ELK SURVIVAL AND MORTALITY FACTORS IN THE BLUE MOUNTAINS OF WASHINGTON, 2003-2006

Scott McCorquodale, Paul Wik, Pat Fowler, Tom Owens

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Prepared By:
Scott McCorquodale, Paul Wik,
Pat Fowler, Tom Owens

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Washington Department of Fish and Wildlife
600 Capitol Way North
Olympia, WA 98501-1091

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EXECUTIVE SUMMARY

Due to uncertainty about cumulative human-caused elk mortality in the Washington Blue Mountains, in particular the magnitude of illegal kills during 2000-2002, we implemented a study to estimate survival rates of elk ≥ 1 year-old and document sources of human-caused elk mortality, 2003-06. Our study area was focused on Game Management Units (GMUs) 162, 166, 169, and 175.

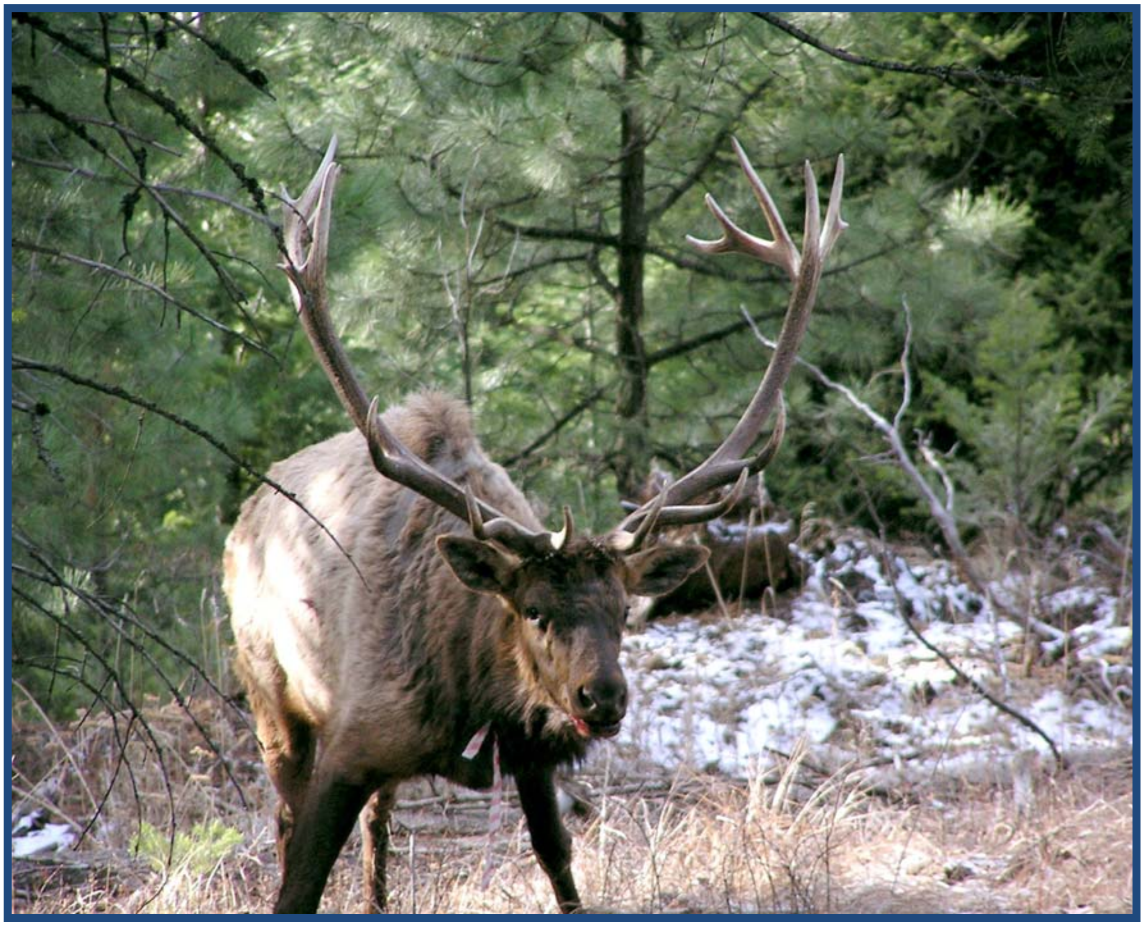
We radiomarked 190 elk (82 bulls and 39 cows > 1 year-old and 65, 11-month-old bulls). We marked most elk with both rumen implant radios and standard neck radiocollars, but we marked 60 elk in February 2003 with rumen radios only. We estimated annual survival rates using known fate models and explored various hypotheses about factors affecting elk survival using 3 alternate datasets and 9 *a priori* survival models.

