool aspect, hunter density, topographic roughness, contagion of vegetation	<0.001	0.07	1969.77	13.72	0.00

^a Number of parameters.

^b Global likelihood ratio test.

Table 14. Best model relating habitat to mortality during hunting season for bull elk in the Coeur d'Alene (CDA), Lochsa, and Sand Creek (SC), Idaho, study areas at the large extent (1352.22 ha).

P ^a	Variables	B ^b	SE (B) ^c	p value	Hazard ratio ^d	95% confidence intervals	
8	Road density	0.036	0.013	0.006	1.036	1.010	1.063
	Percent cool aspect	-2.520	0.995	0.014	0.086	0.012	0.602
	Topographic roughness*strata (CDA)	-0.023	0.016	0.144	0.977	0.947	1.008
	Topographic roughness*strata (Lochsa)	-0.021	0.010	0.027	0.979	0.960	0.990
	Topographic roughness*strata (SC)	0.014	0.006	0.014	1.014	1.003	1.025
	Contagion*strata (CDA)	-0.003	0.013	0.799	0.997	0.972	1.023
	Contagion*strata (Lochsa)	-0.014	0.008	0.074	0.987	0.972	1.001
	Contagion*strata (SC)	-0.096	0.023	<0.001	0.909	0.869	0.950

^a Number of parameters.

^b Parameter estimate.

^c Standard error for parameter estimates.

^d Hazard ratios indicate the relationship between the variable and the mortality rate. If the hazard ratio is >1, there is a positive, increasing relationship between mortality and the habitat variable. If hazard ratio = 1, then no relationship is detected. If the 95% confidence interval of Hazard Ratio includes 1, then it is difficult to interpret the relationship between the mortality rate and the predictor. We used study area as stratum and looked at study area by predictor interactions.

Table 15. Fit statistics for best vulnerability models at large (1352.22 ha) extent for bull elk in all 3 populations (Coeur d’Alene, Lochsa and Sand Creek, Idaho) at 3 different times during hunting season (week).

Scale	Week	Statistics	Full model fit ^a	BSTRP model fit
Large	1	Somers’ Dxy	0.113	0.070
	1	R square	0.101	0.032
	1	Concordance	0.556	0.535
	7.5	Somers’ Dxy	0.274	0.255
	7.5	R square	0.101	0.034
	7.5	Concordance	0.637	0.627
	13	Somers’ Dxy	0.275	0.259
	13	R square	0.101	0.033
	13	Concordance	0.638	0.629

^a Full model fit statistics were calculating using the full data set. They include Somers’ Dxy, a modified R square value, and a concordance index. Data were then bootstrapped 500 times and models were refit for each group. Fit statistics were calculated for each group and then averaged over the 500 replications to obtain bootstrapped (BSTRP) model fit statistics.

Table 16. Seven best models from small-scale (70.28 ha) analysis relating mortality rate to habitat for bull elk at all 3 study areas: Lochsa, Coeur d’Alene (CDA), and Sand Creek (SC), Idaho, monitored between 1 September and 30 November, 1984-1994.

Scale	Model	P ^a Variables	p value ^b	R square	AIC	Delta AIC	AIC weights
Small	4.1	15 Topographic roughness, road density, percent cool aspect, percent forest, hunter density, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), road density*strata (Lochsa), road density*strata (Sand Creek), percent cool aspect*strata (Lochsa), percent cool aspect*strata (Sand Creek), percent forest*strata (Lochsa), percent forest*strata (Sand Creek), hunter density*strata (Lochsa), hunter density*strata (Sand Creek)	<0.001	0.12	1979.42	0.00	0.67
	4.2	15 Topographic roughness, road density, percent cool aspect, contagion of vegetation, hunter density, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), road density*strata (Lochsa), road density*strata (Sand Creek), percent cool aspect*strata (Lochsa), percent cool aspect*strata (Sand Creek), contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek), hunter density*strata (Lochsa), hunter density*strata (Sand Creek)	<0.001	0.12	1981.31	1.89	.026
	4.3	8 Road density, hunter density, topographic roughness, percent forest, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), percent forest*strata (Lochsa), percent forest*strata (Sand Creek)	<0.001	0.09	1985.17	5.76	0.04
	4.4	5 Road density, percent cool aspect, hunter density, topographic roughness, contagion of vegetation	<0.001	0.08	1987.08	7.66	0.01
	4.5	8 Road density, percent cool aspect, topographic roughness, contagion of vegetation, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek)	<0.001	0.09	1987.57	8.16	0.01
	4.6	9 Road density, hunter density, topographic roughness, contagion of vegetation, topographic roughness*strata (Lochsa), topographic roughness*strata (Sand Creek), contagion of vegetation*strata (Lochsa), contagion of vegetation*strata (Sand Creek)	<0.001	0.09	1988.66	9.24	0.01
	4.7	4 Road density, topographic roughness, contagion of vegetation, topographic roughness	<0.001	0.07	1989.48	10.06	0.00

^a Number of parameters.

