

AN ABSTRACT OF THE THESIS OF

Spencer N. Rearden for the degree of Master of Science in Wildlife Science presented on March 14, 2005.

Title: Juvenile Survival and Birth-site Selection of Rocky Mountain Elk in Northeastern Oregon.

Abstract approved:

Signature redacted for privacy.

Robert G. Anthony

With declining populations and low calf recruitment in northeastern Oregon, much interest has been generated to study the survival rates and causes of mortality of Rocky Mountain elk (*Cervus elaphus nelsoni*). I investigated the causes of elk calf mortality and the effects of predation risk on birth-site selection by cow elk. Cow elk were captured in March of 2002–2004 to determine their pregnancy status and condition (percent fat, mass, and age). Pregnant cows had temperature-sensitive vaginal implant transmitters inserted that were expelled at parturition in order to locate newborn calves and birth sites later during the calving season. Elk calves were captured in two adjacent study areas, the Wenaha and Sled Springs, with the use of vaginal implant transmitters, a helicopter and net gun, and ground searching. A total of 222 calves were captured during the spring and summer of 2002–2004. Calves were sexed, aged, weighed, and fitted with radio-transmitting collars that had mortality sensors integrated into the circuitry. Monitoring of the radio-collared calves

was done from fixed-wing aircraft. Calf collars in mortality mode were located on foot to investigate and determine cause of death. Predator-related mortalities were marked with a global positioning unit and the most likely spot where the calf was killed was flagged.

I took microhabitat measurements that described horizontal and vertical cover at each birth and predation site and 2 paired random sites. During the summers of 2003 – 2004, I measured 49 birth sites and 62 predation sites along with 2 paired random sites for each. Using a geographic information system (GIS) I obtained slope and aspect for each site. I also used GIS to obtain macrohabitat data on birth, predation, and 80 random sites (for comparison). For each site, I measured the percent canopy cover and the amount of forest edge within a 250, 500, and 1,000 m radius circle. In addition, I also obtained the distance from each site to the nearest edge.

I found differences in annual survival rates between the two adjacent study areas, with calves in Wenaha having lower survival (0.26; 95% CI = 0.15 to 0.42) rates than calves in Sled Springs (0.52; 95% CI = 0.37 to 0.56). Overall, predation was the main proximate cause of death. In 2003 - 2004, cougars (*Felis concolor*) killed 54% and 35% of radio-collared calves in Wenaha and Sled Springs, respectively. Annual calf survival was influenced by birth date ($\beta = -0.35$; 95% CI = -0.64 to -0.06). Both birth date ($\beta = -0.253$; 95% CI = -0.502 to -.0003) and birth weight ($\beta = 0.13$; 95% CI = -0.14 to 0.39) influenced summer calf survival, with earlier and heavier-born calves having higher survival rates than late and light-born calves. I found no differences in annual survival rates between the sexes in this

study. However, I did find differences in summer survival rates between the sexes depending on the area. In Wenaha, females (0.57; 95% CI = 0.42 to 0.72) had higher survival than males (0.42; 95% CI = 0.27 to 0.59), and in Sled Springs, males (0.82; 95% CI = 0.66 to 0.91) had higher survival than females (0.46; 95% CI = 0.31 to 0.61). Preliminary analyses suggested that cow condition did not influence calf survival, nor was cow condition correlated with the estimated birth date and birth weight of calves. However, the analyses that examined the effects of cow condition on calf survival were preliminary and inconclusive due to small sample sizes.

I found that birth-site selection of cow elk was influenced by predation risk at the microhabitat scale. Cow elk selected birth sites that had less horizontal cover (0.97 times the odds; 95% CI = 0.94 to 0.99) and more overhead density of vegetation (1.022 times the odds; 95% CI = 1.005 to 1.040) than paired-random sites. Although predation sites also had less horizontal cover (0.985 times the odds; 95% CI = 0.973 to 0.998) than random sites, birth sites had less horizontal cover (0.983 times the odds; 95% CI = 0.967 to 1.001) and more overhead density of vegetation (1.02 times the odds, 95% CI = 1.01 to 1.04) than predation sites. I found no evidence that cow elk were influenced by predation risk at the macrohabitat scale. Cow elk chose birth sites with less canopy cover than random sites within a 500 m-radius circle. Cow elk were likely more influenced by forage availability rather than predation risk when selecting a birth site at the macrohabitat scale. When birth sites were compared to predation sites at this scale, I found no differences, further suggesting that birth-site selection was not influenced by predation risk. Cow elk were likely selecting broad areas for parturition that had sufficient forage to meet high nutritional demands due to

lactation. Within these areas, cow elk selected birth sites that had high visibility at the microhabitat scale, presumably to detect predators visually and to avoid predation on calves.

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Juvenile Survival and Birth-site Selection of Rocky Mountain Elk in Northeastern
Oregon

by
Spencer N. Rearden

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Spencer N. Rearden, Author

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CONTRIBUTIONS OF AUTHORS

Dr. Bruce K. Johnson acquired funding, assisted with the study design, data collection, data analyses, interpretation of results, and provided editorial comments for chapter 2. Dr. Bruce K. Johnson also assisted with data collection and interpretation of results for chapter 3. Dr. Robert G. Anthony provided input on the study design, assisted with data collection, data analyses, interpretation of results, and provided extensive editorial comments for both manuscripts.

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JUVENILE SURVIVAL AND BIRTH-SITE SELECTION OF ROCKY
MOUNTAIN ELK IN NORTHEASTERN OREGON

CHAPTER 1

GENERAL INTRODUCTION

Spencer N. Rearden

Elk (*Cervus elaphus*) populations have declined in some wildlife management units (WMUs) in northeastern Oregon during the last 2 decades. In recent years, the recruitment of juvenile elk into the yearling age class has declined to less than 20 calves per 100 cows in certain WMUs (Schommer 1991a, 1991b; Carter 1992; Oregon Department of Fish and Wildlife 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000). During the time of population declines in northeastern Oregon, elk populations have increased in other parts of the state, where recruitment into the yearling age class has been >40 calves per 100 cows (Schommer 1991a, 1991b; Carter 1992; Oregon Department of Fish and Wildlife 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000). However in the two WMUs where this study was conducted, the Wenaha WMU had a 28 and 25 calves per 100 cows and the Sled Springs WMU had 14 and 21 calves per 100 cows in 2002 and 2003, respectively (Victor Coggins, District Biologist, pers. Comm.). Despite no legal hunting of cow elk in northeastern Oregon, except for a few agricultural damage hunts, recruitment has remained low and elk populations have not increased. With the high economic and social values of elk, the dwindling elk populations have reduced hunting and recreational opportunities, thus decreased revenues to local communities and the Oregon Department of Fish and Wildlife. As elk populations continued to decline, pressure on the Oregon Department of Fish and Wildlife to provide answers and to increase elk populations in northeastern Oregon has increased.

The proximate causes of elk calf mortality often result from predation, making ultimate causes of mortality, such as nutrition, difficult to study and understand.

Nutrition can affect virtually every aspect of reproduction and recruitment in elk. Nutritional condition affects elk weight at birth (Thorne et al. 1976), calf growth in summer (Haigh and Hudson 1993, Cook et al. 2004), calf survival in winter (Cook et al. 2004), and cow pregnancy rates (Trainer 1971, Kohlmann 1999, Cook et al. 2001c). In addition, several studies have demonstrated direct relationships between female condition and juvenile survival in ungulates (Clutton-Brock et al. 1987, Bartmann et al. 1992, Cameron et al. 1993, Cook et al. 2004). Physical condition of young at the time of birth can affect survival (Clutton-Brock et al. 1987, Whitten et al. 1992, Fairbanks 1993, Sams et al. 1996, Singer et al. 1997, Smith and Anderson 1998, Keech et al. 2000), which can be a result of cow condition.

Data collected by the Oregon Department of Fish and Wildlife (ODFW) on body condition and pregnancy rates from cow elk harvested in northeastern Oregon during November-December indicated that habitat was not causing poor body condition or low pregnancy rates (Oregon Department of Fish and Wildlife 2003). Pregnancy rates have been consistently above 90%, and the physical condition of cow elk were some of the highest in the state of Oregon, yet the calf/cow ratios were some of the lowest (Oregon Department of Fish and Wildlife 2003). Condition of cow elk and predation are potential causes for the low calf survival and calf/cow ratios, but the overall cause(s) of the decline in northeastern Oregon elk populations is unclear.

Understanding the causes of juvenile elk mortality is important, as well as the role of habitat selection in survivorship and successful reproduction (Pulliam and Danielson 1991, Rosenzweig 1981). Although ungulates usually select habitat that can support their nutritional demands, they are also confronted with risk of predation,

especially at the time of parturition (Alldredge et al. 1991 [pronghorn, *Antilocapra americana*], Barten et al. 2001 [caribou, *Rangifer tarandus*], Bergerud et al. 1984 [caribou], Bowyer et al. 1999 [Alaskan moose, *Alces alces gigas*], Rachlow and Bowyer 1998 [Dall's sheep, *Ovis dalli dalli*]). At parturition, a new-born ungulate is highly vulnerable to predation, and nutritional constraints on the cow are high due to energy demands of lactation. When access to good forage quality increases along with the risk of predation, a tradeoff between the two must occur (Lima and Dill 1990). With high nutritional demands and the need to carefully select a birth site to ensure survival of a newborn, the importance of habitat selection may be magnified.

Understanding causes of mortality and habitat selection can eventually lead to better management and understanding of elk population dynamics. In chapter 2, "Factors influencing elk calf survival in northeastern Oregon," I investigated direct and underlying causes of elk calf mortality and the effects of sex, birth date, and birth weight on survival rates. Although I was able to test for the effects of these life-history characteristics and report direct causes of mortality along with survival rates, I had limited data to look into the effects of cow condition on elk calf survival. In chapter 3, "Does Predation Risk Affect Selection of Birth Sites by Rocky Mountain Elk?," I investigated how birth sites differed in habitat concealment from random and predation sites. I also investigated how predation sites differed from random sites. Understanding the strategies elk use to cope with the risk of predation can lead to a better understanding of mortality factors. The data collected are part of a long-term study scheduled to last through at least May 2008. Additional information will be collected that will likely clarify the role of nutritional condition on calf elk survival.

CHAPTER 2

FACTORS INFLUENCING ELK CALF SURVIVAL IN NORTHEASTERN OREGON

Spencer N. Rearden, Bruce K. Johnson, and Robert G. Anthony

Introduction

The proximate causes of elk (*Cervus elaphus*) calf mortality often result from predation, making ultimate causes of mortality, such as nutrition and disease, difficult to study and understand. Nonetheless, it is important to understand the complex interactions of predation and nutrition in order to properly manage elk populations. Understanding top-down influences from predation versus bottom-up influences from nutrition can be challenging. With the high economic and social values of elk, proper management based on sound information is important. Neonatal survival can be influenced by both nutrition and predation. Discerning which is responsible for the mortality of young is difficult especially because a poor-conditioned calf is presumably more likely to be predisposed to predation than a well-conditioned calf.

Nutrition can affect virtually every aspect of reproduction and recruitment in elk. Nutritional condition affects elk weight at birth (Thorne et al. 1976), calf growth in summer (Haigh and Hudson 1993, Cook et al. 2004), calf survival in winter (Cook et al. 2004), and cow pregnancy rates (Trainer 1971, Kohlmann 1999, Cook et al. 2001c). Physical condition of cow elk was the prime determinant of successful breeding (Trainer 1971), and elk in poor condition did not ovulate (Cook et al. 2001c). Cow elk that faced high energy demands from lactation and fed on forage with low digestible energy in summer did not rebuild sufficient fat reserves by autumn to go into estrous (Cook et al. 2004). However, non-lactating cows accumulated sufficient fat reserves to enter estrous under these conditions (Cook et al. 2004).

Studies on ungulates have demonstrated direct relationships between female

condition and juvenile survival (Clutton-Brock et al. 1987, Bartmann et al. 1992, Cameron et al. 1993, Cook et al. 2004). Physical condition of young at the time of birth can affect survival (Clutton-Brock et al. 1987, Whitten et al. 1992, Fairbanks 1993, Sams et al. 1996, Singer et al. 1997, Smith and Anderson 1998, Keech et al. 2000), which can be a result of cow condition. A study on Alaskan moose (*Alces alces gigas*) did not find a direct relationship between cow condition and survival of offspring, but found that cow condition affected birth weight, birth date, and litter size, which in turn affected calf survival (Keech et al. 2000). As a result, Keech et al. (2000) suggested that cow condition can indirectly determine calf survival through the effects of other life-history characteristics.

There is much concern about declining populations of Rocky Mountain elk (*Cervus elaphus nelsoni*) in northeastern Oregon, which appears to be due to low recruitment. Data collected by the Oregon Department of Fish and Wildlife (ODFW) on body condition and pregnancy rates from cow elk harvested in northeastern Oregon during November-December indicate that habitat is likely not inhibiting reproduction or causing poor body condition (Oregon Department of Fish and Wildlife 2003). Pregnancy rates have been consistently above 90%, and the nutritional conditions of cow elk were some of the highest in the state of Oregon, yet the calf/cow ratios were some of the lowest (Oregon Department of Fish and Wildlife 2003). Habitat changes and predation are potential causes for the low recruitment, but the overall cause(s) of the decline in populations is unclear.

The major predators of elk calves in northeastern Oregon are black bears (*Ursus americanus*), coyotes (*Canis latrans*), and cougars (*Felis concolor*). In

northwest Wyoming, all neonatal mortality of elk calves had occurred by July 15 and totaled 15% of marked calves, with 68% from predation by black bears and coyotes (Smith and Anderson 1996). All calves killed by black bears and coyotes were 2-23 days old and no calves >27 days old died until the fall hunting season. Similarly, most of the predation by black bears and brown bears (*Ursus arctos*) on elk calves in Yellowstone National Park occurred during the first 28 days (Singer et al. 1997). Of the calf mortalities, 16.9% were from brown bears, 1.5% from black bears, 4.6% from unknown bear species, and 16.9% from coyotes (Singer et al. 1997). Due to sheer numbers, coyotes were thought to be the major elk predator on calves in Yellowstone National Park (Crabtree and Sheldon 1999). In southeastern Washington, cougars killed 48.6% of marked elk calves, while black bears and coyotes killed only 15.9% and 4.7%, respectively (Myers et al. 1999).

Although cougar numbers are usually lower than black bears and coyotes, they specialize in preying on deer (*Odocoileus spp.*) and elk. Deer and elk made up the majority (70%) of cougar's winter diet in Central Idaho, with 75% of the elk 1.5 years old or less (Hornocker 1970). Fifty-three percent of the elk mortalities were calves. Deer were more abundant, yet more elk were killed by cougars, which suggested that either cougars were selecting elk or elk were more vulnerable to cougar predation (Hornocker's 1970). Hornocker (1970) suggested that elk were expanding into extremely rough terrain, where cougars were able to hunt them more successfully due to ideal hunting conditions. In northeastern Oregon, the most frequently consumed prey by cougars in December was mule deer (*Odocoileus hemionus*), followed by elk (Maser and Rohweder 1983).

To better understand the reasons for the low recruitment in elk populations in northeastern Oregon, I investigated the effects of predation and cow nutrition on calf survival. The following hypotheses were developed to help understand low recruitment: (1) Predation is not directly responsible for >50% mortality of elk calves, (2) black bears are the main predators on young (0-28 days old) calves, (3) cougars are the main predators on older (28 days-1 year) calves, and (4) the nutritional condition of cow elk is an important factor in calf survival. The specific objectives of this study were to: (1) describe causes of mortality of calves from birth to recruitment at 1 year of age, (2) estimate time-specific survival of calves from birth to recruitment, and (3) investigate the influence of cow condition on pregnancy rates and survival of calves.

This study is ongoing and up to 4 more years of data (2004-2005, 2005-2006, and 2006-2007) will be collected. Additional information will increase sample sizes for testing the above hypotheses as well as strengthen the analyses on the effects of cow nutritional condition on calf survival. Consequently, the analyses of the effect of cow condition on calf survival are preliminary, and the analyses for that part of my study illustrate how these data will be analyzed.

Study sites

Two adjacent study sites in the Wenaha and Sled Springs wildlife management units were selected in northeastern Oregon for this study (Figure 2.1). Both are at the northernmost reach of the Blue Mountains. Ponderosa pine (*Pinus ponderosa*) dominates the lower elevations while subalpine fir (*Abies lasiocarpa*) dominates the highest elevations. In the intermediate elevations, mixed stands of

ponderosa pine, lodgepole pine, (*Pinus contorta*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), Douglas fir (*Pseudotsuga menziesii*), and Engleman spruce (*Picea engelmannii*) can be found. Sled Springs varies in elevation from about 700-1350 meters and Wenaha varies in elevation from about 700-1600 meters. Climate is characterized by cold, snowy winters and warm, dry summers. Annual precipitation in northeastern Oregon ranges from 43-63 cm with most falling as snow in winter and rain in spring and autumn with extreme dryness mid to late summer. Each site has both winter and summer elk ranges. The Sled Springs Wildlife Management Unit (WMU) has a winter range that encompasses approximately 70 km² in the southwest portion of the WMU with a winter population of approximately 400 elk. The summer range is about 300 km². The majority of the Sled Springs winter range was owned and managed by Boise Cascade Corporation. The Wenaha WMU has a winter range that encompasses about 100 km² in the eastern portion of the WMU with a winter population of approximately 600 elk. The summer range includes about 400 km². This area is comprised mostly of public lands, which is mostly managed by the U. S. Forest Service. The Oregon Department of Fish and Wildlife (ODFW) manages the Wenaha Wildlife Management area in the eastern part of the Wenaha WMU.

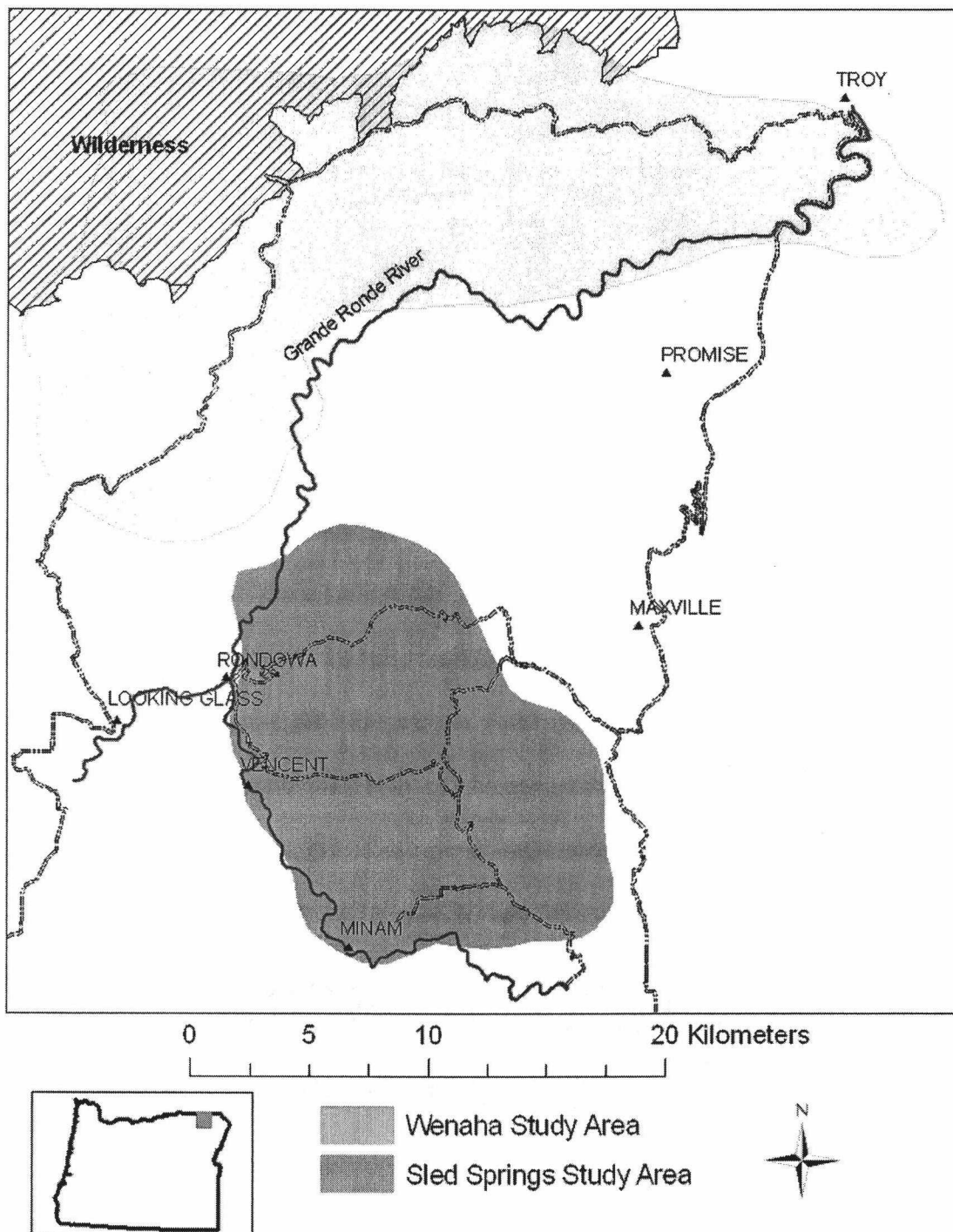


Figure 2.1. Study areas within the Wenaha and Sled Springs wildlife management units in northeastern Oregon. Boundaries of study areas defined by home range kernel estimator using an 80% kernel from locations of 1,114 radio-collared calves and 2,201 radio-collared cows from December 2001 to March 2004.