Our 9 survival models invoked possible survival differences between subadult (2-3 yr-olds) and adult bulls (≥ 4 yr-olds), differences in bull survival west and east of the Tucannon River, and differences in branch-antlered bull survival during 2003-05 vs. 2006. We used multi-model inference to select a subset of models that best explained our observed data.

We found that 90% of the available model weight was accounted for in a subset of 5 models for each alternate dataset. Four of the best models were common to all 3 datasets. Simpler models (3-4 parameters) generally had more support in the data than more complex models. We found little support for differences in survival between younger and older branch-antlered bulls or for differences in survival west and east of the Tucannon River for yearling bulls. We found modest support for survival differences east and west of the Tucannon River for branch-antlered bulls, and we found some evidence that branch-antlered bull survival was lower in 2006 relative to 2003-05.

Using estimates from the best-supported models, we estimated annual survival for yearling bulls was 0.41; for adult cows, survival estimates ranged 0.80-0.84 and for branch-antlered bulls, estimates ranged 0.80-0.85, depending on dataset. In models allowing different survival estimates for branch-antlered bulls east and west of the Tucannon River, we estimated annual survival was 0.79-0.83 and 0.80-0.86, respectively, across the 3 datasets. In models allowing survival to differ for branch-antlered bulls in 2003-05 vs. 2006, we estimated survival was 0.83-0.86 during 2003-05 and was 0.73-0.76 in 2006.

We recorded 78 deaths of our radiomarked elk during our study. Human-caused deaths predominated among general causes (n = 55). Most human-caused deaths were of yearling bulls killed by state-licensed hunters (n = 28). Most subadult bull deaths were from tribal hunting (n = 5), and most mature bulls died from natural causes (n = 6). We detected few illegal kills (n = 4). We detected deaths in every month of the year, but most mortalities occurred during Sept-Nov. Overall, tribal hunting was a nontrivial source of mortality, but its magnitude was only about 29% of that of state-licensed hunters. Mortalities of branch-antlered bulls were highest in 2006 (n = 13), with deaths almost equally split between natural causes (n = 6) and human-caused mortalities (n = 7).



Radiomarked mature bull elk in the Washington Blue Mountains, February 2005.

We explored a variety of landscape factors as predictors of hunting mortality risks for yearling bulls using logistic regression models. We detected a relationship between road variables (distance-to-road and road density) and risks of hunting mortality, but other landscape factors (*e.g.*, habitat class, ownership, topography) were not related to hunting mortality risks for our data. Risks of hunting mortality increased modestly as yearling bulls used areas closer to roads and as local road densities increased. Our models were not good absolute predictors of the fate of yearling bulls, suggesting other factors affected mortality risks or that vulnerability was variable across our study area. Our modest sample size of kill sites likely limited our ability to detect significant landscape effects (*e.g.*, cover and topography) on elk harvest risks.

We concluded that aggressive enforcement efforts during 2000-03 greatly reduced illegal hunting activity in our study area. We also concluded that current spike-only general season regulations allow sufficient annual recruitment of young branch-antlered bulls to meet management objectives. Tribal harvest was a nontrivial source of mortality, suggesting that the reporting of off-reservation tribal harvest would be useful for state-tribal collaborative management of the Washington Blue Mountains elk herd.