^b Global likelihood ratio test.

Table 17. Best model relating habitat to mortality during hunting season for bull elk in the Coeur d'Alene (CDA), Lochsa, and Sand Creek (SC), Idaho, study areas at the small extent (70.28 ha).

P ^a	Variables	B ^b	SE (B) ^c	p value	Hazard ratio ^d	95% confidence intervals	
15	Percent cool aspect*strata (CDA)	-0.435	0.976	0.656	0.647	0.095	4.386
	Percent cool aspect*strata (Lochsa)	-2.092	0.798	0.009	0.124	0.026	0.590
	Percent cool aspect*strata (SC)	-1.755	1.656	0.290	0.173	0.007	4.445
	Road density*strata (CDA)	0.048	0.018	0.007	1.049	1.013	1.087
	Road density*strata (Lochsa)	0.030	0.014	0.025	1.031	1.004	1.059
	Road density*strata (SC)	2.472	0.925	0.008	11.852	1.933	72.663
	Hunter density*strata (CDA)	-366.739	120.609	0.002	1.640E-24	7.240E-06	0.000
	Hunter density*strata (Lochsa)	-21.907	69.667	0.753	0.000	0.000	6123E+49
	Hunter density*strata (SC)	1116.000	402.241	0.006	0.000	8.350E-76	1.26E-13
	Percent forest*strata (CDA)	-2.273	2.010	0.258	0.103	0.002	5.296
	Percent forest*strata (Lochsa)	-1.910	0.798	0.017	0.148	0.031	0.708
	Percent forest*strata (SC)	2.364	1.034	0.022	10.633	1.400	80.748
	Topographic roughness*strata (CDA)	0.001	0.009	0.864	1.001	0.985	1.019
	Topographic roughness*strata (Lochsa)	-0.007	0.003	0.013	0.993	0.987	0.999
	Topographic roughness*strata (SC)	0.246	0.145	0.090	1.278	0.963	1.698

^a Number of parameters.

^b Parameter estimate.

^c Standard error for parameter estimates.

^d Hazard ratios indicate the relationship between the variable and the mortality rate. If the hazard ratio is >1, there is a positive, increasing relationship between mortality and the habitat variable. If hazard ratio = 1, then no relationship is detected. If the 95% confidence interval of Hazard Ratio includes 1, then it is difficult to interpret the relationship between the mortality rate and the predictor. Strata are almost like blocking by that variable. We used study area as stratum and looked at study area by predictor interactions.

Table 18. Seven best models from small-scale (70.28 ha) analysis relating mortality rate to habitat for bull elk at each study area: Lochsa, Coeur d’Alene (CDA), and Sand Creek, Idaho, monitored between 1 September and 30 November.

Population	Scale Model ^a	P ^b Variables	p value ^c	R square	Delta AIC	AIC weights
Lochsa	Small	4 Topographic roughness, road density, percent cool aspect, percent forest	<0.001	0.092	0.000	0.510
	5.1					
	5.2	5 Topographic roughness, road density, percent cool aspect, percent forest, hunter density	<0.001	0.092	1.890	0.191
	5.3	4 Topographic roughness, road density, percent cool aspect, contagion of vegetation	<0.001	0.085	2.380	0.150
	5.4	5 Topographic roughness, road density, percent cool aspect, percent forest, hunter density	<0.001	0.086	4.320	0.046
	5.5	2 Topographic roughness, percent cool aspect	0.001	0.067	4.870	0.041
	5.6	3 Topographic roughness, road density, percent forest	0.002	0.072	4.990	0.041
CDA	5.7	3 Topographic roughness, road density, contagion of vegetation	0.003	0.067	6.920	0.021
	6.1	5 Topographic roughness, road density, percent cool aspect, percent forest, hunter density	0.006	0.099	0.000	0.490
	6.2	5 Topographic roughness, road density, percent cool aspect, contagion of vegetation, hunter density	0.009	0.093	1.050	0.290
	6.3	2 Road density, percent forest	0.037	0.042	3.770	0.070
	6.4	1 Percent forest	0.037	0.027	0.130	0.060
	6.5	2 Age-class 2.5, age-class 3.5	0.006	0.036	4.090	0.050
	6.6	2 Road density, contagion of vegetation	0.071	0.033	4.760	0.040
Sand Creek	6.7	1 Contagion of vegetation	0.073	0.020	5.150	0.010
	7.1	5 Topographic roughness, road density, percent cool aspect, contagion of vegetation, hunter density	<0.001	0.265	0.000	0.477
	7.2	5 Topographic roughness, road density, percent cool aspect, percent forest, hunter density	<0.001	0.251	1.590	0.216
	7.3	4 Topographic roughness, road density, percent cool aspect, contagion of vegetation	<0.001	0.224	2.650	0.127
	7.4	3 Topographic roughness, road density, contagion of vegetation	<0.001	0.202	2.990	0.107
	7.5	2 Age-class 2.5, age-class 3.5	0.001	0.166	4.700	0.045