Methods

Cow Capture

Personnel from the ODFW and National Council for Air and Stream Improvement (NCASI) captured cow elk during 3 springs (March 2002-2004) and 2 fall seasons (November/December 2001-2003) with the use of helicopter and dart gunning. The first time cow elk were captured, they were radio-collared with VHF transmitters (obtained from a variety of manufacturers). In subsequent capture work, personnel attempted to catch the same cows in the spring as they did in the fall of each year to monitor changes in body condition and pregnancy status. Each time a cow was captured, ultrasound was used to determine pregnancy status, and ultrasound and body-condition scoring were used to measure percent fat (Cook et al. 2001a, b). Girth measurements were made to estimate body mass (Cook et al. 2003). In addition, during the first capture, a canine tooth was extracted from each cow to determine age through cementum analysis (Fancy 1980). Also, during the fall capture, lactation status of each cow was determined, indicating calf survival at the time of cow capture (Fleet and Peaker 1978, Noble and Hurley 1999).

In the spring, vaginal implant transmitters (VIT; ATS, Isanti, Minnesota, USA; Bowman and Jacobson 1998) were inserted into pregnant cows (Table 2.1). Radio collars on cows were used in conjunction with VITs because radio transmitters put out stronger signals, allowing field personnel to locate and monitor pregnancy status of cows easier. A directional yagi H-antenna (Telonics, Mesa, Arizona, USA) was used to locate the radio-collared cows and VITs from aircraft or the ground, which helped narrow the search for newborn calves. Once a cow was found, we

Table 2.1. Summary of cow capture, pregnancy rates, and number of VITs inserted in cow elk in northeastern Oregon during the Springs of 2002-2004. Wenaha cows are listed first (Wenaha/Sled Springs).

Dates of cow capture	No. of cows captured	No. of cows pregnant	No. of VITs inserted	Percent pregnant	Overall percent pregnant for each year
March 11-14, 2002	^a 24 / 23	23 / 22	20 / 20	96% / 96%	96%
March 22-24, 2003	^b 25 / ^c 24	23 / 19	^d 19 / 19	100% / 90%	95%
March 15-18, 2004	24 / ^e 27	19 / 24	^f 19 / 19	79% / 89%	84%

^aIncludes 1 1-year old cow that was pregnant

^bPregnancy status was not determined on 2 of the cows

^cPregnancy status was not determined on 3 of the cows

^d20 VITs inserted, but one failed leaving 19.

^eTotal captured includes 1 1-year old cow that was not pregnant

^f21 VITs inserted, but 2 failed leaving 19. 1 VIT was put in a non-pregnant cow and 1 pregnant cow did not have a VIT inserted due to pregnancy misdiagnosis.

switched to the weaker VIT signal so that we could check on its status. The VITs were temperature sensitive and doubled in pulse rate when shed from the cow, indicating a newborn calf. By using maternal calves (calves caught with the use of VITs), I was able to analyze calf survival as it relates to cow condition in March.

Calf Capture

Flights from a fixed-wing aircraft fitted with directional antennas were conducted daily, weather permitting from about May 19 to June 30 to determine if any calves were born to cows with VITs (maternal calves). A VIT that was determined to be in fast pulse, indicating a birth, was marked with a global positioning system (GPS) to obtain an approximate location. The frequency of the VIT and coordinates were then relayed to a ground crew, who attempted to find and catch the calf. Additional calves were caught by ground searching (discovery calves) and with the use of a helicopter with net guns. Random searching from the ground

was conducted throughout the calving season to find calves or cows that appeared to have a calf. A helicopter was used to capture newborn calves during a few days in late May or early June (helicopter calves; Table 2.2). A person was set on the ground and then directed to the calf by the helicopter pilot and the calf was captured by hand. If groups of cows and calves were located, a net gun was used to aid in catching mobile calves. If there were more than 1 calf in a group, the smallest (youngest) calf was captured. Two extra calves were caught in a trap on the Wenaha WMU during February 2004 (2003-born calves) while the rest of the calves caught were from the middle of May to early July, with peak captures occurring in late May / early June during helicopter capture.

Table 2.2. Summary of number of calves captured by each method in northeastern Oregon, 2002-2004.

Year	No. of maternal calves	No. of discovery calves	Dates of helicopter capture	No. of helicopter-captured calves	Total
2002	5	11	June 3-11	46	62
2003	18	^a 18	May 29-June 1	49	87
2004	14	26	May 29-June 1	33	73

^aTwo additional calves were caught in February with a portable elk trap.

Once a calf was caught, it was blindfolded and hobbled if necessary for easier handling. Each calf was fitted with an expandable collar with a radio-transmitter attached, most were weighed, sexed, aged, ear tagged, and had blood drawn (for future analysis). The radio transmitters had a mortality sensor integrated in the circuitry that was activated by 6 hours of no movement (Telonics, Mesa, Arizona, USA), resulting in an accelerated pulse indicating that a calf was dead or the collar

was shed. With precaution, abandonment by the cow was likely reduced to an insignificant level (Larsen and Gauthier 1989), and with proper handling and tagging, most mortality of neonates was not affected (Ozoga and Clute 1988, Byers 1997).

The age of the calf was estimated based on the combination of coat and ear wetness, hoof condition, state of navel healing, tooth eruption, and gum color (Johnson 1951). A calf with a wet coat or wet inner ears was judged to be hours old (this technique was not used on rainy days). A calf with yellow, soft, and rough hooves indicated a young calf (<1 day of age), and a calf with black, hard, and smooth hooves indicated an older calf (≥ 3 days of age). We observed the navel to determine how wet, bloody, and/or dry and scabbed it was. The teeth were inspected to determine state of eruption and extent of eruption was measured, and the gum color was determined on a scale from pink to gray.

Monitoring and Forensics

Radio-collared elk calves were monitored from fixed-wing aircraft or from the ground at least once daily from the day of the first calf capture until June 30, 3 times a week in July, and 2-3 times a week from August through May, except for days of inclement weather that grounded the aircraft. Some variation occurred with each year and weather conditions. The purpose of monitoring was to determine if the calf was alive or dead. Flights were usually done in early mornings to ensure enough time to get to mortality sites the same day. When a mortality signal was detected, coordinates were taken with a GPS to help a ground crew find the calf collar.

Most collars on mortality mode were reached by foot within 4-8 hours of initially being detected except for a few mortalities that were in remote areas and they

were usually located within 24 hours. Some were difficult to reach due to high snowfall in the winter in which case we had to wait until conditions allowed travel to the site. Once a dead calf was located, we first searched the vicinity for signs of predation and scavenging. We looked for hair, scat, tracks, claw marks, bed sites, vegetative disturbance, blood, and calf carcass parts. Hair and scat samples were collected for analysis when found. If signs of predation were present, the carcass was skinned and examined for evidence of hemorrhaging, claw and bite marks, bleeding, and crushed bones. We determined the cause of death by observing predator-specific wounds, concealment of the carcass, and consumption habits (Henne 1975, Wade and Bowns 1985). We also inspected internal organs for signs of disease and starvation. Photographs were often taken of the mortality site as a permanent record. Soon after a carcass was processed, the details of the evidence found were discussed with another biologist to obtain a final conclusion on the fate of the calf. Intact carcasses were taken to a veterinarian for necropsy.

Statistical analyses

Survival analyses were conducted with “known fate” models in program MARK (White and Burnham 1999). Program MARK uses a modified Kaplan-Meier (1958) estimator that allows for staggered entry and censoring (Pollock et al. 1989). This allowed much flexibility in my analyses in that late-born calves were added to the data set at the time of birth. In addition, calves that moved off of study areas were censored from the data set for the time periods gone and then added back into the analysis if they returned.

Differences in calf survival based on sex, study area, and year were tested as

group effects, and modeling of survival as a function of covariates was incorporated into the analyses. Each model tested was ranked by the small sample size bias-corrected form of Akaike's Information Criterion (AIC_c ; Burnham and Anderson 1998) leading me to choose the best and any competing model(s). The best model was the one with the lowest AIC_c , and any model within 2 AIC_c values of the best model was considered competing (Burnham and Anderson 1998) and therefore taken into consideration. The best models were used to interpret results. Variables that were not in the best model were either added or substituted in for a variable in the best model for interpretation. Coefficients were reported based on the best model since competing models had similar variables and results.

I developed models that incorporated sex, year, area, a constant survival rate for each group and time period (\cdot), variable time (t), and time trend (T). Variable time-specific (t) and time trend (T) were incorporated into models to explain survival rates. The $S(\cdot)$ model (constant survival rate) was used as a baseline for comparison to other models to help determine differences among groups and/or effects of variables. The $S(t)$ model involves separate parameters for each time period. The $S(T)$, $S(T+TT)$ and $S(\ln T)$ models involve 1 parameter to describe survival over a linear time trend (T), quadratic time trend ($T+TT$), and curvilinear time trend ($\ln T$). Covariates obtained from calf measurements included birth date (BD) and birth weight (BW). Birth weight was calculated by taking the weight and estimated age at capture and backtracking by the average weight gain of elk calves, 870 g d^{-1} as reported by Hudson and Adamczewski (1990). Covariates obtained from cow measurements included percent spring fat (SF; Cook et al 2001a, b), cow age (CA),

and spring cow mass (SCM; Cook et al. 2003), which measured cow condition.

Annual survival analysis

To estimate annual survival I used calves born in 2003 ($n = 87$). Grouping variables were based on sex and study area, and the covariates used were BD and BW. I analyzed survival on a monthly-basis up to 1 year (June 1, 2003-May 31, 2004). Two of the calves that moved off the Wenaha study area in late fall and then came back in spring were censored and then added back into the analysis. The two calves that moved from the Wenaha study area to the Sled Springs study area were censored from the Wenaha group and then added into the analysis as Sled Springs calves. Calves that lost their collars were censored from the analysis at the time they were last known alive.

A subset of the data from the 2003-2004 annual analysis was used to analyze the effects of BD and BW on survival more accurately (*see* Appendix A for complete results). This data set consisted of all calves (maternal, discovery, and helicopter calves) that were ≤ 4 days of age and 1 5-day old calf that was captured by ground discovery. My ability to accurately estimate age of calves, and thus BW, diminished for calves > 4 days of age. Schlegel (1976) believed it was difficult to accurately age calves beyond 2-4 days. I decided to include the 1 5-day old calf in the analysis because we caught the calf from the ground, making it not likely older than 5 days. With this data set, I found similar results as I did using the full data set to test the effects of birth date and birth weight on survival of calves, so interpretations of results are from the full set of data.

6-month maternal and lactation calves analysis

My ability to simultaneously test influences of calf covariates and cow condition on calf survival was hindered by small sample sizes. I used the 2002 and 2003 maternal and lactation calves to analyze the effects of cow condition on calf survival. Lactation calves are elk calves that were considered alive or dead based on the lactation status of the cow at the end of November and early December (Fleet and Peaker 1978, Noble and Hurley 1999), the times of fall cow captures. These are calves that were not caught and collared due to logistics and unforeseen problems as explained in the results, but were included in the analysis to increase the sample size from 18 (maternal calves) to 61 (maternal and lactation calves). Using lactation status to indicate survival of the calf up until fall cow capture was used only on cows that were known to be pregnant the previous spring. Grouping variables were area and year, and our covariates representing cow condition were spring fat (SF), cow age (CA), and spring cow mass (SCM). I could not include fall cow measurements because of large amounts of missing data. The spring cow measurements should still represent the previous fall cow measurements to some degree because they were highly correlated (SF correlation with fall fat, $r = 0.66$, $n = 28$, $p\text{-value} = 0.0002$; SCM correlation with fall cow mass, $r = 0.70$, $n = 28$, $p\text{-value} = <0.0000$). With this analysis, survival was analyzed on a monthly basis from June to November. Since I was not able to determine the date of death for lactation calves, I modeled time of death after time-specific mortality in the annual analysis, where the time of death for each calf was known. This analysis was considered preliminary since survival is analyzed only up to 6 months, the accuracy of using lactation status to determine elk

calf survival in the late fall is unknown, and the time of death for lactation calves was unknown. I considered this analysis as a protocol for future analyses when more data is obtained; therefore, no conclusions on the effects of cow condition on calf survival can be made from this analysis.

Annual maternal calves survival analysis

To further investigate the effects of cow condition and calf covariates on calf survival, I analyzed a complete, but much smaller data set on the 18 maternal calves from 2003 through the first 12 months. This analysis allowed me to simultaneously test influences of calf covariates and spring cow condition on calf survival up until recruitment. With this data set, I was able to include sex and area as group variables and all calf and spring cow covariates. Although similar to my other analyses, this analysis was only used to look for trends and was not used for interpretation of final results due to the small sample size and preliminary nature of the results. I was not able to make conclusions on the effects of cow condition on elk calf survival due to the small sample size.

Summer survival analysis

I investigated summer calf survival up to 15 weeks ($n = 222$) by including all maternal, discovery, and helicopter calves collared from the 3 years. For this analysis, 55 calves were censored due to shed collars. This survival analysis started May 12, the earliest birth date recorded, and ended on August 25. The time span was dictated by the results of the 2003 annual survival analysis, where time-specific survival rates became relatively constant from there on. Time intervals were set at 1 week for a total of 15. Group variables were gender, year, and area. Birth date (BD)

and birth weight (BW) of calves were also included in this analysis. Calves that lost their collars were censored from the analysis at the point of the last known date they were alive.

To determine if the effects of BD and BW were different from the results of the summer survival analysis, I used a subset of this data ($n = 93$) using only maternal and discovery calves (*see* Appendix B for complete results). I considered the maternal and discovery calves to be more randomly selected through time than the calves that were captured with the helicopter at fixed time periods near the peak of parturition. In addition, most of the maternal and discovery calves were <4 days of age, allowing me to analyze the effects of BW and BD more accurately since age could be better estimated at the time of capture for young calves. This analysis produced similar results to using all calves in the summer survival analysis. Although a large proportion of the helicopter calves were sampled at fixed time periods and on average were older than maternal and discovery calves at the time of capture, I do not believe that the addition of these calves to the survival analysis created bias. The slight differences between the two analyses are not different enough to justify further interpretation of the analysis on just the maternal and discovery calves. In all survival analyses, some missing data occurred. These values were estimated by using medians and averages for the year or were randomly assigned. In 2002, 1 calf had a missing birth date (median = June 1st), 2 calves had missing birth weights (mean = 21.7 kg) and the sex of 1 calf was randomly assigned to female. In 2003, 2 calves had missing birth dates (median = June 26), 2 had missing birth weights (mean = 21.0 kg), and the sex of 3 calves was randomly assigned (all male). In 2004, 1 calf had a missing birth

date (median = June 27), 3 calves had missing birth weights (mean = 19.0 kg), and the sex of 2 calves were randomly assigned (1 male and 1 female). In 2002, 3 cows had missing spring cow mass (mean = 209 kg). In 2003, 2 cows had missing spring cow mass (mean = 217 kg) and 2 had missing percent spring fat (mean = 6%).

Relationships of cow condition to birth date and birth weight

I computed correlation coefficients to determine relationships between cow condition (SF, SCM, and age) and birth date (n = 55) and birth weight (n = 36) of calves to look for indirect effects of cow condition on calf survival. Associated P-values were also presented for measures of significance. For birth date, the data consisted of all the known birth dates of calves associated with cows captured and measured the previous springs for all three years. This included data from calves that we did (maternal calves) and did not capture, but knew the birth date for each due to the day the VITs were shed. VITs not found near birth sites (disturbed circular areas) were considered to have been possibly prematurely shed and were not used to indicate the birth dates of calves. This is a conservative approach to determining birth date, because some of the cows may have shed the VIT and moved a short distance and given birth. For birth weight, I used data obtained from maternal calves captured that had associated cow condition measurements.

Results

During 2002-2003, 45 of the 62 calves lost their collars before recruitment (1 year of age), with 23 of the 45 lost collars falling off by July 16th. In addition, of the 40 VITs deployed, 3 stayed in until parturition and only 5 maternal calves were captured. By recruitment, the fates of only 16 calves were determined (Table 2.3). Only 1 managed to make it to recruitment with its collar still attached, 14 died from predation with their collars still attached, and 2 were killed by hunters after recruitment. Overall, data were limited for the 2002-2003 sample.

Improved collars and different VITs were used during calf and cow capture in the springs of 2003 and 2004. As a result, only 6 of the 87 calves caught in 2003 lost their collars prior to recruitment and only 4 of the 73 calves caught in 2004 lost their collars prior to August 25, 2004 (research is ongoing). We were able to determine the fates of 82 calves for 2003-2004 up until recruitment and 68 for 2004 as of August 25, 2004 (Table 2.3). The improved VITs also allowed us to capture more maternal calves; 18 in 2003 and 14 in 2004.

Estimated birth dates ranged from May 12 to July 7 and the median was May 29 for calves that had birth dates estimated at the time of capture ($n = 218$). The median and range of estimated birth dates was the same for calves ≤ 4 day of age at capture ($n = 140$). Median birth dates were only 1 day apart for female (May 28) and male calves (May 29) and were the same for male and female calves ≤ 4 day of age at capture (May 29). Estimated birth weight of female calves ($n = 110$) averaged 19.4 kg and for male calves ($n = 101$) 21.7 kg. Estimated average birth weight of females ≤ 4 days of age at capture ($n = 69$) was 16.6 kg and males ($n = 67$) was 19.5 kg.

Table 2.3. Fates of radio-collared elk calves on two study sites in northeastern Oregon, 2002-2004.

Study area	Study year	No. radio collared calf elk	No. censored due to lost collars	Cause of mortality							Total mortalities
				Black bear	Cougar	Other	Unknown predator	Neonate starvation	Hunter/Vehicle	Unknown	
Wenaha	2002	30	20	1	9				1		11
Sled Springs	2002	32	25	4	1				1		6
Wenaha	2003	44	3	3	22			1		2	28
Sled Springs	2003	43	3	3	10	^a 1	1	1	2	3	21
Wenaha	^b 2004	34	3		9			^c 2		1	12
Sled Springs	^b 2004	39	1	3	8	^d 2		^c 1			14
Total		222	55	14	59	3	1	5	4	6	92

^aMortality due to pneumonia.

^b2004 results up to August 25, 2004.

^cStarvation deaths likely related to capture.

^d1 coyote and 1 bobcat kill.

Influence of cow condition on pregnancy rates

Spring pregnancy rates were 84-96% during the study (Table 2.1). Of the 78 cows that had both pregnancy and lactation status determined in the fall, 5 were not pregnant (Table 2.4). Due to the energy demands of lactation, I categorized the cow elk captured in the fall into 4 groups based on pregnancy and lactation status (Table 2.4). The average percent fall fat for pregnant/non-lactating cows was not different from the average percent fall fat for non-pregnant/non-lactating cow elk (overlapping 95% confidence intervals). I was not able to determine if pregnant/lactating cows differed statistically in fall percent fat from non-pregnant/lactating cows, because only 1 non-pregnant/lactating cow was in the sample. With many pregnant cows and few non-pregnant cows, I did not find evidence that cow condition, as described by percent fall fat, negatively influenced pregnancy rates. All cows that were pregnant in the fall and recaptured the following spring were still pregnant; thus, there was no evidence that cows aborted or absorbed their fetuses before parturition. Additional data from the rest of the study will help clarify these comparisons.

Table 2.4. Number of pregnant and lactating cows captured in northeastern Oregon in late November / early December 2001-2003. Includes only cows that had both pregnancy and lactation status determined.

	No. of cows	No. of cows pregnant	No. of cows pregnant and lactating	No. of cows not pregnant and lactating	No. of cows pregnant and not lactating	No. of cows not pregnant and not lactating
Number	78	73	38	1	35	^a 4
Average fall fat (%)			7.95	3.99	12.11	7.85
95% CI			7.16 - 8.74		11.3 - 12.92	1.69 - 14.01

^a1 1-year old cow part of total - fall fat = 14.23%.