Our results suggested that managing the density of open roads could be an effective strategy to reduce elk harvest vulnerability where that is a management objective.

INTRODUCTION

Washington's Blue Mountains elk herd is an important public resource.

The Blue Mountains elk population in southeast Washington is 1 of 10 major elk herds in the state and has provided important subsistence, recreational, and tribal harvests of elk for more than 100 years. However, recreational hunter participation and harvests declined in recent decades after peaking in the 1970s. (Fowler 2001). A number of factors likely contributed, including large-scale forest health declines resulting from decades of fires suppression and chronic drought (Johnson 1994), redistribution of hunter effort in eastern Washington, and elk population changes.

During the 1970s and 1980s, Blue Mountains elk managers documented highly skewed adult elk sex ratios and extended conception periods in cow elk (Fowler 2001, unpublished Washington Department of Fish and Wildlife [WDFW] data). Skewed adult sex ratios resulted from high hunting pressure and general season hunting regulations that allowed hunters to harvest any antlered bull elk.

The so-called *open bull* regulation resulted in low overall bull survival and a bull subpopulation with very few older age-class individuals. The scarcity of mature bulls had predictable effects on elk breeding biology (Noyes et al. 1996) and resulted in bulls >3 years of age being rare in annual hunter harvests for many years (<3% of 7,097 bulls aged at WDFW check stations during 1962-1988 were more than 3-years-old; WDFW file data).

In an attempt to increase bull survival and improve adult sex ratios, WDFW adopted a *spike-only* general hunting season regulation in the Washington Blue Mountains in 1989 (WDFW 2000). Under the new regulations, general season bull elk hunters could only harvest spike bulls (*i.e.*, a bull with a maximum of a single tine on at least one antler). As bull survival into older age classes increased, as was predicted, branch-antlered bull hunting opportunity was provided via special, limited-entry *any bull* permits. Although *spike-only* management focused hunting mortality on yearling bulls, those that survived the hunting season had much higher chances of surviving to maturity than under *open bull* regulations, which increased older bull numbers and trophy hunting opportunity.

By the mid 1990s, bull permit holders in the Washington Blue Mountains were regularly harvesting 350+ Boone and Crockett bulls, and some 400+ bulls were being taken. This unique elk hunting resource became well-known regionally, and bull permits were highly prized by permit applicants. However, additional sources of human-caused mortality also removed bulls from the population.

Many older age-class bulls were killed illegally in the Washington Blue Mountains during 2001-2003.

Two Native American Tribes, the *Confederated Tribes of the Umatilla Indian Reservation* and (CTUIR) the *Nez Perce Tribe* (NPT) have federal treaty-reserved hunting rights in the Blue Mountains and court-affirmed autonomy to self-regulate hunting by their tribal members (McCorquodale 1999). Neither tribe has shared harvest data with WDFW, but it has been assumed that tribal hunters harvest some substantive number of elk annually, including mature bulls. CTUIR hunting is regulated by a formal legal code with many elements common to state hunting regulations (*e.g.*, seasons, caliber restrictions, no spotlighting, no shooting from motorized vehicles, wastage restrictions). CTUIR hunters may hunt elk only during Aug-Dec by tribal regulation, with branch-antlered bull hunting closed during the rut and the month of December. Hunting by the NPT is largely unrestricted by minimal tribal regulations governing hunting by tribal members.

Additionally, the availability of high trophy-value bulls in the Washington Blue Mountains predictably drew elk poachers to the area. By 2001, WDFW enforcement officers were documenting increasing poaching levels on the Blue Mountains elk herd (T. Vandivert, *pers. comm.*). The perpetrators included some well-organized groups of poachers that appeared to be targeting trophy-class bull elk.

Table 1. Known branch-antlered bulls harvested illegally in the Blue Mountains of Washington, 2001-2003.

Year	Non-legal Bull Kills
2001	26
2002	23
2003	4
TOTAL	**53**

Source: WDFW Enforcement Program.