Table 18. Continued.

Population	Scale Model ^a	P ^b Variables	p value ^c	R square	Delta AIC	AIC weights
	7.6	2 Road density, contagion of vegetation	0.002	0.146	6.700	0.017
	7.7	4 Topographic roughness, road density, percent cool aspect, percent forest	0.003	0.178	7.530	0.011

^a The same models were fit to each population separately.

^b Number of parameters.

^c Parameter estimate.

Table 19. Best model from small scale (70.28 ha) analysis relating mortality rate to habitat for bull elk at each study area: Lochsa, Coeur d'Alene, and Sand Creek, Idaho, monitored between 1 September and 30 November.

Population	P ^a	Variables	B ^b	SE (B) ^c	p value	Hazard ratio ^d	95% confidence intervals	
Lochsa	4	Topographic roughness	-0.007	0.993	0.014	0.993	0.988	0.999
		Road density	0.030	1.030	0.027	1.030	1.003	1.058
		Percent cool aspect	-2.111	0.121	0.008	0.121	0.026	0.575
		Percent forest	-1.888	0.151	0.018	0.151	0.032	0.723
Coeur d'Alene	5	Topographic roughness	0.001	0.009	0.860	1.050	0.985	1.020
		Road density	0.048	0.018	0.007	1.000	1.010	1.090
		Percent cool aspect	-0.435	0.977	0.660	0.647	0.095	4.390
		Percent forest	-2.273	2.010	0.260	0.103	0.002	5.300
		Hunter density	-33.300	10.951	0.002	3.450E-15	1.64E-24	7.24E-06
Sand Creek	5	Topographic roughness	0.344	0.132	0.009	1.410	1.090	1.827
		Road density	1.994	0.927	0.032	7.350	1.190	45.242
		Percent cool aspect	-1.843	1.721	0.280	0.158	0.005	4.623
		Contagion of vegetation	-0.050	0.018	0.006	0.951	0.918	0.986
		Hunter density	-85.151	40.599	0.036	0.000	0.000	0.004

^a Number of parameters.

^b Parameter estimate.

^c Standard error for parameter estimates.

^d Hazard ratios indicate the relationship between the variable and the mortality rate. If the hazard ratio is >1, there is a positive, increasing relationship between mortality and the habitat variable. If hazard ratio = 1, then no relationship is detected. If the 95% confidence interval of Hazard Ratio includes 1, then it is difficult to interpret the relationship between the mortality rate and the predictor. Strata are almost like blocking by that variable. We used study area as stratum and looked at study area by predictor interactions.

Table 20. Fit statistics for best vulnerability models at small (70.28 ha) extent for bull elk in each population (Coeur d'Alene, Lochsa and Sand Creek, Idaho) at 3 different times during hunting season (week).

Scale	Population	Week	Statistics	Full model fit ^a	BSTRP model fit
Small	Coeur d'Alene	1	Somers' Dxy	-0.320	-0.257
		1	R square	0.105	0.078
		1	Concordance	0.340	0.371
		7.5	Somers' Dxy	-0.320	-0.258
		7.5	R square	0.105	0.078
		7.5	Concordance	0.340	0.371
		13	Somers' Dxy	-0.320	-0.255
		13	R square	0.105	0.078
		13	Concordance	0.340	0.372
	Lochsa	1	Somers' Dxy	-0.259	-0.244
		1	R square	0.094	0.084
		1	Concordance	0.370	0.378
		7.5	Somers' Dxy	-0.259	-0.246
		7.5	R square	0.094	0.085
		7.5	Concordance	0.370	0.377
		13	Somers' Dxy	-0.259	-0.243
		13	R square	0.094	0.083
		13	Concordance	0.370	0.379
	Sand Creek	1	Somers' Dxy	-0.480	-0.461
		1	R square	0.260	0.270
		1	Concordance	-0.460	0.270
		7.5	Somers' Dxy	-0.480	-0.463
		7.5	R square	0.279	0.237
		7.5	Concordance	0.260	0.268
		13	Somers' Dxy	-0.480	-0.459
		13	R square	0.279	0.234
		13	Concordance	0.260	0.271

^a Full model fit statistics were calculated using the full data set. They include Somers' Dxy, a modified R square value, and a concordance index. Data were then bootstrapped 500 times and models were refit for each group. Fit statistics were calculated for each group and then averaged over the 500 replications to obtain bootstrapped (BSTRP) model fit statistics.