Causes of mortality

Throughout the study, 1 coyote and 1 bobcat kill were recorded. Two of the unknowns in Wenaha and 2 in Sled Springs were likely cougar-related deaths due to cougar sign found at each mortality site. No diseases were identified in deaths due to predation. At least 3 of the 5 deaths due to starvation were likely capture-related (Table 2.3), as these calves were probably separated from their dams during capture and were never united. With minimal data from 2002-2003 and ongoing research from 2004-2005, I chose to describe mortality rates and causes of mortality over an entire year using only data from 2003-2004. Not including calves that lost their radio-collars for the 2003-2004 study period, 48% of the radio-collared elk calves were killed by predators. In Wenaha, 61% of the radio-collared calves were killed by predators ($n = 25$) with 54% of radio-collared calves killed by cougar ($n = 22$). In Sled Springs, 35% of the radio-collared calves were killed by predators ($n = 14$) with 25% of radio-collared calves killed by cougar ($n = 10$). Of the 87 calves captured, 6 lost their collars and 32 lived to yearling age class. The first 3 months had a higher percentage of calf mortalities than the last 9 for year 2003 (Figure 2.2).

During the first month of life (calves <28 days of age), cougars were the main predators on elk calves over the 3 study years; however, slight differences occurred between study areas. Of the 40 calf mortalities, cougars killed 20, with 15 of the cougar kills occurring in Wenaha. There were 3 more black bear kills than cougar kills in Sled Springs, making black bears the main predators on calves 0-28 days old. During capture in 2004, 3 calves were found in Sled Springs caught in wire fences. Once collared and released, these calves showed sign of injury, which may have

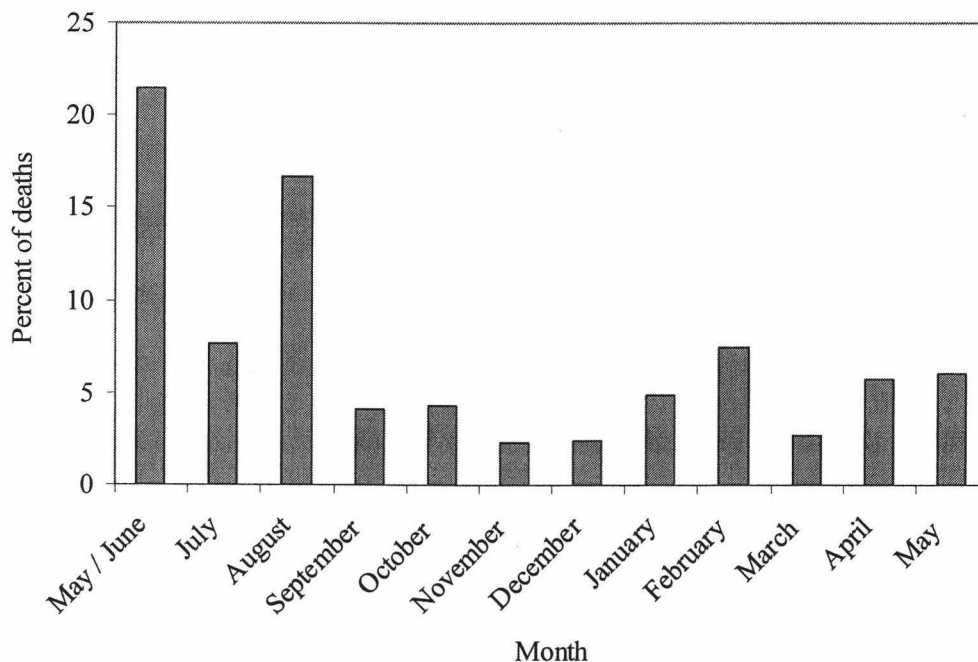


Figure 2.2. Percent of deaths out of number of calves living for each month in northeastern Oregon, 2003-2004 (n = 89).

resulted in death. Two of the injured calves were killed by cougars 4 and 30 days after capture and 1 died of starvation 3 days after capture. During ground and helicopter capture, 7 dead elk calves were found: 1 pneumonia, 1 cougar, and 5 bear kills. These calves were not included in any analyses.

I only used 2003-2004 data to describe mortality rates and causes of mortality for calves 29 days-1 year. For calves 29 days-1 year old, cougars were the main predators. Of the 31 calf mortalities, cougars killed 23, with 14 of the cougar kills occurring in Wenaha. No kills by black bear were recorded for calves older than 28 days of age in 2003. Other causes of mortality on elk calves that were 29 days-1 year old were: 1 unknown predator kill, 1 hunter kill, 1 vehicle collision, and 5 unknowns.

Annual survival

The best model for estimating annual survival was $S(\text{area}+\ln T+\text{BD})$ and there were no competing models (Table 2.5). This model had almost 3 times the weight as the next best model, indicating the likelihood of this model over the other models tested. The best model indicated that survival differed between the two study areas, followed a curvilinear time trend, and was affected by the birth date of calves (BD). The probability of survival for 12 months in Wenaha and Sled Springs was 0.26 (95% CI = 0.15 to 0.42) and 0.52 (95% CI = 0.37 to 0.56), respectively, a twofold difference (Figure 2.3). Survival rates changed most dramatically from August (month 3) to September (month 4; Figure 2.4). Neonatal survival was lower in later-born calves than in early-born calves (Figure 2.5a & b). The effects of study area and birth date were significant as the 95% confidence intervals for each variable did not include zero (Figure 2.6). Survival rates did not differ between sexes, and birth weight (BW) of calves did not affect survival estimates, as shown by the larger AIC_c value over the best model. The confidence intervals for these two variables also overlapped 0 to a large extent (Figure 2.6).

Table 2.5. Model selection results for annual survival for 2003-2004 collared calves in northeastern Oregon (n = 89). Variable definitions: BD = birth date, BW = birth weight, T = linear time trend, lnT = curvilinear time trend, T² = exponential time trend, t = time-specific.

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(area+lnT+BD)	313.802	0.000	0.479	4	305.731
S(area+lnT+BD+BW)	315.837	2.036	0.173	5	305.731
S(area+lnT)	316.721	2.919	0.111	3	310.678
S(lnT+BD)	317.461	3.660	0.077	3	311.419
S(area+lnT+BW)	318.443	4.642	0.047	4	310.372
S(sex+lnT+BD)	318.946	5.145	0.037	4	310.875
S(lnT)	319.196	5.394	0.032	2	315.175
S(T+T ²)	319.645	5.843	0.026	3	313.602
S(sex+lnT)	321.061	7.259	0.013	3	315.018
S(T)	323.876	10.074	0.003	2	319.855
S(area+BD)	326.188	12.387	0.001	3	320.146
S(t)	329.628	15.827	0.000	12	305.066
S(area)	331.494	17.692	0.000	2	327.472
S(sex*area)	331.951	18.149	0.000	4	323.880
S(BD)	332.132	18.331	0.000	2	328.111
S(sex+BD)	333.285	19.484	0.000	3	327.243
S(sex+area)	333.515	19.713	0.000	3	327.472
S(sex+BD+sex*BD)	333.646	19.844	0.000	4	325.575
S(BD+BW)	334.134	20.332	0.000	3	328.091
S(.)	335.782	21.981	0.000	1	333.775
S(BD+BW+BD*BW)	336.116	22.314	0.000	4	328.045
S(BW)	337.573	23.771	0.000	2	333.552
S(sex)	337.589	23.788	0.000	2	333.568
S(sex+BW+sex*BW)	337.833	24.031	0.000	4	329.762
S(sex+BW)	339.409	25.608	0.000	3	333.367
S(t*sex*area)	357.868	44.066	0.000	48	252.804

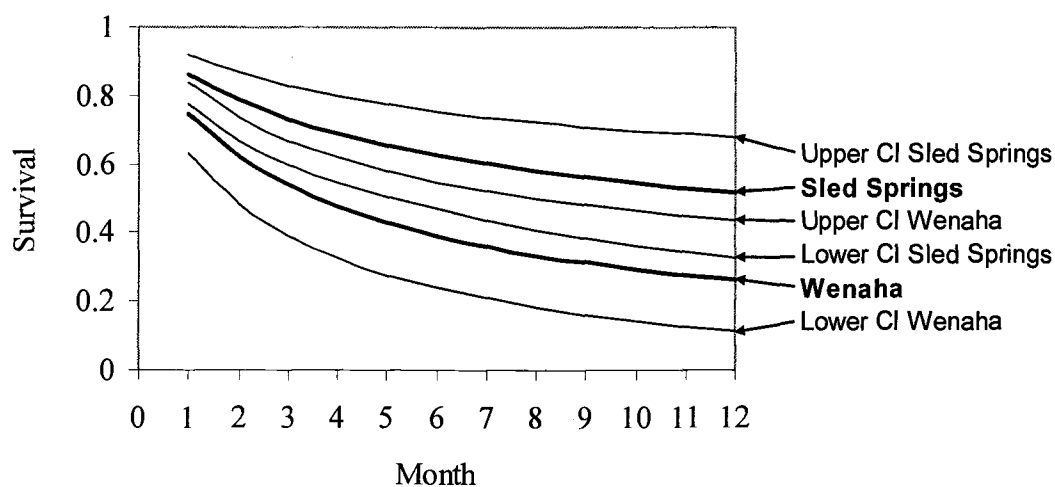


Figure 2.3. Compounded survival estimates and associated 95% confidence intervals for radio-collared elk calves in two adjacent study areas in northeastern Oregon, June 2003 – May 2004 ($n = 89$). Estimates generated from the minimum AIC_c model, $S(\text{area}+\ln T+BD)$.

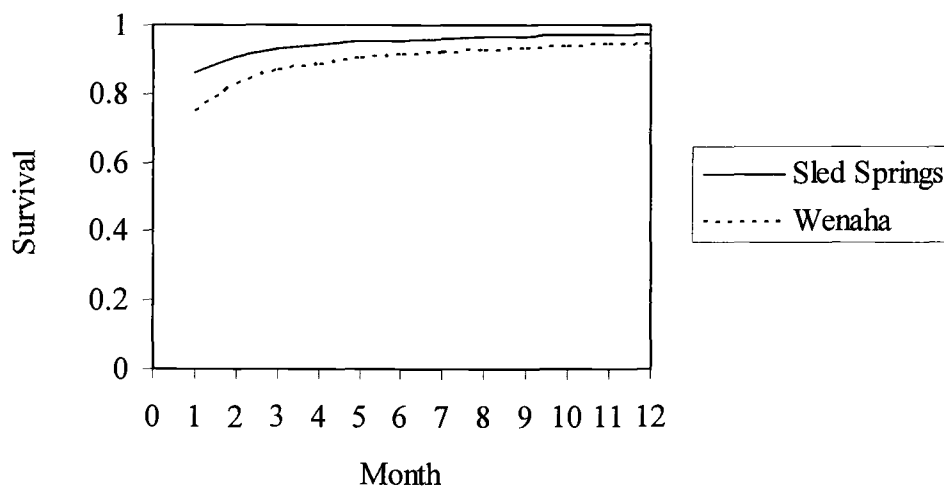


Figure 2.4. Survival estimates for each month for radio-collared elk calves in two adjacent study areas in northeastern Oregon, June 2003 – May 2004 ($n = 89$). Estimates generated from the minimum AIC_c model, $S(\text{area}+\ln T+BD)$.

Figure 2.5a.

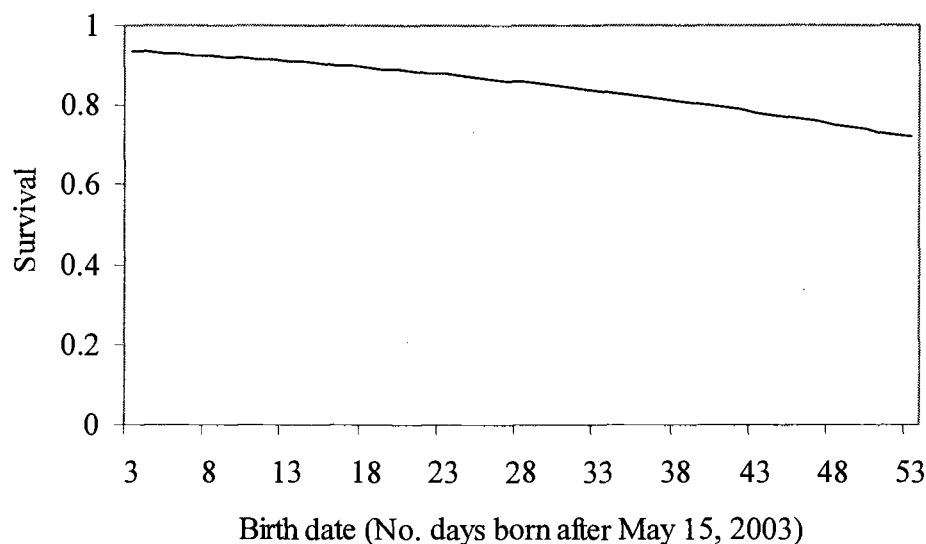


Figure 2.5b.

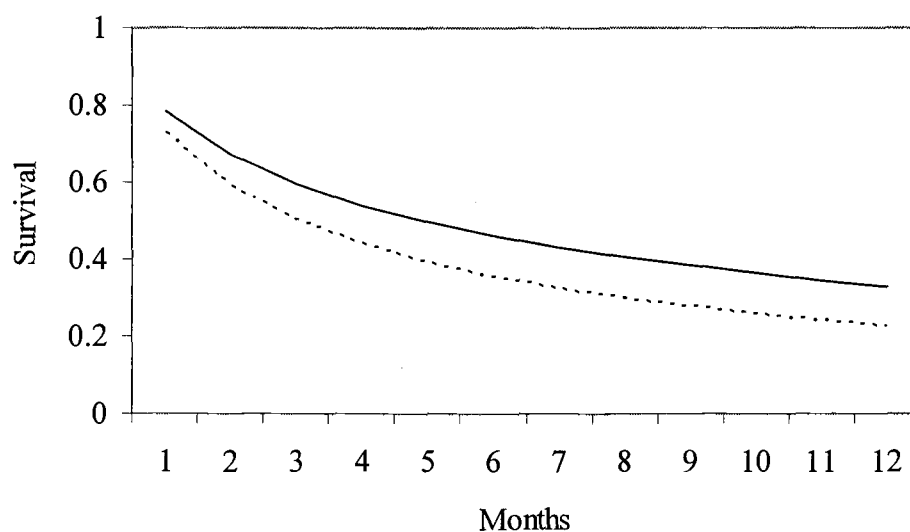


Figure 2.5. The effect of birth date on elk calf survival in northeastern Oregon, 2003-2004 ($n = 89$). Figure 2.5a shows only the effect of BD in Wenaha, while other variables are held constant. Estimates generated from model $S(\text{area} + \ln T + \text{BD})$ using equation $\text{logit}(S) = 1.837 + -0.745(\text{area}) + 0.704(\ln T) + -0.035(\text{BD})$. Area = 0.5 and $\ln T = 1.869$, which are the medians. Figure 2.5b shows the differences in survival probability for a calf born 8 days after May 15 (solid line) and a calf born 15 days after May 15 (dotted line) in Wenaha.

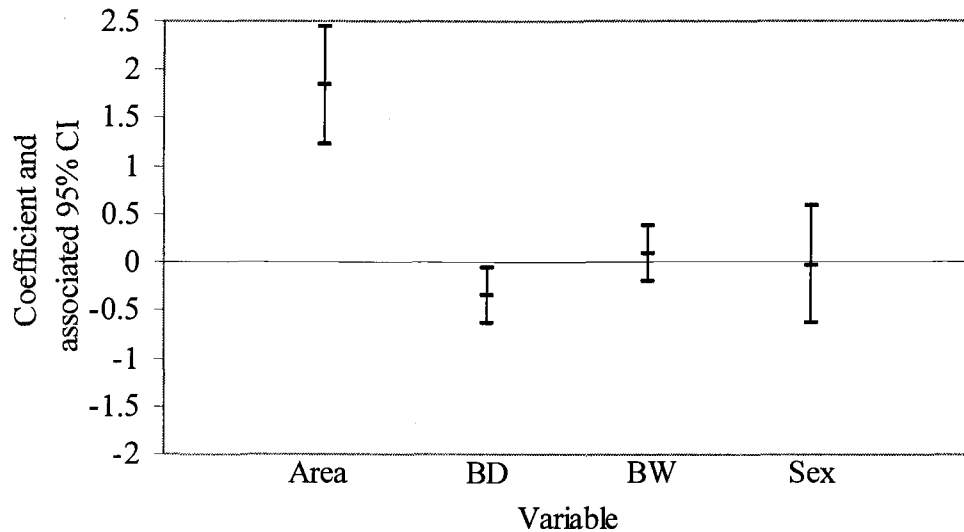


Figure 2.6. Regression coefficients with associated 95% confidence intervals for each variable generated from model S(area+lnT+BD) for the 2003-2004 annual survival analysis (n = 89).

The analysis on the maternal calves from 2003 showed that the best model was S(lnT+BD) (Table 2.6). This model also indicated that annual survival followed a curvilinear trend and was affected by the birth date of calves. Again, survival was lower in later-born calves than in early-born calves as indicated by the negative coefficient (Figure 2.7). There was evidence of a birth date effect due to the 95% confidence interval slightly overlapping 0. Competing models included models that consisted of different types of time-effects and models that added the variables area and sex to the best model. Although area and sex appeared in competing models, there is no evidence for differences in survival rates between areas and sexes because the 95% confidence intervals substantially overlapped 0 (Figure 2.7). In addition, the models including only these variables had higher AIC_c values than the S(.) model (Table 2.6). Models that incorporated cow age (CA), spring cow mass (SCM), and spring fat (SF) were >2 AIC_c scores away from the best model (Table 2.6). Ninety-

Table 2.6. Model selection results for annual survival for 2003-2004 maternal calves in northeastern Oregon (n = 18). Variable definitions: BD = birth date, BW = birth weight, T = linear time trend, lnT = curvilinear time trend, T² = exponential time trend, SCM = spring cow mass, SF = spring fat, CA = cow age.

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(lnT+BD)	73.154	0.000	0.157	3	66.854
S(lnT)	73.534	0.380	0.130	2	69.386
S(T+T ²)	74.108	0.954	0.097	3	67.808
S(area+lnT+BD)	74.830	1.677	0.068	4	66.324
S(sex+lnT+BD)	74.971	1.818	0.063	4	66.465
S(T)	74.990	1.837	0.063	2	70.842
S(BD)	75.210	2.057	0.056	2	71.062
S(lnT+BD+SCM)	75.213	2.059	0.056	4	66.707
S(area+lnT)	75.343	2.189	0.052	3	69.043
S(lnT+SCM)	75.477	2.323	0.049	3	69.177
S(sex+lnT)	75.668	2.515	0.045	3	69.368
S(BW)	76.512	3.358	0.029	2	72.364
S(area+lnT+BD+CA)	76.611	3.457	0.028	5	65.841
S(sex+lnT+BD+CA)	77.130	3.976	0.021	5	66.361
S(area+lnT+CA)	77.545	4.391	0.017	4	69.038
S(.)	77.743	4.590	0.016	1	75.694
S(SF)	77.906	4.752	0.015	2	73.758
S(area+lnT+BD+CA+SCM)	78.773	5.620	0.009	6	65.682
S(area)	79.219	6.066	0.008	2	75.071
S(SCM)	79.441	6.288	0.007	2	75.293
S(CA)	79.827	6.673	0.006	2	75.679
S(sex)	79.842	6.689	0.006	2	75.694
S(sex+area)	81.353	8.199	0.003	3	75.052
S(sex*area)	83.055	9.901	0.001	4	74.548
S(t)	88.744	15.590	0.000	12	60.350
S(t*area*sex)	239.177	166.023	0.000	45	40.230

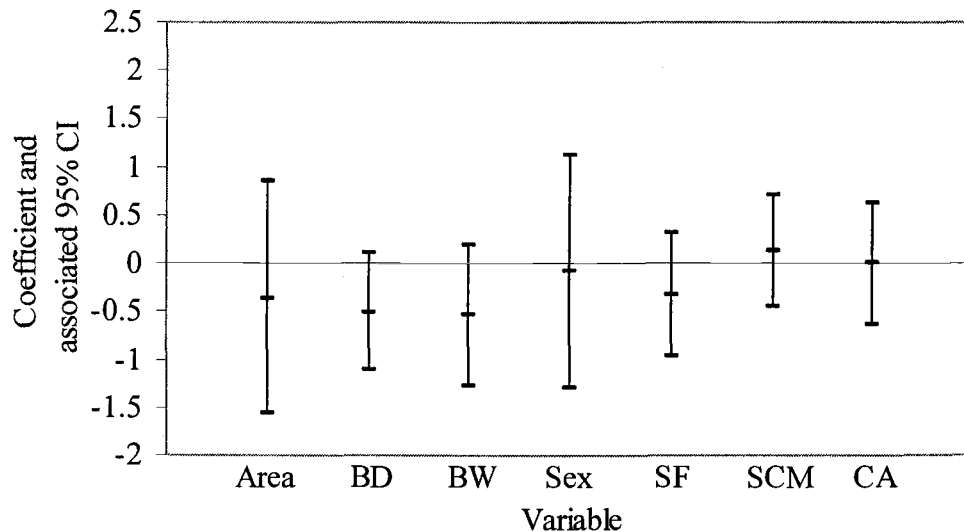


Figure 2.7. 2003-2004 annual maternal calves survival analysis ($n = 18$). Regression coefficients with associated 95% confidence intervals for each variable generated from model $S(\ln T + BD)$. Variables area, BW, sex, SF, SCM, and CA were substituted in for BD.

five percent confidence intervals for each cow condition variable overlapped 0 suggesting that cow condition had no effect on calf survival (Figure 2.7). Both birth weight (BW) and spring fat (SF) had negative effects on calf survival (Figure 2.7), a correlation that made no biological sense. Consequently, BW and SF were not included in additional models. This is a preliminary analysis because it only includes 1 year of at least 3 years of data that will be analyzed on maternal calves.

Influence of cow condition on calf survival

The best model from the 6-month analysis that used maternal and lactation calves from 2002 and 2003 was $S(T)$ (Table 2.7). This model indicated that survival followed a linear trend up to 6 months. I found no evidence for an effect of cow condition on calf survival in this analysis. The models $S(SF)$, $S(CA)$, and $S(SCM)$ all had higher AIC_c scores than model $S(.)$. The cow variables spring fat (SF), cow age

Table 2.7. Model selection results for 6-month survival using 2002 and 2003 maternal and lactation calves in northeastern Oregon (n = 61). Variable definitions: T = linear time trend, lnT = curvilinear time trend, T² = exponential time trend, t = time-specific, SCM = spring cow mass, SF = spring fat, CA = cow age.

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(T)	191.486	0.000	0.215	2	187.430
S(lnT)	192.333	0.848	0.140	2	188.277
S(T+T ²)	192.900	1.414	0.106	3	186.788
S(T+CA)	193.239	1.753	0.089	3	187.127
S(T+SCM)	193.409	1.923	0.082	3	187.297
S(year+T)	193.412	1.926	0.082	3	187.300
S(area+T)	193.537	2.052	0.077	3	187.425
S(.)	194.112	2.627	0.058	1	192.094
S(SF)	195.135	3.650	0.035	2	191.080
S(CA)	195.773	4.287	0.025	2	191.717
S(year)	195.972	4.486	0.023	2	191.916
S(SCM)	195.991	4.506	0.023	2	191.935
S(area)	196.142	4.656	0.021	2	192.086
S(area*year)	197.506	6.020	0.011	4	189.318
S(area+year)	198.012	6.526	0.008	3	191.899
S(t)	198.392	6.906	0.007	6	185.994
S(t*area*year)	234.998	43.512	0.000	24	180.780

(CA), and spring cow mass (SCM) also were determined to not affect survival as shown by the 95% confidence intervals overlapping over 0 (Figure 2.8). The models $S(T+CA)$ and $S(T+SCM)$ are competing models only because the linear time effect (T) was strong enough to allow these models to come within 2 AIC_c values of the best model. Similar results were found in the 2003 annual maternal calves analysis. Models that included only the cow condition variables had higher AIC_c values than the $S(.)$ model (Tables 2.6 and 2.7), and the 95% confidence intervals for the cow condition variables overlapped 0 (Figures 2.7 and 2.8).

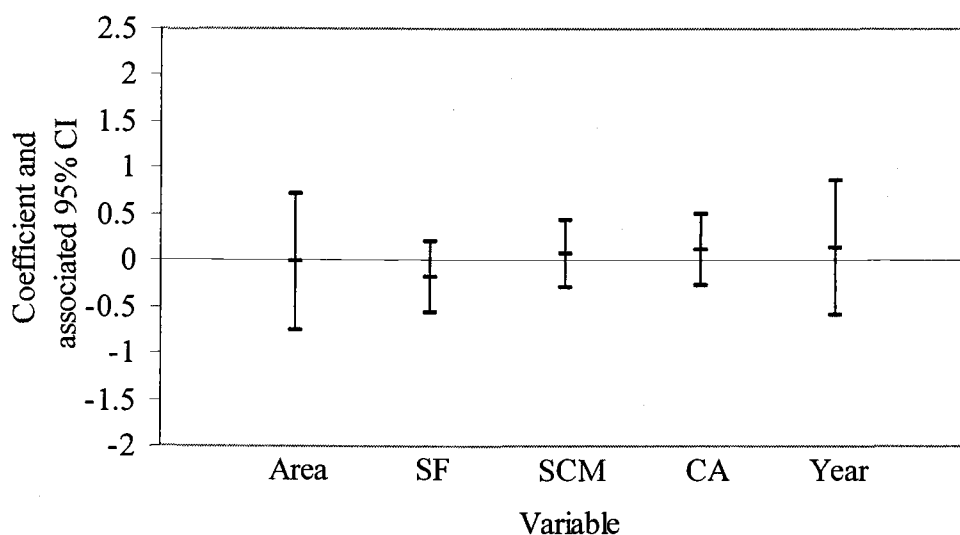


Figure 2.8. 2002 and 2003 maternal and lactation calves survival analysis ($n = 61$). Regression coefficients with associated 95% confidence intervals for each variable. Variables area, SF, SCM, CA, and year were added to the $S(T)$ model to compute values.

I found no relationship between cow condition and birth date and birth weight of calves (Table 2.8). All *r*-values were near 0 and all associated *p*-values were >0.09 ; therefore, there was no evidence that cow condition affected birth weight and birth date of calves. Consequently, I found no evidence that cow condition had an indirect effect on calf survival through birth weight and birth date effects.

Table 2.8. Correlation coefficients between cow condition variables (SF, SCM, cow age) and BD or BW with associated *p*-values (*r* / *p*-value) using 55 calves for birth date and 36 calves for birth weight. Data from northeastern Oregon, 2002-2004.

Cow condition variable	Birth date (BD)	Birth weight (BW)
Spring fat (SF)	-0.14 / 0.29	-0.29 / 0.09
Spring cow mass (SCM)	-0.13 / 0.34	0.03 / 0.86
Cow age	0.09 / 0.50	-0.03 / 0.87

Summer survival

The best model from the summer survival analysis using 2002-2004 data was $S(\text{sex} \cdot \text{area} + \ln T + \text{BD})$ and the 2 other competing models were very similar (Table 2.9). The difference in the second model was the addition of the variable BW, and the difference in the third model was that BD was not included. This suggested that the addition of BW only increases the AIC_c value, weakening the model, and that BD had a significant effect on survival rates.

Similar to the annual survival analysis, this analysis indicated that birth date had a negative effect on survival rates, with later-born calves having lower neonatal survival (Figure 2.9). There was some evidence that heavier-born calves had higher survival than light-born calves; the coefficient for BW was positive and the 95% confidence intervals slightly overlapped 0. The effects of sex and area were analyzed

Table 2.9. Model selection results for survival during the first 15 weeks of life in northeastern Oregon, 2002-2004 (n = 222). Variable definitions: BD = birth date, BW = birth weight, T = linear time trend, lnT = curvilinear time trend, T² = exponential time trend, t = time-specific.

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(sex*area+lnT+BD)	578.745	0.000	0.411	6	566.704
S(sex*area+lnT+BD+BW)	580.127	1.383	0.206	7	566.073
S(sex*area+lnT)	580.369	1.625	0.182	5	570.340
S(sex*area+lnT+BW)	581.460	2.716	0.106	6	569.419
S(sex*area)	583.121	4.377	0.046	4	575.101
S(sex+lnT+BD)	588.059	9.314	0.004	4	580.039
S(lnT)	588.365	9.620	0.003	2	584.359
S(T)	588.370	9.626	0.003	2	584.364
S(sex*area*year+lnT+BD)	588.400	9.655	0.003	14	560.194
S(lnT+BD)	588.411	9.667	0.003	3	582.400
S(T+BW)	588.461	9.716	0.003	3	582.449
S(lnT+BW)	588.502	9.757	0.003	3	582.490
S(area+lnT+BD)	588.672	9.928	0.003	4	580.653
S(sex+area+lnT+BD)	588.690	9.946	0.003	5	578.661
S(lnT+BD+BW)	588.785	10.041	0.003	4	580.766
S(sex+lnT)	588.788	10.044	0.003	3	582.776
S(T+BD)	588.871	10.127	0.003	3	582.859
S(sex+lnT+BD+BW)	589.038	10.293	0.002	5	579.009
S(area+lnT)	589.102	10.357	0.002	3	583.090
S(sex+lnT+BW)	589.379	10.634	0.002	4	581.359
S(sex+area+lnT+BW)	589.958	11.214	0.002	5	579.929
S(T+TT)	589.998	11.254	0.001	3	583.986
S(.)	592.918	14.173	0.000	1	590.916
S(sex)	593.115	14.371	0.000	2	589.109
S(BW)	593.216	14.472	0.000	2	589.210
S(area)	593.309	14.564	0.000	2	589.303
S(sex+area)	593.922	15.177	0.000	3	587.910
S(BD)	594.086	15.342	0.000	2	590.080
S(04 vs. 02 + 03)	594.350	15.605	0.000	2	590.344
S(sex+BD+sex*BD)	594.496	15.751	0.000	4	586.476
S(BD+BW)	594.576	15.832	0.000	3	588.565
S(03 vs. 02 + 04)	594.667	15.922	0.000	2	590.661
S(sex*area*year)	594.965	16.220	0.000	12	570.812
S(year)	595.748	17.004	0.000	3	589.737
S(BD+BW+BD*BW)	596.422	17.678	0.000	4	588.403
S(year*area)	597.877	19.133	0.000	6	585.836
S(t)	604.639	25.895	0.000	15	574.405
S(t*sex*area*year)	802.544	223.799	0.000	169	434.158

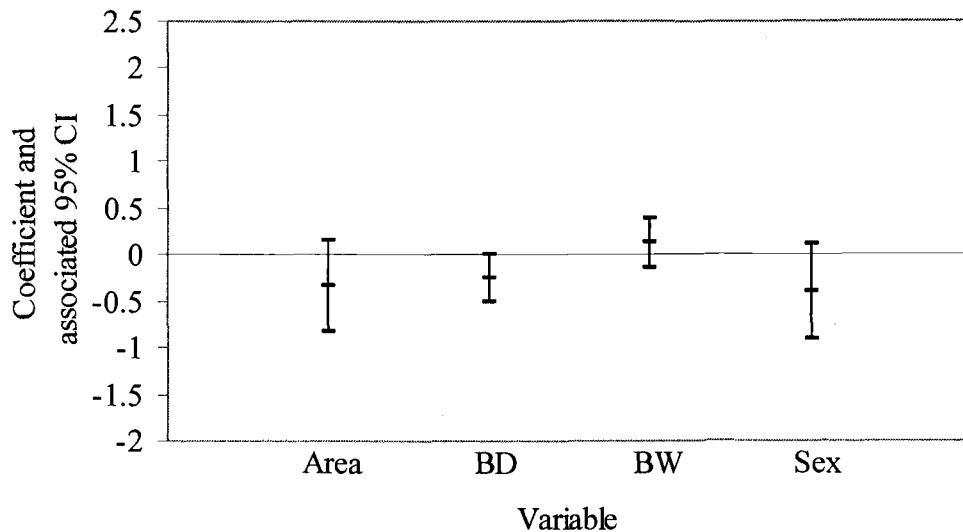


Figure 2.9. 2002–2004 summer survival analysis ($n = 222$). Regression coefficients with associated 95% confidence intervals for each variable. Variables BD and BW were added to model $S(\text{sex} \times \text{area} + \ln T)$ and sex and area were added to model $S(\ln T + \text{BD})$ to compute values. Year was not presented because of extremely large confidence intervals.

from models $S(\text{sex} + \ln T + \text{BD})$ and $S(\text{area} + \ln T + \text{BD})$ to determine their effects individually. The 95% confidence intervals for sex and area slightly overlapped 0, suggesting some evidence of a difference in survival between the sexes and areas (Figure 2.9). However, the interaction between sex and area ($\text{sex} \times \text{area}$) was stronger than the sex or area effect individually. The $\text{sex} \times \text{area}$ was important in all 5 of the top models for a combined weight of 0.95 (Table 2.9). In Wenaha, female calves had higher summer survival (0.57; 95% CI = 0.42 to 0.72) than male calves (0.42; 95% CI = 0.27 to 0.59). In contrast, in Sled Springs female calves had lower summer survival (0.46; 95% CI = 0.31 to 0.61) than male calves (0.82; 95% CI = 0.66 to 0.91; Figure 2.10).

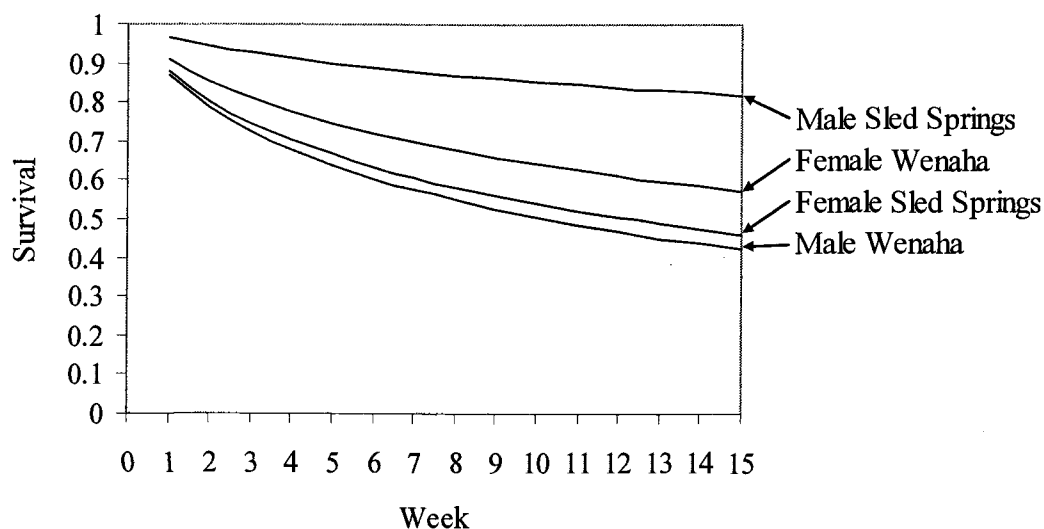


Figure 2.10. Summer survival estimates from model $S(\text{sex} \times \text{area} + \ln T + \text{BD})$ for radio-collared elk calves in northeastern Oregon, May 26 – August 25, 2002-2004 ($n = 222$).

Discussion

Birth date and birth weight of calves

I found strong evidence that birth date affected summer and annual calf survival. Other research on cervids has also shown that birth date can affect neonatal survival when predators are involved (Whitten et al. 1992, Adams et al. 1995, [caribou, *Rangifer tarandus*]; Singer et al. 1997, Smith and Anderson 1998, [elk]; Keech et al. 2000, [moose]; Gregg et al. 2001, [pronghorn, *Antilocapra americana*]). Birth date affected both summer and winter survival in red deer (*Cervus elaphus*) in an area where there were no predators (Clutton-Brock et al. 1982). Late-born calves are presumably energetically disadvantaged (Clutton-Brock et al. 1982) and the importance of body size going into winter has been demonstrated by Cook et al. (2004). Early-births should allow for a survival advantage by ensuring that the calves

are present when the dams can maximize the use of high-quality forage during the growing season, thus reaching optimal milk production (Keech et al. 2000). Cook et al. (2004) found that early births allowed calves more time to grow before the onset of winter and that larger calves lived longer due to greater tolerance of nutritional deficiencies and winter weather. Similarly, small moose calves not only lost a larger proportion of their body mass during winter, but also more weight than large calves (Cederlund et al. 1991).

The effect of birth weight on survival rates was positive in two analyses; however, there was not enough evidence to support a birth weight effect in the analysis of annual calf survival in this study. The effect of birth weight was stronger during the first 15 weeks of life than for the full year. These results suggest that birth weight has more of an influence on neonatal survival <15 weeks, but additional years of data are needed to clarify this point.

Calves born at a weight below a threshold are unlikely to survive. In a captive population, elk calves with birth weights >16 kg had a 90% chance of surviving to 4 weeks of age, whereas calves with birth weights of <11.4 kg had <50% chance of survival (Thorne et al. 1976). In this study, 83% of the calves weighed >16 kg. Of the 4 calves with estimated weights below 11.4 kg in this study; 2 were killed by cougars (42 and 57 days of age), 1 died of starvation (3 days of age), and 1 shed its collar (21 days of age). Heavier-born calves are likely to further increase their chances of survival over lighter-born calves because larger calves grow more rapidly through early summer than do smaller calves (Cook et al. 2004).

Similar to my findings, both birth weight and birth date of calves affected

summer calf survival of red deer, but only birth date affected winter survival (Clutton-Brock et al. 1982). If the size and condition of calves at the start of winter was the most important factor in determining survival (Cook et al. 2004), then differences in growth may have obscured any effects of birth weight (Clutton-Brock et al. 1982). Birth date effects can create larger differences in calf weight at any point in time than birth weight effects. Potentially, a 3-week difference in birth date can result in a >18 kg difference, assuming that elk calves gain 870 g d^{-1} . None of the birth weights in this study were different to this extent. Nelson and Leege (1982) suggested that cow elk in central Washington which gave birth after 15 June would not be able to find sufficient protein in available forage for optimal milk production when lactation demands peak at about 48 days post partum.

The results from the full set of 2003 data and that from just the maternal calves were similar in most ways. However, the large difference is in the interpretation on how birth weight may affect survival. The coefficient for BW was positive in the analysis on the full set of 2003 data, suggesting that heavier-born calves have higher survival. The coefficient for BW in the analysis on just the 18 maternal calves was negative, suggesting that lighter-born calves have higher survival. It does not make biological sense for lighter-born calves to have higher survival than larger calves. Due to small sample size ($n = 18$) in the analysis on the maternal calves, these results have little support in determining factors that influence calf survival.

Survival Rates

Sex and Area - In this study, I found suggestive evidence that males had

higher survival rates than females during the first 15 weeks of life. This may be a result of a difference in size. Birth weights may be higher due to greater maternal investment in males than females (Clutton-Brock et al. 1982). Smith et al. (1997) and Cook et al. (2004) also found that growth rates of males were higher than females. Clutton-Brock et al. (1982) suggested that male calves more frequently demand milk, stimulating their mothers to produce more milk. Males had estimated average birth weights of >2 kg than females in this study. In contrast, I didn't find differences in survival rates between the sexes during the first year of life. The size at which a calf elk enters winter may have obscured any survival differences between the sexes. Cook et al. (2004) found similar mass loss between sexes during winter and calves ≥ 105 kg at the beginning of winter had a high probability of surviving at least 90 days.

Although I found evidence for differences in summer survival rates between the sexes overall, these differences were not consistent between study areas. In Wenaha, females had higher survival than males, and in Sled Springs, males had higher survival than females for the first 15 weeks of life. The reasons for these different results are not clear.

Significant differences in annual survival rates between study areas occurred in 2003, because cougars killed more elk calves in Wenaha than in Sled Springs. In 2003, there was more than twice the number of cougar kills in Wenaha than in Sled Springs which was likely due to high cougar densities. During the summer of 2003, cougar densities were determined to be high in a particular area of Wenaha where many groups of elk resided (Bruce Johnson, pers. comm). Of the 15 cougars radio-

collared in Wenaha, 12 were located at least 1 time during the calving period in an estimated 80 km² area, where many of the collared calves died due to cougar predation.

Overall, there were likely higher densities of cougars residing in Wenaha near groups of elk than in Sled Springs. These differences may be attributed to differences in topography (Hornocker 1970), amount of cover, and the amount of human disturbances due to logging practices. In Wenaha, there is higher elevation, rougher terrain, and deeper canyons than in Sled Springs. Also, the higher human disturbance coupled with less cover in Sled Springs may make the area less suitable to cougars.

Curvilinear trend - It was not surprising to find that time-specific survival followed a curvilinear trend (lnT), because younger calves were more susceptible to predation than older calves. Calves that reached 3 months of age had higher monthly survival rates. Eighty-five percent of calf mortality occurred between May and September in southeastern Washington (Myers et al. 1999). Similarly, survival was higher after the initial phase of predator mortality when elk calves were young in Idaho (Schlegel 1976).