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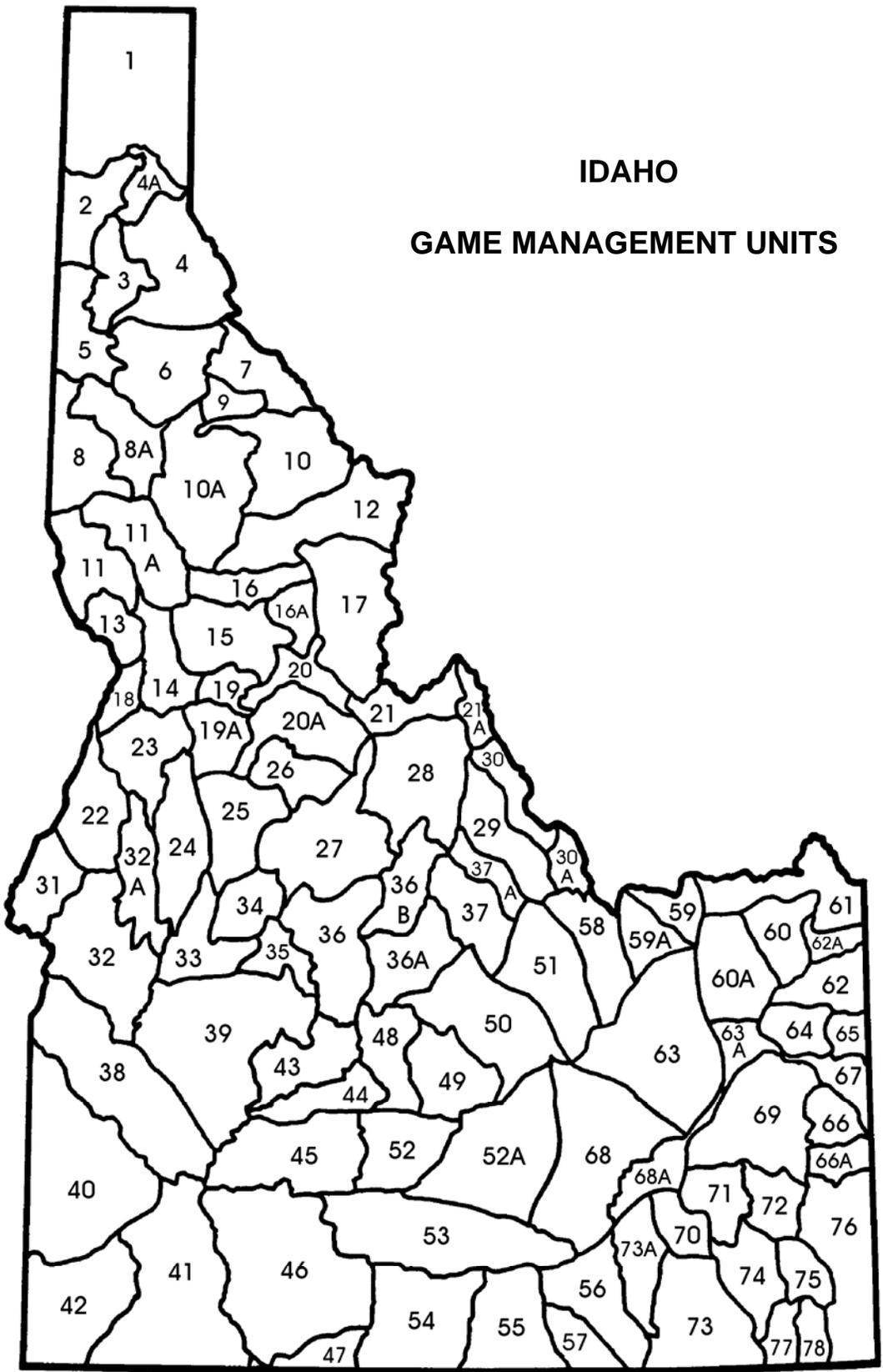
Principal Wildlife Research Biologist

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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.