Causes of Mortality

Predation was directly responsible for 48% of the mortality of radio-collared elk calves born in 2003 during their first year of life. However, there were 5 calves killed from unknown causes that could have been predator-related, as all 5 were eaten by bears and/or cougars. Predation likely was responsible for >50% of the collared calves (hypothesis 1). If only 2 of the unknown mortalities were considered to have been predator-related, then predation would have been responsible for >50% of the

radio-collared elk calves. Predation rates also differed between study areas; predation was responsible for 61% and 35 % of the radio-collared calves in Wenaha and Sled Springs, respectively. My hypothesis that black bears were the main predators on young (0-28 days old) calves was only partially correct. The main predators on young calves in Sled Springs were black bear; however the overall major predators on young calves were cougar, with most cougar kills occurring in Wenaha. Although black bears are efficient predators on young elk (Schlegel 1976, Smith and Anderson 1996), cougars killed more young calves in this study. Only 15% of the predator-related deaths of elk calves in Idaho were due to cougar predation, while 74% of the predator-related deaths were due to black bears (Schlegel 1976). Smith and Anderson (1996) reported no cougar mortalities in Wyoming, and Singer et al. (1997) reported only 1 cougar mortality throughout their study in Yellowstone National Park. These differences likely indicate that bear densities were lower and/or cougar densities higher in this study than in Idaho, Wyoming, and Yellowstone National Park. Similar to this study, cougars were the main predator and killed more elk calves than did black bears in southeastern Washington (Myers et al. 1999).

My results did support the hypothesis that cougars were the main predators on older (28 days-1 year old) calves, (hypothesis 3). This dominance of cougar predation carried over from the early calf mortality through the first year of life. Besides the fact that black bears were hibernating for much of the year, cougars were likely more capable than black bears at catching and killing older elk.

Predator deaths on elk calves in Wyoming were from black bears and coyotes and were on calves 2-23 days of age (Smith and Anderson 1996). All black bear and

brown bear predation in Yellowstone National Park occurred during the first 28 days (Singer et al. 1997). This is similar to what I found, suggesting that bears have a short time period to prey on calves, as only 1 calf >28 days old was killed by a black bear. Black bears have other foods available after the peak calving period, such as insects and vegetation (Bull et al. 2001). With other foods easily obtainable, black bears may reduce their efforts in searching for young elk calves after peak calving. In southeastern Washington, 88% of calf mortalities due to black bear occurred before August, while cougar predation occurred over longer periods (Myers et al. 1999). Myers et al. (1999) suggested that any elk calves found by black bears were likely young and using a hiding strategy since black bears were observed hunting for calves with their sense of smell. Cougars tend to be visual hunters, which might allow mobile calves to be more vulnerable to cougar predation (Myers et al. 1999).

Pregnancy rates

In the summer and fall, non-lactating cows can more easily achieve a higher level of condition than lactating cows, thus increasing their chances of ovulating and becoming pregnant (Cook et al. 2004). Lactation requires 3 to 4.5 times the energy as pregnancy in large herbivores (Oftedal 1985); consequently, a cow elk without a calf can build fat reserves more easily than a lactating cow. Hence, a population of elk with high calf mortality during summer may have higher pregnancy rates. The majority of the calf mortality in this study occurred during summer, which may have allowed cows without calves to build sufficient fat reserves and increase their chances of ovulating and becoming pregnant. In this study, only 5 of 78 cows were not pregnant in the fall following the rut, 1 of which was lactating, compared to 73 cows

determined to be pregnant; therefore little comparison could be made to determine the effect of cow condition on pregnancy rates. However, the average percent fat during fall was higher for pregnant/non-lactating cows (12%) than non-pregnant/non-lactating cows (8%) and pregnant/lactating cows (8%) than the 1 non-pregnant/lactating cow (4%). Differences between these values are small, making it difficult to determine if nutrition affected pregnancy rates in this study.

If a cow is able to reach an adequate nutritional level before the breeding season, regardless of lactation status, she is likely to become pregnant. Cook et al. (2004) found that confined and tame elk showed a threshold of condition of about 9% body fat below which the probability of pregnancy rapidly declined. If nutrition was high enough to allow lactating and non-lactating cows to reach such a threshold, then the effects of lactation may be insignificant in influencing pregnancy rates. In this study, percent fat was measured during the late fall, which did not allow me to compare cows from this study to the 9% threshold, that was determined by Cook et al. (2004) during the rut. However, during the fall, there were 38 cows pregnant and lactating and 35 cows pregnant and not lactating which may suggest that lactation had little influence on pregnancy rates in elk in this study. Nutrition was likely high enough to overcome any potential effects of lactation on pregnancy rates in these study areas.

Influence of cow condition on calf survival

I found no evidence that cow condition affected calf survival in northeast Oregon during this study (i.e. no support for hypothesis 4); however, these results are preliminary and more data over more years are needed to truly investigate the effects

of cow condition on calf survival. Because of small sample sizes and low precision of estimates, I did not find evidence for an effect of cow age, spring fat, or spring cow mass on survival rates of their calves. Ongoing research will provide larger sample sizes (>18) over more years which will increase precision of estimates to test this hypothesis. In addition, I did not find an indirect link between cow condition and birth date and birth weight of calves which had an effect on calf survival. The analyses performed in this thesis that examined the effects of cow condition on calf survival were inconclusive; however, they provide a possible protocol by which the final data sets can be analyzed to test this hypothesis.

Additive versus compensatory mortality

Whether predation was mainly compensatory or additive could not be fully addressed. Although the removal of predators could decrease predation on elk calves, it is unknown if the population will have higher survival and recruitment. Bartmann et al. (1992) tested for compensatory mortality in mule deer fawns (*Odocoileus hemionous hemionus*) and found that there was no change in fawn survival after coyote removal. Although the removal of coyotes resulted in less predation, starvation mortalities increased suggesting that there was compensatory mortality after coyote removal (Bartmann et al. 1992). In contrast, Kunkel and Pletscher (1999) suggested that predation was more additive than compensatory in Glacier National Park, because they found that annual deer survival rates decreased when predation rates by wolves (*Canis lupus*) and cougars increased. Prime-aged and healthy deer, elk, and moose were also readily killed by cougars and wolves (Kunkel and Pletscher 1999). There were no differences in age or femur marrow fat for white-

tailed deer (*Odocoileus virginianus*) killed by coyotes and those of road-killed deer in southwestern Nova Scotia (Patterson and Messier 2003). Although Patterson and Messier (2003) suggest that mortality may be additive based on their results, they point out that no manipulative experiment was done to verify their speculations. Variation in winter severity, relative density, and density of alternate prey may have influenced coyote selection of deer based on age or condition (Patterson and Messier 2003). With regard to elk calves, Singer et al. (1997) state that "...summer mortality of calves due to predation was partially compensatory but severe environmental conditions produced largely additive components to both summer (increased predation) and winter (increased malnutrition) mortality". Such variation in wild ungulates from year to year suggests the importance of long-term survival studies.

The main proximate cause of elk calf mortality in this study was from cougars. Cougars most often select the weaker prey, thus the most vulnerable (Kunkel et al. 1999), but are capable of killing healthy elk (Kunkel and Pletscher 1999), suggesting that predation mortality is not completely compensatory. Although some literature suggests that calf survival is highly influenced by the condition of the mother (Clutton-Brock et. 1987, Bartmann et al. 1992, Cameron et al. 1993, Cook et al. 2004), which may result in compensatory mortality by predisposing elk calves to predation, cougars do kill healthy elk calves and adults. The true effects of predation on elk population dynamics in northeastern Oregon could not be determined from this study since this study did not involve manipulation (i.e. removal of cougars) over a long period of time.

CHAPTER 3

DOES PREDATION RISK INFLUENCE BIRTH-SITE SELECTION BY ROCKY MOUNTAIN ELK?

Spencer N. Rearden, Robert G. Anthony, and Bruce K. Johnson

Introduction

Selection of habitat by ungulates at parturition can be influenced by the risk of predation (Alldredge et al. 1991 [pronghorn, *Antilocapra americana*], Barten et al. 2001 [caribou, *Rangifer tarandus*], Bergerud et al. 1984 [caribou], Bowyer et al. 1999 [Alaskan moose, *Alces alces gigas*], Rachlow and Bowyer 1998 [Dall's sheep, *Ovis dalli dalli*]). At parturition, a new-born ungulate is highly vulnerable to predation, thus the importance of selecting proper concealment by the mother is magnified in order to raise her young successfully. In addition to predator risk, ungulates are also constrained to selecting birth sites based on forage availability and quality to satisfy the high nutritional demands of lactation (Barten et al. 2001, Bowyer et al. 1998, 1999, Kohlmann et al. 1996, Nicholson et al. 1997) and/or reduce the time needed to feed and increase time to tend to young. When the risk of predation increases along with forage quality, a tradeoff between the two must occur (Lima and Dill 1990). Thus, female ungulates are faced with the need to select birth sites within easy access to forage and avoid predation on their young during and shortly after parturition.

Female moose made tradeoffs between food and the risk of predation when selecting birth sites, as birth sites differed from random sites in forage and visibility (Bowyer et al. 1999). Visibility was likely related to the cow's ability to see a predator before the predator was aware of her and her calf (Bowyer et al. 1999). Bowyer et al. (1999) also found that visibility was inversely related to abundance of forage, and the risk of predation varied directly with food abundance. Because moose remain at or near the birth site for several weeks, forage was highly influential in birth-site selection compared to other ungulates. In contrast, female caribou with

neonates may have reduced the risk of predation without subjecting themselves to huge nutritional costs (Barten et al. 2001). There was no viable model for explaining habitat selection in minimizing predation and maximizing foraging with black-tailed deer (*Odocoileus hemionus columbianus*) neonates in California (Bowyer et al. 1998). Black-tailed deer neonates were seen with their mothers and other adult deer foraging in meadows, and they did not stay near the birth site (Bowyer et al. 1998). The amount of edge, amount of non-timber, and average slope best explained birth-site selection by black-tailed deer in southern Oregon (Pamplin 2003). Does tended to choose birth sites with more edge, non-timber, and flatter slopes (Pamplin 2003). Pamplin (2003) suggested that selection for amount of edge and non-timber implied that does foraged in open areas to support high energy demands during lactation.

Elk (*Cervus elaphus*) are herding animals and within a day of giving birth, a cow may join other cows in the vicinity of the birth site (Harper et al. 1967) and visit the calf periodically (Geist 1982). Within a week, cows and calves join other cows and calves (Geist 1982). Like black-tailed deer, elk leave the birth site soon after parturition. The literature on birth-site selection by elk are limited and mixed. Some suggest elk are selective on where to calve (Altmann 1952, Anderson 1954), while others found no apparent selection (Stevens 1966, Harper et al. 1967). In Oregon, Roosevelt elk (*C. e. roosevelti*) used benches, stream bottoms, and areas of gentle terrain for calving (Harper 1971). On Afognak Island, Alaska, where there are brown bears (*Ursus arctos*), cow elk used treeless areas on open grassy slopes for calving (Troyer 1960). Rocky Mountain elk (*C. e. nelsoni*) have been found to calve in ecotones between sagebrush and conifer forests (Johnson 1951, Picton 1960), and

newborn elk were often found a short distance into the forest edge in southwestern Montana (Johnson 1951). In the Sawtooth Mountains of Idaho, Rocky Mountain elk calved in areas with overstory ranging from 20–60% cover and on slopes of about 35% (Phillips 1974). The preference for certain slope and aspect is probably more of a function of availability (Skovlin et al. 2002). Altmann (1952) found that southerly exposures were used more frequently in the Jackson Hole area of Wyoming, and Phillips (1974) found that northwesterly exposures were used in the Sawtooth Mountains of Idaho during calving for Rocky Mountain elk.

The purpose of this study was to determine if predation risk affected birth-site selection of Rocky Mountain elk cows. Cow elk may be selecting birth sites based on the amount and type of cover (horizontal and vertical) that conceals their young from predators. If the risk of predation has a positive relationship with the amount of forage and cow elk are attempting to reduce predation risk, then cow elk should choose birth sites that will have less forage. The following hypotheses were developed to understand if birth-site selection was affected by predation risk: (1) Birth sites have more horizontal and vertical cover than paired random sites (microhabitat scale), (2) the areas surrounding birth sites have more canopy cover and less forest edge than random sites (macrohabitat scale), (3) predation sites have less horizontal and vertical cover than paired random sites (microhabitat scale), and (4) the areas surrounding predation sites have less canopy cover and more forest edge than random sites (macrohabitat scale). Vegetation is often distributed heterogeneously across landscapes due to forest overstory canopy cover (Cook et al. 2002). If results suggest that cow elk chose birth sites based on cover rather than

forage (i.e. less canopy, less overhead density of vegetation, more forest edge within the surrounding areas, and closer to forest edge), then there would be evidence that predation risk influenced birth-site selection by cow elk. The specific objectives of my study were to: (1) Describe differences between birth and random sites and (2) describe differences between predation and random sites. In addition, I was interested in comparing the characteristics of birth to predation sites. In northeastern Oregon, predation risk comes from black bears (*Ursus americanus*), coyotes (*Canis latrans*), and cougars (*Felis concolor*). I found that predation on elk calves by black bears and cougars was common in this study area (see chapter 2). Cougar numbers are usually the lowest among all three predators, but they specialize in preying upon deer (*Odocoileus* spp.) and elk (Hornocker 1970).

Study Site

Portions of two adjacent wildlife management units (WMUs; Wenaha and Sled Springs) separated by the Grande Ronde River were selected in northeast Oregon as the study site (Figure 3.1). The study site is at the northernmost reach of the Blue Mountains. Ponderosa pine (*Pinus ponderosa*) dominates the lower elevations while subalpine fir (*Abies lasiocarpa*) dominates the highest elevations. In the intermediate elevations, mixed stands of ponderosa pine, lodgepole pine, (*Pinus contorta*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), Douglas fir (*Pseudotsuga menziesii*), and Engleman spruce (*Picea engelmannii*) can be found. Sled Springs varies in elevation from about 700-1350 meters and Wenaha varies in elevation from about 700-1600 meters. Climate is characterized by cold, snowy winters and warm, dry summers. Annual precipitation in northeastern Oregon ranges

from 43-63 cm with most falling as snow in winter and rain in spring and autumn with extreme dryness mid to late summer. Each site has both winter and summer elk ranges. The Sled Springs Wildlife Management Unit (WMU) has a winter range that encompasses approximately 70 km² in the southwest portion of the WMU with a winter population of approximately 400 elk. The summer range is about 300 km². The majority of the Sled Springs winter range was owned and managed by Boise Cascade Corporation. The Wenaha WMU has a winter range that encompasses about 100 km² in the eastern portion of the WMU with a winter population of approximately 600 elk. The summer range includes about 400 km². This area is comprised mostly of public lands, which is mostly managed by the U. S. Forest Service. The Oregon Department of Fish and Wildlife (ODFW) manages the Wenaha Wildlife Management area in the eastern part of the Wenaha WMU.

Methods

Personnel of Oregon Department of Fish and Wildlife (ODFW) and National Council for Air and Stream Improvement (NCASI) captured cow elk in March of 2002, 2003, and 2004 with the use of a helicopter and dart gun. Each cow's pregnancy status was determined with ultrasound. Cow elk that were pregnant had vaginal implant transmitters inserted (VIT; ATS, Isanti, Minnesota, USA) (Bowman and Jacobson 1998) and were collared with radio transmitters (Telonics, Mesa, Arizona, USA). The radio collars were used to locate cows because they produced a much stronger signal than the VITs.

Cow elk were located before and during the calving seasons using aerial telemetry from a fixed-wing aircraft. Once a cow was located, we checked on the

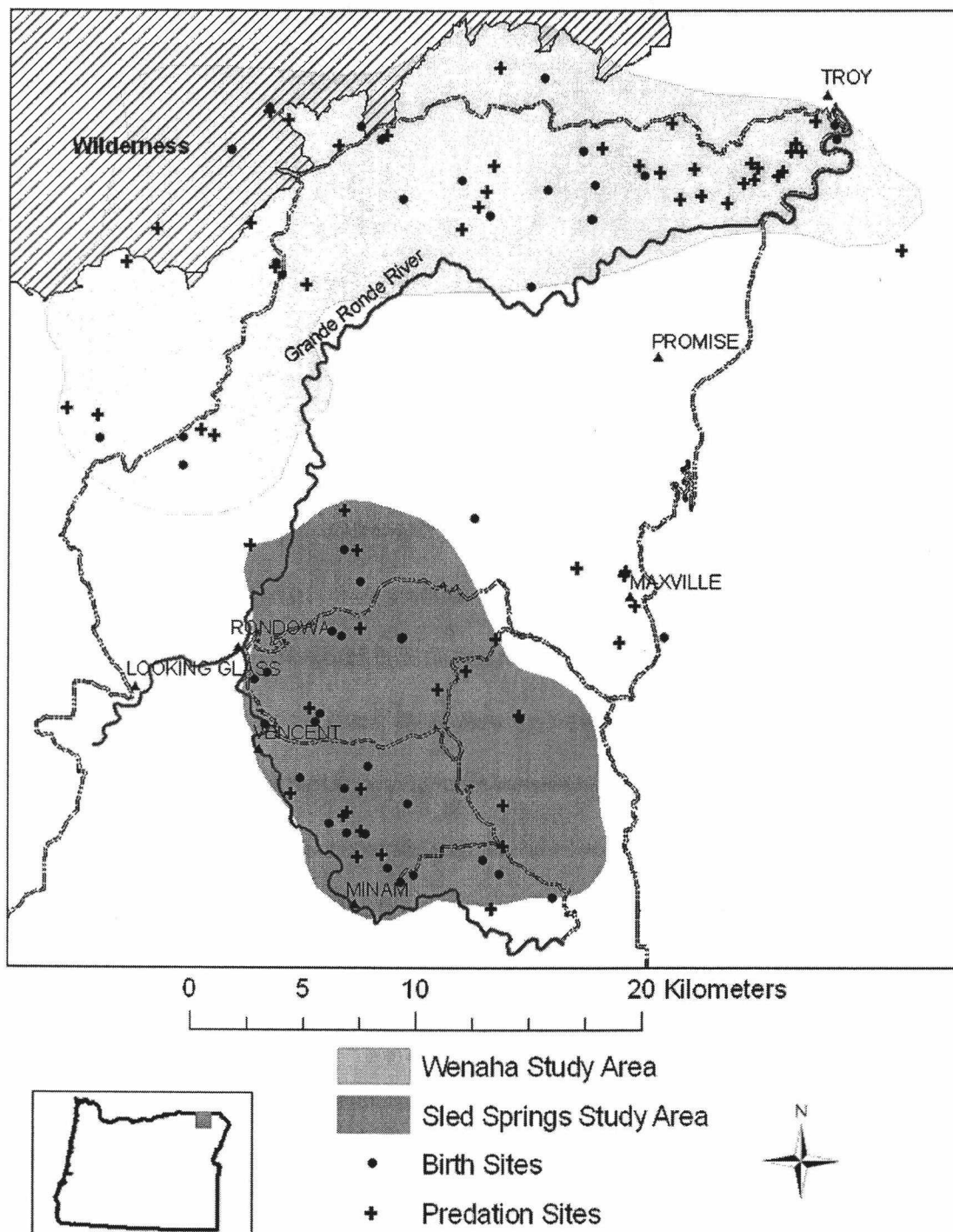


Figure 3.1. Study site with birth and predation sites in northeastern Oregon within the Wenaha and Sled Springs wildlife management units in northeastern Oregon. Boundaries of study areas defined by home range kernel estimator using an 80% kernel from locations of 1,114 radio-collared calves and 2,201 radio-collared cows from December 2001 to March 2004.

status of the VIT. The temperature-sensitive VITs double in pulse rate when shed from the cow indicating a birth. A ground crew then located the VIT and radio-collared cow, which helped narrow our search for newborn calves and birth sites. Birth sites were usually at or near the location of the shed VIT. The exact location of birth sites was considered to be an area that had disturbed vegetation in a circular pattern. Often, signs of afterbirth and blood were found at the birth sites. If a newborn calf and/or birth site could not be found in the vicinity of the VIT, we concluded that the VIT was shed before birth and these sites were not included in the measurements. Areas that contained birth sites were flagged and the location recorded with a global positioning system (GPS) so that I could return to take measurements after the cow and calf had left (Figure 3.1).

Calves were captured by locating the VITs, ground searching, and with the use of a helicopter and net gun. Each calf was fitted with an expandable radio-transmitting collar that had a mortality sensor integrated into the circuitry that was set to accelerate in pulse after 6 hours of no movement (Telonics, Mesa, Arizona, USA). Once collared, elk calves were monitored using telemetry from a fixed-wing aircraft to determine their status. Calf collars in mortality mode were reached by foot. If the investigator(s) found elk calf remains and determined the cause of death to be predator-related, the investigator(s) marked the most likely spot where the calf was killed with flagging (Figure 3.1). The location was also recorded with a GPS. Predation sites were determined by careful observations and searched for hair, disturbed soil, and blood.

Microhabitat measurements

I chose 2 random sites that were within 200 to 400 m and at random directions from the birth/predation sites to describe birth-site selection and areas of predation at the microhabitat scale. Each time I measured a birth or predation site, I measured the paired random sites the same day. At each birth, predation, and random site, I took horizontal and vertical measurements.

A cover pole (CP) that was 2 m in height and divided into 20-cm segments was used to measure concealment (Griffith and Youtie 1988). Percent cover was determined by recording the proportion of segments that were covered by at least 50% vegetation or land features from four cardinal directions at a distance of 10 m and at an eye level of 1.5 meters. I also estimated "percent view" at 25 m and 50 m (View25 and View50). Percent view is the estimated number of 30-degree increments out of 360 degrees that does not conceal a cougar-sized animal out to an estimated 25 m and 50 m from a standing position. I estimated vertical cover (overhead density of vegetation; Dens) with a spherical densitometer by averaging 4 measurements taken at the cardinal directions (Lemmon 1957). I also obtained slope and aspect for each site with a geographic information system (GIS; ArcView, Redlands, CA) using a 10 m digital elevation model (DEM).

Macrohabitat measurements

To understand habitat use by maternal females, sampling at >1 spatial scale may be necessary (Rachlow and Bowyer 1998). I investigated birth-site selection and areas of predation on a series of larger scales (macrohabitat) using GIS-derived data (ArcView and ArcGIS, ESRI, Redlands, CA). I generated 80 random points within

the study area for comparison to the birth and predation sites. I generated a 1,000 m buffer around the birth and predation sites and used the outermost buffers as a basis to draw my boundary. Within the boundary is where I generated my random points. Both birth and predation sites were integrated in the overall area so I considered the area within the boundary as habitat available to elk and predators .

At each birth, predation, and random site, I examined landscape attributes within 3 circular areas with a radius of 250, 500, and 1,000 m centered on each site, similar to Pamplin's (2003) analysis on birth-site selection of black-tailed deer. These scales were selected because they likely incorporated characteristics of birth and predation sites. Vore and Schmidt (2001) found that cow elk from parturition to 4 days after, cow elk in northwest Montana averaged 240 m from the birth site and had average daily movements of 305 m/d. As cows moved to their calving areas, the mean distance from eventual birth sites during the 4 days prior to parturition was 1,554 m (Vore and Schmidt 2001). Not including maternal females within 4 days of parturition, average daily movements of cow elk was 712 m/d (Vore and Schmidt 2001).

Using GIS (ArcGIS, ESRI, Redlands, CA), I classified orthophotos to 2 classes so that I could obtain a layer that described each pixel as either a tree (value = 1) or non-tree (value = 0). I averaged the pixel values within each circular plot to compute average percent canopy cover (Canopy). To obtain the amount of edge (Edge) within each circular plot, I used the nearest neighbor function to dissolve small areas composed of pixels that were classified as tree or non-tree into what the surrounding pixels were. This was done to eliminate small areas that had a high edge

to area ratio. I then created edge where the tree and non-tree pixels met and took the total number of pixels that described edge within each circular plot. Using the same data layer, I also obtained the distance to the nearest edge (Dist. edge) from each birth and predation site. Finally, slope and aspect were obtained from a digital elevation model (DEM) for the 80 random sites. Aspect was transformed using the formula from Roberts and Cooper (1989):

$$ASP = \frac{1 - \cos(\text{aspect} - 30)}{2}$$

This transformation assigns the lowest values to land oriented in a north-northeast direction, the coolest and wettest orientation and highest values for south-southwest slopes in Utah. I considered this transformation sufficient for Northeastern Oregon. I used GIS to characterize all 49 birth sites and 60 of the 62 predation sites. Two of the predation sites were outliers from the main study area and so were censored for all macrohabitat analyses because I did not want to generate random points between all other points and the two censored points, where we had no birth and predation sites.

Statistical analyses

I conducted 6 sets of analyses: Birth and predation sites compared to random sites at the microhabitat and macrohabitat scales and birth sites compared to predation sites at the microhabitat and macrohabitat scales to determine which variable(s) best explained birth-site selection and predation sites at multiple scales. Each model tested was ranked by the small sample size bias-corrected form of Akaike's Information Criterion (AIC_c ; Burnham and Anderson 1998). The best model had the lowest AIC_c value, and any model within 2 AIC_c values of the best model was considered competing (Burnham and Anderson 1998) and therefore taken into

consideration.

Comparisons of birth and predation sites to paired-random sites on the microhabitat scale were done with matched-paired logistic regression (Hosmer and Lemeshow 2000; S-plus 6.1). For each birth and predation site, 1 of 2 matched-random sites was randomly chosen for comparison. This process was repeated 10 times for each model and the coefficients, standard errors, and deviances were then averaged for accuracy. Comparisons of birth and predation sites to random sites on the macrohabitat scale and comparisons of birth sites to predation sites on both the microhabitat and macrohabitat scale were done using logistic regression (Hosmer and Lemeshow 2000; S-plus 6.1). The same random sites were used to compare to both the birth and predation sites. I only used predation sites from calves that died prior to August 25 ($n = 48$), the date at which I found the most dramatic change in survival rates (*see* chapter 2) to compare to all birth sites. Using these predation sites for comparison to birth sites helped ensure that I was using predation sites that are within the spring and summer elk ranges, where birth sites were found. In all macrohabitat analyses, distance to edge (Dist. edge), slope, and aspect were the same values for each scale since these variables were derived from the exact location of birth, predation, and random sites. The effects of each variable were interpreted from lowest AIC_c models.

Results

During the summers and falls of 2002-2004, I measured 49 birth sites and 62 predation sites along with 2 paired random sites for the microhabitat analyses. The majority of the predation was due to cougars. I measured 39 cougar, 18 black bear,

and 5 unknown predator sites.

Birth sites vs. random sites at the microhabitat scale

The best model for birth sites compared to random sites included cover pole (CP) and densiometer (Dens) measurements at the microhabitat scale (Table 3.1). Interpretation from this model indicated that birth sites had less horizontal cover (0.97 times the odds; 95% CI = 0.94 to 0.99), as measured from a cover pole at 10 m (CP), and more overhead density of vegetation (1.022 times the odds; 95% CI = 1.005 to 1.040) as measured from a densiometer (Dens) than paired random sites. Both View25 and View50, also measures of horizontal cover, explained similar differences as CP due to high correlation between them (CP and View25; $r = 0.72$, CP and View50; $r = 0.65$). View25 and view50 also indicated that birth sites had less horizontal cover than paired random sites as measured from view25 (0.97 times the odds; 95% CI = 0.96 to 0.99) and view50 (0.978 times the odds; 95% CI = 0.959 to 0.997). Birth sites on average had 13.1+% less horizontal cover and 21.1% more overhead density of vegetation than random sites (Figure 3.2a; Appendix C). Two models were competing: {CP + Dens + Slope} and {CP + Dens + Aspect}. The addition of slope or aspect to the best model decreased the AIC_c value ~ 2.0 ; therefore neither slope nor aspect explained differences between birth and random sites (Slope = 1.03 times the odds, 95% CI = 0.93 to 1.14; Aspect = 1.13 times the odds, 95% CI = 0.16 to 8.20).

Table 3.1. Model selection results at the microhabitat scale comparing 49 birth sites to 49 random sites. Data from northeastern Oregon, 2002-2004.

Model	AICc	Delta AICc	AICc weight	K	Deviance
CP+Dens	53.911	0.000	0.474	3	47.377
CP+Dens+Slope	55.742	1.832	0.190	4	46.833
CP+Dens+Aspect	55.986	2.075	0.168	4	47.077
CP+Dens+Slope+Aspect	57.865	3.954	0.066	5	46.469
CP	59.134	5.224	0.035	2	54.874
CP+Aspect	60.929	7.019	0.014	3	54.396
CP+Slope	60.968	7.057	0.014	3	54.435
Dens	61.004	7.093	0.014	2	56.743
Slope+Dens+Aspect+View25	61.683	7.772	0.010	5	50.287
CP+Slope+Aspect	62.816	8.906	0.006	4	53.907
View25	62.880	8.969	0.005	2	58.619
Slope+Dens+Aspect+View50	63.828	9.917	0.003	5	52.433
View50	65.695	11.784	0.001	2	61.434
Null	70.014	16.103	0.000	1	67.928
Aspect	71.120	17.210	0.000	2	66.859
Slope	71.754	17.844	0.000	2	67.494

Figure 3.2a

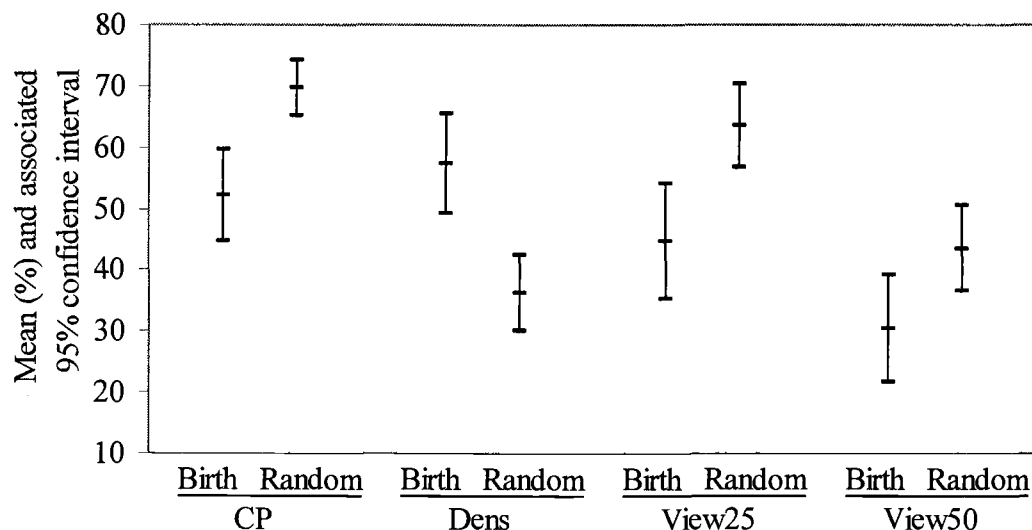


Figure 3.2b

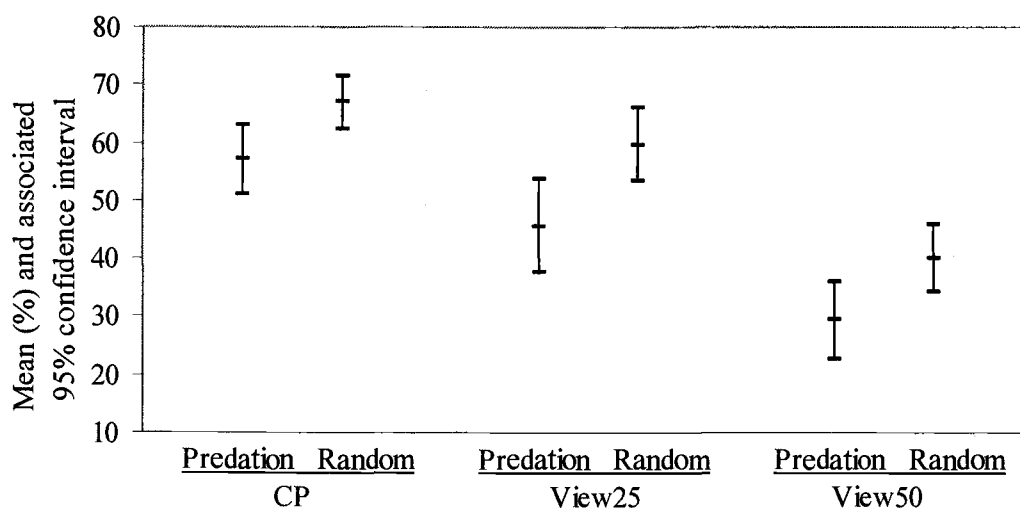


Figure 3.2. Means with associated 95% confidence intervals for variables that explained differences between birth and random sites (Figure 3.2a; $n = 49$ birth sites and 98 random sites) and predation and random sites (Figure 3.2b; $n = 62$ predation sites and 124 random sites) at the microhabitat scale. Variable definitions: CP = horizontal cover measured from a cover pole, Dens = overhead density of vegetation, View25 = horizontal cover measured as percent view at 25 m, View50 = horizontal cover measured as percent view at 50 m.

Predation sites vs. random sites at the microhabitat scale

At the microhabitat scale, the best model for predation sites compared to random sites included a single variable, View25 (Table 3.2). This model indicated that predation sites had less horizontal cover than random sites, as measured by percent view at 25 m. There were 9 competing models, in which all but 2 models included View25. Only measures of horizontal cover (View25, View50, and cover pole (CP)) explained differences between predation and paired random sites with predation sites having less horizontal cover than random sites (View25 = 0.985 times the odds, 95% CI = 0.973 to 0.998; View50 = 0.985 times the odds, 95% CI = 0.970 to 0.999; CP = 0.983, 95% CI = 0.967 to 0.999). Predation sites on average had less horizontal cover than random sites by 9.9+% (Figure 3.2b; Appendix D). Although slope, aspect, and densiometer (Dens) appeared in competing models, they were not significant because 95% confidence intervals overlapped 1 (Slope = 1.03 times the odds, 95% CI = 0.97 to 1.10; Aspect = 0.38 times the odds, 95% CI = 0.08 to 1.94; Dens = 0.99 times the odds, 95% CI = 0.98 to 1.01).

Birth sites vs. random sites at the macrohabitat scale

At the macrohabitat scale, the best model for birth sites compared to random sites included canopy and slope at the scale of a 500 m-radius circle (Table 3.3). This model indicated that birth sites had less canopy cover (0.05 times the odds, 95% CI = 0.01 to 0.34) and were on gentler slopes (0.951 times the odds, 95% CI = 0.907 to 0.998) than random sites. Birth sites on average had 11.2% less canopy cover and had 3.3% less slope than random sites (Figure 3.3; Appendix E). The 3 models competing were similar to the best model. Each competing model was at the scale of

Table 3.2. Model selection results at the microhabitat scale comparing 62 predation sites to 62 random sites. Data from northeastern Oregon, 2002-2004.

Model	AICc	Delta AICc	AICc weight	K	Deviance
View25	83.802	0.000	0.140	2	79.599
View25+Slope	84.488	0.685	0.100	3	78.074
View25+Aspect	84.523	0.721	0.098	3	78.110
CP	84.740	0.937	0.088	2	80.536
View25+CP	84.886	1.083	0.082	3	78.472
View25+Dens	85.004	1.202	0.077	3	78.590
View50	85.058	1.255	0.075	2	80.854
View25+Slope+Aspect	85.226	1.424	0.069	4	76.524
View25+Aspect+Dens	85.236	1.433	0.069	4	76.534
View25+Slope+Dens	85.597	1.794	0.057	4	76.895
View25+Slope+Aspect+CP	86.651	2.849	0.034	5	75.580
View25+Slope+Aspect+Dens	87.596	3.793	0.021	5	76.524
Aspect	87.850	4.047	0.019	2	83.646
Slope+Dens+Aspect+View50	87.920	4.117	0.018	5	76.848
Null	88.017	4.214	0.017	1	85.950
Slope+Dens+Aspect+CP	88.532	4.730	0.013	5	77.461
Slope	88.929	5.126	0.011	2	84.725
Slope+Aspect+CP+Dens+View25 +View50	89.825	6.023	0.007	7	73.751
Dens	89.934	6.131	0.007	2	85.731

Table 3.3. Model selection results at the macrohabitat scale comparing 49 birth sites to 80 random sites. Data from northeastern Oregon, 2002-2004.

Model	AICc	Delta AICc	AICc weight	K	Deviance
500 / Canopy+Slope	163.027	0.000	0.244	3	156.835
500 / Canopy+Slope+Dist.edge+Edge	163.496	0.469	0.193	5	153.009
500 / Canopy+Slope+Dist.edge	163.624	0.597	0.181	4	155.302
500 / Canopy+Slope+Edge	164.224	1.197	0.134	4	155.901
500 / Canopy	165.581	2.554	0.068	2	161.486
500 / Canopy+Dist.edge	166.647	3.619	0.040	3	160.455
500 / Edge+Canopy	166.814	3.786	0.037	3	160.622
500 / Edge+Canopy+Dist.edge	166.898	3.871	0.035	4	158.575
250 / Canopy	168.435	5.408	0.016	2	164.340
250 / Canopy+Dist.edge	169.366	6.339	0.010	3	163.174
250 / Edge+Canopy	170.517	7.490	0.006	3	164.325
1000 / Edge+Canopy+Dist.edge	170.714	7.687	0.005	4	162.392
Slope	170.880	7.853	0.005	2	166.785
1000 / Canopy+Dist.edge	171.176	8.149	0.004	3	164.984
1000 / Canopy	171.240	8.213	0.004	2	167.145
Dist.edge	172.149	9.121	0.003	2	168.053
1000 / Edge+Canopy	172.259	9.232	0.002	3	166.067
1000 / Edge+Dist.edge	172.273	9.246	0.002	3	166.081
Slope+Aspect	172.951	9.924	0.002	3	166.759
Null	173.340	10.313	0.001	1	171.309
500 / Edge+Dist.edge	173.535	10.508	0.001	3	167.343
250 / Edge+Dist.edge	174.233	11.206	0.001	3	168.041
250 / Edge	174.531	11.504	0.001	2	170.436
1000 / Edge	174.925	11.897	0.001	2	170.829
Aspect	175.240	12.212	0.001	2	171.144
500 / Edge	175.397	12.370	0.001	2	171.302
250 / Edge+Canopy+Dist.edge	176.376	13.349	0.000	4	168.053

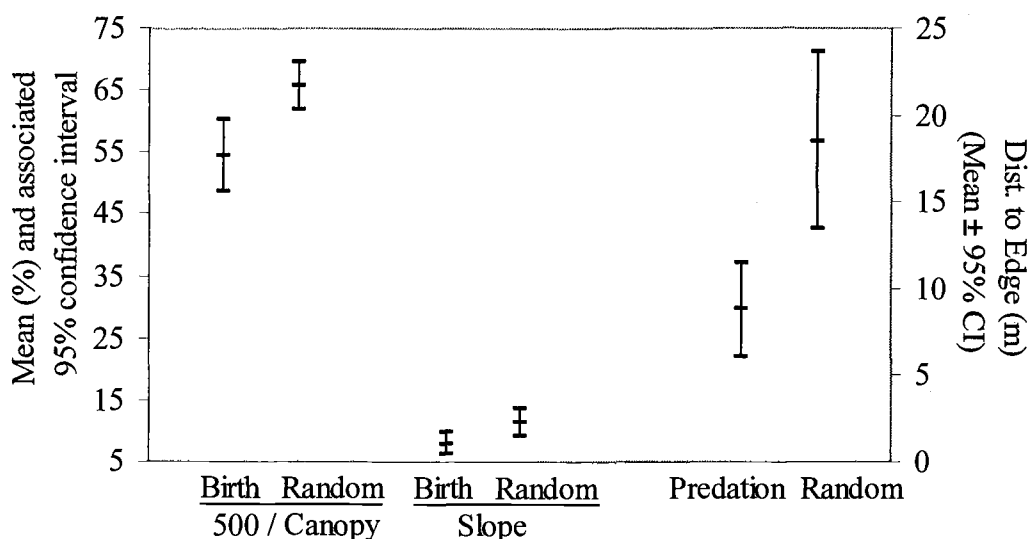


Figure 3.3. Means with associated 95% confidence intervals for variables that explained differences between birth and random sites and predation and random sites at the macrohabitat scale ($n = 49$ birth sites, 60 predation sites, and 80 random sites). Variable definitions: 500 / Canopy = canopy cover at the scale of a 500 m radius, Dist. to Edge = distance to nearest edge.

a 500 m-radius circle and included slope and canopy. The addition of variables edge and distance to edge increased the AIC_c values indicating little support for these 2 variables. Model {Edge + Canopy + Dist.edge + Slope} indicated that edge and distance to edge have little support in explaining differences between birth and random sites (Edge = 0.99998 times the odds, 95% CI = 0.99995 to 1.00001; Dist.edge = 0.980 times the odds, 95% CI = 0.956 to 1.004). The addition of aspect to the variable slope (Slope + Aspect model) increased the AIC_c value compared to the {Slope} model. From the {Slope + Aspect} model, aspect was insignificant due to the 95% CI overlapping over 1 (Aspect = 0.92, 95% CI = 0.32 to 2.66). None of the models at the 250 m and 1000 m scales had much support, but most models at these scales were better than the null mode (Table 3.3).

Predation sites vs. random sites at the macrohabitat scale

At the macrohabitat scale, the best model for predation sites compared to random sites included edge, canopy, and distance to edge at the scale of a 1,000 m-radius circle (Table 3.4). In the best model, distance to edge was significant while edge and canopy had 95% confidence intervals that overlapped 1 (Dist.edge = 0.96 times the odds, 95% CI = 0.93 to 0.99; Edge = 0.999994 times the odds, 95% CI = 0.99 to 1.00; Canopy = 0.15 times the odds, 95% CI = 0.02 to 1.26). The distance to edge variable indicated that predation sites were closer to edges than random sites. On average predation sites were 10 m closer to the nearest edge than random sites (Figure 3.3; Appendix F). All competing models included the variable distance to edge. The top 4 models were all very similar to the best model in that they consisted of some of the same variables at a 1,000 m-radius circle. The next 2 competing models were {Canopy + Dist.edge}; 1 at a 500 m-radius circle and 1 at a 250 m-radius circle. The 6th competing model was similar to the best model except that it included slope and was also at the 1,000 m-radius scale. The 7th competing model, which is also at the 1,000 m-radius scale, was different from the best model in that slope was included and edge was excluded from the model. The 8th and 9th competing models also were similar to the best model in that they included distance to edge. Since distance to edge has the same values at all levels of the macrohabitat scales, multiple scales (250, 500, and the 1,000 m-radius) were competing. Only the variable distance to edge helped explain differences between predation and random sites. Slope and aspect did not help explain differences between predation and random sites (Slope = 0.99 times the odds, 95% CI = 0.95 to 1.03; Aspect = 0.81, 95% CI = 0.30 to 2.12).

Table 3.4. Model selection results at the macrohabitat scale comparing 60 mortality sites to 80 random sites. Data from northeastern Oregon, 2002-2004.

Model	AICc	Delta AICc	AICc weight	K	Deviance
1000 / Edge+Canopy+Dist.edge	184.585	0.000	0.100	4	176.289
1000 / Canopy+Dist.edge	184.680	0.095	0.095	3	178.504
Dist.edge	184.770	0.185	0.091	2	180.683
1000 / Edge+Dist.edge	185.615	1.029	0.060	3	179.438
500 / Canopy+Dist.edge	185.626	1.041	0.059	3	179.450
250 / Canopy+Dist.edge	186.102	1.517	0.047	3	179.926
1000 / Edge+Canopy+Dist.edge +Slope	186.290	1.705	0.043	5	175.842
1000 / Canopy+Dist.edge+Slope	186.374	1.789	0.041	4	178.078
Dist.edge+Slope	186.475	1.889	0.039	3	180.298
1000 / Canopy+Dist.edge+Aspect	186.602	2.016	0.037	4	178.305
1000 / Edge+canopy+Dist.edge +Aspect	186.614	2.029	0.036	5	176.166
Dist.edge+Aspect	186.679	2.094	0.035	3	180.503
500 / Edge+Dist.edge	186.734	2.149	0.034	3	180.558
250 / Edge+Dist.edge	186.761	2.176	0.034	3	180.584
500 / Edge+Canopy+Dist.edge	187.247	2.662	0.026	4	178.951
1000 / Edge+Dist.edge+Slope	187.324	2.739	0.025	4	179.028
500 / Canopy+Dist.edge+Slope	187.336	2.751	0.025	4	179.040
500 / Canopy+Dist.edge+Aspect	187.589	3.004	0.022	4	179.293
1000 / Edge+Dist.edge+Aspect	187.615	3.030	0.022	4	179.319
250 / Canopy+Dist.edge+Slope	187.845	3.260	0.020	4	179.549
250 / Canopy+Dist.edge+Aspect	188.028	3.443	0.018	4	179.732
250 / Edge+Canopy+Dist.edge	188.221	3.636	0.016	4	179.925
500 / Edge+Dist.edge+Slope	188.449	3.864	0.014	4	180.153
250 / Edge+Dist.edge+Slope	188.525	3.940	0.014	4	180.229
500 / Edge+Dist.edge+Aspect	188.686	4.101	0.013	4	180.390
250 / Edge+Dist.edge+Aspect	188.702	4.117	0.013	4	180.406
1000 / Canopy	191.477	6.892	0.003	2	187.390
500 / Canopy	191.486	6.900	0.003	2	187.398
250 / Edge	191.870	7.285	0.003	2	187.783
250 / Canopy	192.166	7.581	0.002	2	188.078
250 / Edge+Canopy	192.701	8.116	0.002	3	186.525
Null	193.243	8.658	0.001	1	191.214
1000 / Edge+Canopy	193.315	8.730	0.001	3	187.139
500 / Edge+Canopy	193.446	8.861	0.001	3	187.270
500 / Edge	194.212	9.627	0.001	2	190.125
Aspect	195.219	10.633	0.000	2	191.131
Slope	195.254	10.669	0.000	2	191.167
1000 / Edge	195.301	10.716	0.000	2	191.214
Slope+Aspect	197.277	12.692	0.000	3	191.101

Birth sites vs. Predation sites at the microhabitat scale

At the microhabitat scale, the best model that explained differences between birth and predation sites was {CP + Dens + Slope} (Table 3.5). This model indicated that birth sites had slightly less horizontal cover (CP = 0.983 times the odds, 95% CI = 0.967 to 1.001), more overhead density of vegetation (Dens = 1.02 times the odds, 95% CI = 1.01 to 1.04) and were on gentler slopes (Slope = 0.96 times the odds, 95% CI = 0.91 to 1.01) than predation sites. However, only suggestive evidence exists for cover pole and slope in explaining differences due to the 95% confidence intervals slightly overlapping 1. Birth sites on average had 8% less horizontal cover, 19.6% more overhead density of vegetation, and 3.1% less slope than predation sites (Figure 3.4; Appendix G). The addition of both variables cover pole and slope to densiometer decreased the AIC_c value from models {Dens}, {CP + Dens}, and {CP + Slope}, which also suggested some evidence of an effect. The 6 competing models included CP or dens indicating similarities to the best model. The addition of aspect to the best model increased the AIC_c value. Interpretation of aspect from model {CP + Dens + Slope + Aspect} indicates that aspect did not explain differences between birth and predation sites (Aspect = 2.27 times the odds, 95% CI = 0.58 to 8.84).

Birth sites vs. Predation sites at the macrohabitat scale

At the macrohabitat scale, the best model for differences between birth and predation sites was {Edge + Dist.edge + Slope} at the 250 m-radius scale (Table 3.6). In the best model, edge and dist.edge had 95% confidence intervals that overlapped 1 while slope had 95% confidence intervals slightly overlapping 1 (Edge = 1.0000, 95% CI = 0.9999 to 1.0001; Dist.edge = 1.02, 95% CI = 0.98 to 1.06; Slope = 0.95,

Table 3.5. Model selection results at the microhabitat scale comparing 49 birth sites to 48 predation sites. Data from northeastern Oregon, 2002-2004.

Model	AICc	Delta AICc	AICc weight	K	Deviance
CP+Dens+Slope	127.710	0.000	0.203	4	119.275
CP+Dens	127.767	0.057	0.197	3	121.509
CP+Dens+Slope+Aspect	128.510	0.800	0.136	5	117.850
Dens	128.729	1.020	0.122	2	124.602
Dens+Slope	128.963	1.253	0.108	3	122.705
CP+Dens+Aspect	129.127	1.418	0.100	4	120.693
Dens+Slope+Aspect	130.152	2.442	0.060	4	121.717
Dens+Aspect	130.357	2.647	0.054	3	124.099
CP+Slope	135.557	7.848	0.004	3	129.299
CP	136.036	8.326	0.003	2	131.908
View50	136.278	8.568	0.003	2	132.150
Null	136.502	8.793	0.002	1	134.460
CP+Slope+Aspect	137.167	9.457	0.002	4	128.732
CP+View50	137.373	9.664	0.002	3	131.115
CP+Aspect	137.971	10.261	0.001	3	131.713
Slope+Aspect	138.079	10.369	0.001	3	131.821
View25	138.299	10.590	0.001	2	134.172
Aspect	138.514	10.804	0.001	2	134.386
Slope	138.570	10.860	0.001	2	134.442

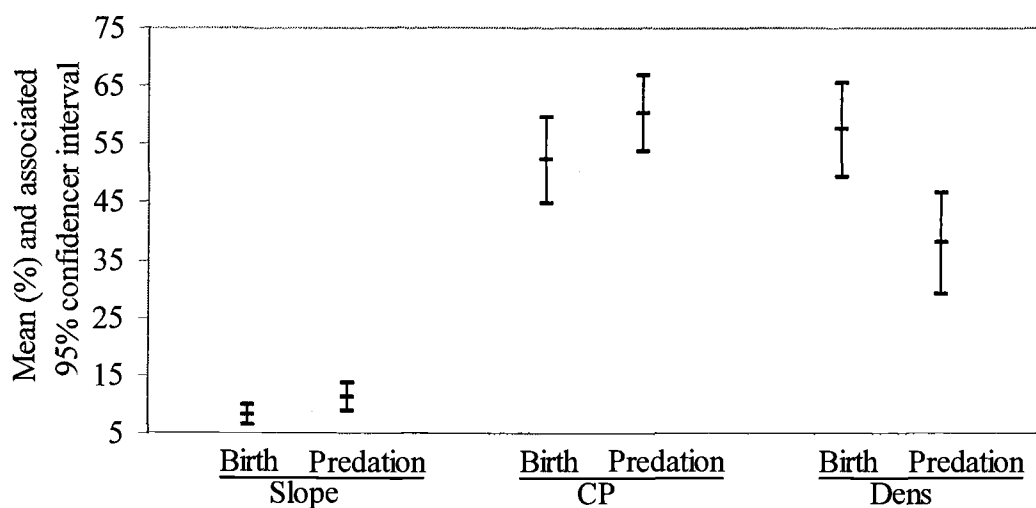


Figure 3.4. Means with associated 95% confidence intervals for variables that explained differences between birth and predation sites at the microhabitat and scale ($n = 49$ birth and 48 predation sites). Variable definitions: CP = horizontal cover measured from a cover pole, Dens = overhead density of vegetation.

95% CI = 0.89 to 1.00). Again, birth sites on average had 3.1% less slope than predation sites since slope has the same values at both microhabitat and macrohabitat scales (Figure 3.4; Appendix H). Interpretation of Canopy from model {Canopy + Dist.edge + Slope} at the 500 m-radius scale and Aspect from model {Edge + Dist.edge + Slope + Aspect} at the 250 m-radius scale indicated that these two variables also did not explain differences between birth and predation sites (Canopy = 0.24 times the odds, 95% CI = 0.03 to 1.97; Aspect = 1.34 times the odds, 95% CI = 0.39 to 4.66). The best model was only 2.6 AIC_c values from the null model and most of the models had higher AIC_c values than the null. This was an indication that the variables explained very little in terms of differences between birth and predation sites, and that birth and predation sites were similar at the macrohabitat scale.

Table 3.6. Model selection results at the macrohabitat scale comparing 49 birth sites to 48 predation sites. Data from northeastern Oregon, 2002-2004.

Model	AICc	Delta AICc	AICc weight	K	Deviance
250 / Edge+Dist.edge+Slope	133.951	0.000	0.070	3	127.693
Slope	134.312	0.361	0.059	2	130.184
Dist.edge+Slope	134.579	0.628	0.051	3	128.321
500 / Canopy+Dist.edge+Slope	134.789	0.838	0.046	4	126.354
250 / Edge+Slope	134.795	0.845	0.046	3	128.537
500 / Edge+Slope	134.806	0.855	0.046	3	128.548
250 / Canopy+Dist.edge+Slope	134.949	0.999	0.043	4	126.514
500 / Canopy+Slope	135.295	1.345	0.036	3	129.037
500 / Canopy+Dist.edge	135.558	1.607	0.031	3	129.300
Dist.edge	135.690	1.739	0.029	2	131.562
250 / Canopy+Dist.edge	135.765	1.815	0.028	3	129.507
250 / Canopy+Slope	135.766	1.816	0.028	3	129.508
1000 / Edge+Slope	135.867	1.917	0.027	3	129.609
250 / Edge+Dist.edge+Slope +Aspect	135.909	1.958	0.026	4	127.474
500 / Edge+Dist.edge+Slope	136.028	2.078	0.025	4	127.593
Slope+Aspect	136.342	2.391	0.021	3	130.084
500 / Edge+Canopy+Dist.edge +Slope	136.381	2.430	0.021	5	125.721
Null	136.502	2.552	0.020	1	134.460
1000 / Edge+Dist.edge+Slope	136.614	2.663	0.019	4	128.179
250 / Edge+Canopy+Dist.edge +Slope	136.623	2.673	0.018	5	125.964
1000 / Canopy+Dist.edge+Slope	136.751	2.800	0.017	4	128.316
500 / Canopy+Dist.edge+Slope +Aspect	136.773	2.822	0.017	5	126.113
250 / Edge+Slope+Aspect	136.818	2.867	0.017	4	128.383
500 / Edge+Slope+Aspect	136.822	2.871	0.017	4	128.387
250 / Canopy+Dist.edge+Slope +Aspect	137.008	3.057	0.015	5	126.349
500 / Edge	137.281	3.330	0.013	2	133.153
500 / Canopy+Slope+Aspect	137.370	3.420	0.013	4	128.936
500 / Canopy	137.390	3.439	0.013	2	133.262
500 / Edge+Canopy+Dist.edge	137.436	3.486	0.012	4	129.002
500 / Edge+Dist.edge	137.456	3.505	0.012	3	131.198
250 / Edge	137.533	3.582	0.012	2	133.405
250 / Edge+Dist.edge	137.660	3.710	0.011	3	131.402
1000 / Edge+Dist.edge	137.728	3.778	0.011	3	131.470
1000 / Canopy+Dist.edge	137.818	3.868	0.010	3	131.560
250 / Edge+Canopy+Dist.edge	137.819	3.868	0.010	4	129.384
250 / Canopy+Slope+Aspect	137.875	3.924	0.010	4	129.440
1000 / Edge+Slope+Aspect	137.884	3.933	0.010	4	129.449
250 / Canopy	137.969	4.018	0.009	2	133.841
1000 / Edge	137.971	4.020	0.009	2	133.843
500 / Edge+Dist.edge+Slope+Aspect	138.022	4.071	0.009	5	127.363

Discussion

At the microhabitat scale, birth sites differed from paired random sites in that there was less horizontal cover and more overhead density of vegetation at the birth sites. Consequently, hypothesis 1 that birth sites would have more horizontal and vertical cover than paired random sites was only correct for the latter variable. At the macrohabitat scale, birth sites had less canopy cover and gentler slopes than random sites at the 500-m scale, but the amount of edge did not explain differences between birth and random sites. Consequently, hypothesis 2 that the areas around birth sites would have more canopy cover and less forest edge than random sites was not supported.

Predation sites had less horizontal cover than paired random sites at the microhabitat scale, but there were no differences in overhead density of vegetation. Consequently, hypothesis 3 that predation sites would have less horizontal and vertical cover than paired random sites was not supported. Predation sites were closer to the nearest edge than random sites, and there were no differences in canopy cover and the amount of edge between predation and random sites at the macrohabitat scale. These findings offered no support for hypothesis 4 that the surrounding areas around predation sites would have less canopy cover and more forest edge than random sites.

In comparing birth sites to predation sites at the microhabitat scale, I found that birth sites had less horizontal cover, more overhead density of vegetation, and were on gentler slopes than predation sites. However, the differences were small and may not be biologically meaningful. At the macrohabitat scale, I found that only slope explained differences between birth and predation sites, but the difference was

small and may not be meaningful biologically also. Slope didn't explain differences between birth and random sites at the microhabitat scale because the distance between birth and the paired-random sites were only 200 – 400 m. A larger distance might result in larger differences in slope between birth and random sites. Although I found evidence of slope explaining differences between birth and random sites and birth and predation sites at the macrohabitat scale, the differences were small (3.3% difference between birth and random sites; 3.1% difference between birth and predation sites). Biologically, cow elk likely did not choose gentler slopes for a birth site, but instead chose small areas that were flat within a larger area. During collection of field data, I often found flat birth sites at a very small scale on steep slopes.

At the macrohabitat scale, it appears that cow elk were selecting areas to give birth that had more forage than random sites. Once a cow selects an area that provides sufficient forage for her nutritional demands and/or to reduce feeding time to allow more time to tend to her calf, she may then select a microhabitat in which to give birth. At the macrohabitat scale, birth-site selection took place at a 500-m radius circle. This is likely due to the fact that cow elk do not tend to move far from newborn calves the first 4 days of parturition, and their average daily movements are within 500 m of the birth site (Vore and Schmidt 2001). Birth sites had less horizontal cover and more overhead density of vegetation than paired-random sites at the microhabitat scale. Similar to cow moose (Bowyer et al. 1999), cow elk appeared to be selecting birth sites that allowed visibility by the cow, which is likely related to the cow's ability to see a predator at a distance. Although horizontal cover at birth sites was less than random sites, there likely was sufficient cover to conceal a calf or

cow elk when lying down. Consequently, cow elk that observed predators before they were seen would have an opportunity to “hide” their calves with alarm calls.

Predation sites and birth sites both had less horizontal cover than random sites at the microhabitat scale. However, birth sites also had less horizontal cover than predation sites and more overhead density of vegetation than both random and predation sites. If the predation sites are assumed to be dangerous or vulnerable areas due to the concealment characteristics for predators, then these findings suggest that predation did affect selection of birth sites by cow elk at the microhabitat scale. When comparing birth and predation sites to the same random sites at the macrohabitat scale, different variables were important in explaining the differences. However, when I compared birth sites to predation sites on the macrohabitat scale, I found little differences. These results indicated that cow elk were not influenced by predation risk when selecting birth sites at the macrohabitat scale, but were influenced by the availability of forage (i.e. less canopy = more open areas). Nearly 50% less biomass was found at sites used by females with young than at sites used by females without young (Barten et al. 2001). Pregnant caribou also moved up in elevation, where lichens were less abundant, presumably to distance themselves from predators. Cow elk likely didn't use elevation to space themselves away from predators in this study since birth and predation sites were intermixed, but instead chose birth sites based on concealment characteristics that were not conducive to predators such as cougars that stalk their prey.

In this study, predation appeared to occur near forest edges and in areas that had less horizontal cover than random sites and the majority of calf mortalities were

due to cougar predation. In Wyoming, cougars selected areas that provided vegetative or topographic cover for hunting advantages (Logan and Irwin 1985). When hunting, cougars use areas that allow an approach within attack distance of prey (Hornocker 1970). Altendorf et al. (2001) found that 72% of mule deer killed by cougars ($n = 58$) were near forest edges and 14% each in forest and open areas. Mule deer had higher levels of vigilance, and there were lower pellet counts in edge areas than in open and forest interiors (Altendorf et al. 2001). Altendorf et al. (2001) suggested that mule deer were not foraging near forest edges due to higher predation risk in those areas. In this study, cow elk likely were able to increase vigilance by choosing birth sites with less horizontal cover and better visibility.

In this study, there was less horizontal cover at predation sites than random sites because most predation likely occurred at or near the forest edges. Due to the effects of cover on forage quantity, ungulates often experience a trade-off between selection of food and cover (Myserud and Østbye 1999), which often is related to foraging and exposure to predation (Lima and Dill 1990). Because cougars stalk their prey (Hornocker 1970, Wilson 1984) and require some degree of cover, they are likely to hunt close to the forest edge where they find elk foraging in open areas.

Understanding birth-site selection and areas where predation is successful can provide an understanding of survival strategies by elk in selecting concealment cover. Cougars actively stalk elk and use areas that are beneficial to their hunting techniques. In contrast, cow elk face the challenge of selecting areas for calving that have sufficient forage to provide high energy demands of lactation and avoid areas that have high predation risk. In this study, parturient elk were selecting large areas

that provided adequate forage to meet nutritional demands. Within these areas, cow elk selected birth sites at a smaller scale that had high visibility, presumably to avoid predation on calves. Habitat selection related to birth sites may help regulate type and amount of care given to the calf by the cow (Rachlow and Bowyer 1994, 1998). The strategy of having high quality forage within short distance and selecting a birth site away from predation sites on the microhabitat scale, likely helped increase the chances of calf survival. Thus, cow elk may have reduced risk of predation without incurring a huge nutritional cost.

The pressure of losing young to predators has shaped adaptations of ungulates for coping with the environments they inhabit (Kie 1999). The data on birth-site selection in this study supports the interpretation that cow elk were attempting to avoid predators at the microhabitat scale. At the macrohabitat scale, the nutritional needs of lactating cow elk were likely the primary determinants of birth-site selection. A calf elk's survival, which is highly vulnerable to predation the first few days of life, likely depends on the cow's selection of a birth sites. When quality and abundance of forage has a positive relationship with the risk of predation, a tradeoff between those environmental factors may occur during birth-site selection. Understanding the nature of that tradeoff is necessary to understand how cow elk cope with their environment while attempting to rear young successfully.

CHAPTER 4

CONCLUSIONS

Spencer N. Rearden

The declining elk populations in northeastern Oregon has led to increased pressure on wildlife managers to determine reasons for the decline. Despite low cow harvest through hunting, elk populations have continued to decline. The reason for the declining elk populations is thought to be due to low calf recruitment and perhaps high cow mortality rates. To understand why elk calf recruitment continues to be low, I analyzed factors affecting elk calf survival in northeastern Oregon. In addition, I also investigated the role of habitat selection in survival of calves by determining if birth-site selection by cow elk was influenced by predation risk.

Differences in annual survival rates of Rocky Mountain elk calves in northeastern Oregon were found between the two adjacent study areas, with calves in Wenaha having lower survival (0.26; 95% CI = 0.15 to 0.42) rates than calves in Sled Springs (0.52; 95% CI = 0.37 to 0.56). These differences occurred because cougars killed more elk calves in Wenaha than in Sled Springs. Fifty-four percent and 35% of radio-collared calves were killed by cougars in Wenaha and Sled Springs, respectively. Overall, predation was the main proximate cause of death. Cougars were more important predators to all ages of elk calves than black bears (the second cause of proximate calf mortality) in northeastern Oregon because cougars killed calves throughout the first year of life, while black bears killed calves only during the first month.

Annual calf survival was influenced by birth date ($\beta = -0.35$; 95% CI = -0.64 to -0.06). Both birth date ($\beta = -0.253$; 95% CI = -0.502 to -.0003) and birth weight ($\beta = 0.13$; 95% CI = -0.14 to 0.39) influenced summer calf survival, with earlier and heavier-born calves having higher survival rates than late and light-born calves.

Other research on elk calves have shown that birth date (Singer et al. 1997, Smith and Anderson 1998, Cook et al. 2004) and birth weight (Thorne et al. 1976, Singer et al. 1997, Cook et al. 2004) can affect neonatal survival. I found no differences in annual survival rates between the sexes in this study; however, I did find differences in summer survival rates between the sexes depending on the area. In Wenaha, females (0.57; 95% CI = 0.42 to 0.72) had higher survival than males (0.42; 95% CI = 0.27 to 0.59), and in Sled Springs, males (0.82; 95% CI = 0.66 to 0.91) had higher survival than females (0.46; 95% CI = 0.31 to 0.61).

Preliminary analyses suggested that cow age, weight, and percent spring fat (all estimates of cow condition) did not influence calf survival, nor was cow condition correlated with the estimated birth date and birth weight of calves. The analyses that examined the effects of cow condition on calf survival in this study were inconclusive due to small sample sizes. Therefore, I could not rule out the potential negative effects that cow condition may have on elk calf survival (Thorne et al. 1976, Haigh and Hudson 1993, Cook et al. 2004), which could be part of the cause for low calf recruitment in northeastern Oregon.

Results indicated that birth-site selection of cow elk was influenced by predation risk at the microhabitat scale. Cow elk selected birth sites that had less horizontal cover (0.97 times the odds; 95% CI = 0.94 to 0.99) and more overhead density of vegetation (1.022 times the odds; 95% CI = 1.005 to 1.040) than paired-random sites. Although predation sites also had less horizontal (0.985 times the odds; 95% CI = 0.973 to 0.998) cover than random sites, birth sites had less horizontal cover (0.983 times the odds; 95% CI = 0.967 to 1.001) and more overhead density of

vegetation (1.02 times the odds, 95% CI = 1.01 to 1.04) than predation sites. Similar to moose in Alaska (Bowyer et al 1999), cow elk appeared to be selecting birth sites that allowed visibility by the cow, which was likely related to the cow's ability to see a predator at a distance. Due to the effects of cover on forage quantity and quality, ungulates often experience a trade-off between selection of forage and cover (Mysterud and Østbye 1999), which often is related to foraging and exposure to predation (Lima and Dill 1990). If the predation sites are considered to be dangerous areas due to the habitat concealment characteristics, then these findings suggest that predation did affect birth-site selection at the microhabitat scale. Because cow elk chose birth sites with less horizontal cover and more overhead density of vegetation, indicated that they were influenced by predation risk (more overhead density of vegetation = less forage).

At the macrohabitat scale, it appears that cow elk were not influenced by predation risk. Cow elk chose birth sites with less canopy cover (0.05 times the odds; 95% CI = 0.01 to 0.34) than random sites within a 500 m-radius circle. Since vegetation varies across landscapes due to canopy cover (Cook et al. 2002), cow elk were likely more influenced by forage rather than predation risk when selecting a birth site at the macrohabitat scale. When birth sites were compared to predation sites, I found no differences, further suggesting that birth-site selection was not influenced by predation risk at the macrohabitat scale. Cow elk were likely selecting broad areas for parturition that had sufficient forage to meet the high nutritional demands of lactation. Within these areas, cow elk selected birth sites that had high visibility at the microhabitat scale, presumably to avoid predation on calves.

Understanding the causes of juvenile elk mortality is important to understand low calf recruitment. In addition, studying the role of habitat selection as it relates to survival of calves can lead to better insight into elk ecology. Uncertainty as to why elk calf recruitment is low and why current management practices are not allowing elk populations to increase demonstrates the need for further research. This study on elk calf mortality was part of a longer study that will continue to investigate elk calf mortality to determine causes of low elk populations in northeastern Oregon.

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APPENDICES

Appendix A. Comparison of the annual survival analysis to a subset analysis that uses only calves caught ≤ 4 days of age and 1 5-day-old calf caught by foot to determine if our ability to age older calves bias results.

The most parsimonious model for both analyses was S(area+lnT+BD). The same top 4 models in the analysis on the full set of data are the same as the top 4 on the analysis on the subset analysis, although they are in different order. With such similarities, these two analyses are basically showing the same results which suggests that our ability to estimate calf age at capture on older calves was likely accurate enough to not alter the results.

Model selection results for annual survival analysis using 2003 collared calves. Data from northeastern Oregon (n = 89).

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(area+lnT+BD)	313.802	0.000	0.479	4	305.731
S(area+lnT+BD+BW)	315.837	2.036	0.173	5	305.731
S(area+lnT)	316.721	2.919	0.111	3	310.678
S(lnT+BD)	317.461	3.660	0.077	3	311.419
S(area+lnT+BW)	318.443	4.642	0.047	4	310.372
S(sex+lnT+BD)	318.946	5.145	0.037	4	310.875
S(lnT)	319.196	5.394	0.032	2	315.175
S(T+T ²)	319.645	5.843	0.026	3	313.602
S(sex+lnT)	321.061	7.259	0.013	3	315.018
S(T)	323.876	10.074	0.003	2	319.855
S(area+BD)	326.188	12.387	0.001	3	320.146
S(t)	329.628	15.827	0.000	12	305.066
S(area)	331.494	17.692	0.000	2	327.472
S(sex*area)	331.951	18.149	0.000	4	323.880
S(BD)	332.132	18.331	0.000	2	328.111
S(sex+BD)	333.285	19.484	0.000	3	327.243
S(sex+area)	333.515	19.713	0.000	3	327.472
S(sex+BD+sex*BD)	333.646	19.844	0.000	4	325.575
S(BD+BW)	334.134	20.332	0.000	3	328.091
S(.)	335.782	21.981	0.000	1	333.775
S(BD+BW+BD*BW)	336.116	22.314	0.000	4	328.045
S(BW)	337.573	23.771	0.000	2	333.552
S(sex)	337.589	23.788	0.000	2	333.568
S(sex+BW+sex*BW)	337.833	24.031	0.000	4	329.762
S(sex+BW)	339.409	25.608	0.000	3	333.367
S(t*sex*area)	357.868	44.066	0.000	48	252.804

Appendix A continued...

Model selection results for annual survival analysis using only calves that were ≤ 4 days of age at the time of capture and 1 calf 5 days old that was captured by foot.

Data from northeastern Oregon, 2003 (n = 58).

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(area+lnT+BD)	200.316	0.000	0.280	4	192.209
S(lnT+BD)	201.573	1.256	0.149	3	195.509
S(area+lnT+BD+BW)	201.719	1.402	0.139	5	191.557
S(area+lnT)	202.472	2.156	0.095	3	196.408
S(sex+lnT+BD)	202.490	2.173	0.094	4	194.383
S(T+T ²)	202.962	2.645	0.075	3	196.897
S(lnT)	203.758	3.442	0.050	2	199.726
S(area+lnT+BW)	203.903	3.586	0.047	4	195.795
S(t)	204.368	4.051	0.037	12	179.513
S(sex+lnT)	205.232	4.915	0.024	3	199.167
S(T)	209.005	8.689	0.004	2	204.973
S(area+BD)	209.021	8.705	0.004	3	202.957
S(BD)	211.820	11.504	0.001	2	207.788
S(sex+BD)	212.003	11.686	0.001	3	205.939
S(sex+BD+sex*BD)	213.152	12.836	0.001	4	205.045
S(area)	213.646	13.329	0.000	2	209.614
S(BD+BW)	213.782	13.466	0.000	3	207.718
S(sex+area)	214.581	14.265	0.000	3	208.517
S(sex+BW+sex*BW)	215.731	15.414	0.000	4	207.624
S(BD+BW+BD*BW)	215.820	15.503	0.000	4	207.713
S(.)	216.452	16.136	0.000	1	214.441
S(sex*area)	216.617	16.300	0.000	4	208.510
S(sex)	217.661	17.345	0.000	2	213.629
S(BW)	218.436	18.120	0.000	2	214.404
S(sex+BW)	219.516	19.200	0.000	3	213.452
S(t*sex*area)	254.649	54.333	0.000	48	144.352

Appendix B. Comparison of the summer survival analysis to a subset analysis that uses only maternal and discovery calves to determine if helicopter-caught calves bias results.

In the subset analysis, the most parsimonious model was $S(\text{sex}+\text{year}+\ln T+\text{BD})$. In the subset analysis, the 4 competing models were different from the most parsimonious model in that they either didn't include a variable that was in the most parsimonious model or that they included the variables area or BW. Both the 95% confidence intervals for area and BW overlapped well over 0 (area; 95% CI = -1.29 to 0.23, BW; 95% CI = -0.31 to 0.51) suggesting that they have no effect on neonatal survival.

Similar to the full data set analysis, the subset analysis showed that survival followed a curvilinear trend, birth date affected survival with later-born calves having lower survival, and differences in survival between the sexes also were found, with males having higher survival than females (95% CI = -1.63 to -0.04). The main difference between the analysis on just the VIT and discovery calves and the analysis on all the calves was that year was part of the top models. However, differences in survival between the 3 years were not supported in this analysis due to large overlapping 95% confidence intervals over 0 when analyzing the most parsimonious model (95% CI = -509.16 to 512.52288).

Appendix B continued...

Model selection results for early survival analysis using 2002-2004 collared calves.

Data from northeastern Oregon (n = 222).

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(sex*area+lnT+BD)	578.745	0.000	0.411	6	566.704
S(sex*area+lnT+BD+BW)	580.127	1.383	0.206	7	566.073
S(sex*area+lnT)	580.369	1.625	0.182	5	570.340
S(sex*area+lnT+BW)	581.460	2.716	0.106	6	569.419
S(sex*area)	583.121	4.377	0.046	4	575.101
S(sex+lnT+BD)	588.059	9.314	0.004	4	580.039
S(lnT)	588.365	9.620	0.003	2	584.359
S(T)	588.370	9.626	0.003	2	584.364
S(sex*area*year+lnT+BD)	588.400	9.655	0.003	14	560.194
S(lnT+BD)	588.411	9.667	0.003	3	582.400
S(T+BW)	588.461	9.716	0.003	3	582.449
S(lnT+BW)	588.502	9.757	0.003	3	582.490
S(area+lnT+BD)	588.672	9.928	0.003	4	580.653
S(sex+area+lnT+BD)	588.690	9.946	0.003	5	578.661
S(lnT+BD+BW)	588.785	10.041	0.003	4	580.766
S(sex+lnT)	588.788	10.044	0.003	3	582.776
S(T+BD)	588.871	10.127	0.003	3	582.859
S(sex+lnT+BD+BW)	589.038	10.293	0.002	5	579.009
S(area+lnT)	589.102	10.357	0.002	3	583.090
S(sex+lnT+BW)	589.379	10.634	0.002	4	581.359
S(sex+area+lnT+BW)	589.958	11.214	0.002	5	579.929
S(T+TT)	589.998	11.254	0.001	3	583.986
S(.)	592.918	14.173	0.000	1	590.916
S(sex)	593.115	14.371	0.000	2	589.109
S(BW)	593.216	14.472	0.000	2	589.210
S(area)	593.309	14.564	0.000	2	589.303
S(sex+area)	593.922	15.177	0.000	3	587.910
S(BD)	594.086	15.342	0.000	2	590.080
S(04 vs. 02 + 03)	594.350	15.605	0.000	2	590.344
S(sex+BD+sex*BD)	594.496	15.751	0.000	4	586.476
S(BD+BW)	594.576	15.832	0.000	3	588.565
S(03 vs. 02 + 04)	594.667	15.922	0.000	2	590.661
S(sex*area*year)	594.965	16.220	0.000	12	570.812
S(year)	595.748	17.004	0.000	3	589.737
S(BD+BW+BD*BW)	596.422	17.678	0.000	4	588.403
S(year*area)	597.877	19.133	0.000	6	585.836
S(t)	604.639	25.895	0.000	15	574.405

Appendix B continued...

Model selection results for 2002 - 2004 15-week collared calves analysis using only calves captured through discovery and VITs. Used to test the effects of birthweight and birthdate on survival using accurate estimates of each and from calves randomly captured over the calving season. Data from northeastern Oregon (n = 93).

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(sex+year+lnT+BD)	268.596	0.000	0.158	6	256.491
S(area+year+sex+lnT+BD)	268.855	0.259	0.139	7	254.714
S(sex+lnT+BD)	268.984	0.388	0.130	4	260.934
S(sex+area+lnT+BD)	269.292	0.695	0.112	5	259.216
S(sex+year+lnT+BD+BW)	270.394	1.798	0.064	7	256.253
S(sex*year+lnT+BD)	270.831	2.235	0.052	8	254.650
S(sex+lnT+BD+BW)	270.906	2.310	0.050	5	260.831
S(sex+lnT)	271.051	2.455	0.046	3	265.021
S(sex*area+lnT+BD)	271.072	2.476	0.046	6	258.966
S(sex+year+lnT)	272.208	3.611	0.026	5	262.132
S(lnT+BD)	272.771	4.175	0.020	3	266.741
S(sex+lnT+BW)	272.965	4.369	0.018	4	264.915
S(lnT)	273.059	4.463	0.017	2	269.044
S(area+lnT+BD)	273.244	4.648	0.016	4	265.194
S(sex)	273.870	5.274	0.011	2	269.855
S(sex+area)	273.903	5.307	0.011	3	267.873
S(lnT+BD+BW)	273.941	5.345	0.011	4	265.891
S(T)	274.493	5.897	0.008	2	270.478
S(lnT+BW)	274.543	5.947	0.008	3	268.513
S(T+BD)	275.027	6.431	0.006	3	268.997
S(T+TT)	275.090	6.493	0.006	3	269.060
S(area+year+sex)	275.102	6.505	0.006	5	265.026
S(sex+year)	275.229	6.633	0.006	4	267.179
S(sex+BD+sex*BD)	275.290	6.694	0.006	4	267.240
S(sex*area)	275.769	7.172	0.004	4	267.718
S(T+BW)	275.887	7.291	0.004	3	269.857
S(area+year)	276.905	8.309	0.003	4	268.855
S(year)	277.115	8.519	0.002	3	271.085
S(.)	277.208	8.612	0.002	1	275.203
S(area)	277.386	8.790	0.002	2	273.371
S(sex*year)	277.513	8.916	0.002	6	265.407
S(year*area)	278.072	9.475	0.001	6	265.966
S(area*year)	278.072	9.475	0.001	6	265.966

Appendix B continued...

Table continued from previous page.

Model	AICc	Delta AICc	AICc weights	Parameters	Deviance
S(BW)	278.375	9.779	0.001	2	274.360
S(03 vs. 02+04)	278.587	9.991	0.001	2	274.572
S(BD)	278.668	10.072	0.001	2	274.653
S(04 vs. 02+03)	279.085	10.489	0.001	2	275.070
S(BD+BW)	279.615	11.018	0.001	3	273.585
S(BD+BW+BD*BW)	281.225	12.629	0.000	4	273.175
S(t)	291.003	22.407	0.000	15	260.392
S(t*area*sex*year)	564.108	295.512	0.000	158	169.968

Appendix C. Summary statistics for habitat characteristics of birth and random sites at the microhabitat scale. Variables in bold were identified by matched-paired logistic regression and AIC_c as explaining differences between birth and random sites.

Habitat Variables	Birth (n=49)			Random (n=98)		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
Slope (%)	8.1	6.3	9.9	7.5	6.1	8.9
Aspect (radians)	0.500	0.410	0.590	0.548	0.481	0.614
CP (%)	52.2	44.8	59.6	69.6	65.1	74.1
Dens (%)	57.3	49.4	65.3	36.2	30.1	42.3
View25 (%)	44.6	35.1	54.0	63.5	56.8	70.2
View50 (%)	30.4	21.7	39.2	43.5	36.6	50.5

Appendix D. Summary statistics for habitat characteristics of predation and random sites at the microhabitat scale. Variables in bold were identified by matched-paired logistic regression and AIC_c as explaining differences between birth and random sites.

Habitat Variables	Predation (n=62)			Random (n=124)		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
Slope (%)	10.6	8.5	12.8	9.6	8.2	11.1
Aspect (radians)	0.472	0.384	0.559	0.535	0.475	0.595
CP (%)	57.0	50.9	63.1	66.9	62.2	71.5
Dens (%)	41.2	33.4	48.9	40.3	34.7	45.9
View25 (%)	45.6	37.6	53.5	59.7	53.5	65.9
View50 (%)	29.3	22.5	36.1	40.1	34.4	45.8

Appendix E. Summary statistics for habitat characteristics of birth and random sites at the macrohabitat scale. Variables in bold were identified by logistic regression and AIC_c as explaining differences between birth and random sites.

Habitat Variables	Birth (n=49)			Random (n=80)		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
500 / Edge (m)	39384	34825	43943	39616	36249	42984
500 / Canopy (%)	54.5	48.6	60.4	65.6	61.7	69.5
Dist.edge (m)	12	8	16	19	13	24
Slope (%)	8.0	6.3	9.8	11.4	9.2	13.6
Aspect (radians)	0.441	0.351	0.532	0.467	0.388	0.546

Appendix F. Summary statistics for habitat characteristics of predation and random sites at the macrohabitat scale. Variables in bold were identified by logistic regression and AIC_c as explaining differences between predation and random sites.

Habitat Variables	Predation (n=60)			Random (n=80)		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
1000 / Edge (m)	160868	148815	172921	160675	148669	172681
1000 / Canopy (%)	58.6	53.7	63.6	64.6	61.1	68.1
Dist.edge (m)	9	6	12	19	13	24
Slope (%)	11.0	8.8	13.2	11.4	9.2	13.6
Aspect (radians)	0.449	0.356	0.541	0.467	0.388	0.546

Appendix G. Summary statistics for habitat characteristics of birth and predation sites at the microhabitat scale. Variables in bold were identified by logistic regression and AIC_c as explaining differences between birth and predation sites.

Habitat Variables	Birth (n=49)			Predation (n=48)		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
Slope (%)	8.1	6.3	9.9	10.5	8.0	12.9
Aspect (radians)	0.500	0.410	0.590	0.481	0.379	0.584
CP (%)	52.2	44.8	59.6	60.2	53.7	66.7
Dens (%)	57.3	49.4	65.3	37.8	28.9	46.6
View25 (%)	44.6	35.1	54.0	48.1	39.1	57.0
View50 (%)	30.4	21.7	39.2	31.3	23.3	39.2

Appendix H. Summary statistics for habitat characteristics of birth and predation sites at the macrohabitat scale. Variables in bold were identified by logistic regression and AIC_c as explaining differences between birth and predation sites.

Habitat Variables	Birth (n=49)			Predation (n=48)		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
250 / Edge (m)	10631	9231	12032	11629	10320	12939
250 / Canopy (%)	0.5	0.5	0.6	0.6	0.5	0.6
Dist.edge (m)	12	8	16	8	5	11
Slope (%)	8.0	6.3	9.8	11.2	8.7	13.7
Aspect (radians)	0.441	0.351	0.532	0.437	0.336	0.537