During 2001-2003, WDFW enforcement investigated the known poaching of at least 53 branch-antlered bulls from the Blue Mountains elk population (Table 1). Although investigations led to several successful prosecutions, substantial concern remained about actual poaching levels, which were unknown.

During this time, WDFW biologists in the Blue Mountains began to document a declining trend in mature bull numbers and adult sex ratios despite *spike-only* general season regulations; suggesting cumulative bull mortality was exceeding that anticipated under current *any bull* permit levels. This trend, coupled with uncertainty about actual elk mortality rates, especially among mature bulls, prompted a reduction in *any bull* permits and a research investigation, which is the subject of this report. The CTUIR also responded to the high level of documented illegal kill of branch-antlered bulls by closing CTUIR harvest of branch-antlered bulls in GMU 162 in 2002 and 2003; CTUIR reopened harvest of branch-antlered bulls in GMU 162 under a lottery issued tag system in 2004 (6 tags), and this system was implemented annually through 2007.

In 2003, we initiated a study of elk mortality in the Washington Blue Mountains. Previously, data were collected on first year survival of elk calves (Myers et al. 1999*a*) and adult elk (Myers et al. 1999*b*) in this population, but those data did not address the information needs identified in 2003. The previous studies were focused on calf and adult cow elk mortality.

Our objectives were to quantify levels of current human-caused elk mortality in the Washington Blue Mountains, including all bulls at least 1-year-old. Our approach focused on following the fate of an annual sample of radiomarked elk over a period of 4 years, documenting sources and rates of elk mortality and survival.

Although our principal objectives focused on elk survival/mortality rates and causes of elk deaths, we believed our study also presented an opportunity to explore the effects of specific landscape features on elk mortality risks in the Blue Mountains.

Previous work had clearly shown that the characteristics of landscapes often had systematic effects on the vulnerability of elk to human-caused mortality (Leptich and Zager 1991, Unsworth et al. 1993, Leptich et al. 1995, Gratson et al. 1997, McCorquodale et al. 2003). We believed that identifying factors specifically affecting elk vulnerability to human-caused mortality in the Blue Mountains would be potentially useful to both managers of this herd and managers of the landscape they occupy.

Our explicit objectives in this study were to:

- Estimate survival rates for radiomarked yearling bulls, subadult bulls (2-3 yr-old), mature bulls (≥ 4 yr-old), and adult cows (≥ 1 yr-old).
- Quantify causes of elk deaths among our radiomarked elk sample.
- Estimate rates of cause-specific hunting-related mortality from our radiomarked elk.
- Model the effects of landscape features on elk hunting-mortality risks.
- By synthesizing results from the analyses supporting these objectives, our final goal was to develop data-based recommendations for managing subadult and adult elk mortality in the Washington Blue Mountains.

STUDY AREA

The ~2,500 km^2 (~965 mi^2) Blue Mountains Elk Herd Area is located in the southeastern corner of Washington, in Walla Walla, Columbia, Garfield, and Asotin Counties (Fig. 1). Approximately 63% of the elk herd range is privately owned; the remaining 37% is public land, including a large area of the Umatilla National Forest. Our study area comprised GMUs 162, 166, 169, and 175. Most of GMU 162 was privately owned, whereas GMUs 166, 169, and 175 mostly consisted of public land. Approximately 550 km^2 (~212 mi^2) of the study area was federal wilderness (Wenaha Wilderness). Road densities varied considerably across the study area, from roadless wilderness in GMU 169 to highly roaded (>1.5 km / km^2; >2.4 mi / mi^2) areas.

Topographically, the Blue Mountains are characterized by diverse, mountainous terrain. Rolling foothills grade into steeply dissected river valleys and higher elevation upland plateaus. Elevations ranged from 400 to 1,850 m (1,320-6,105 ft) within the study area. Much of the Wenaha Wilderness portion of the study area consisted of extremely rugged, high relief terrain.

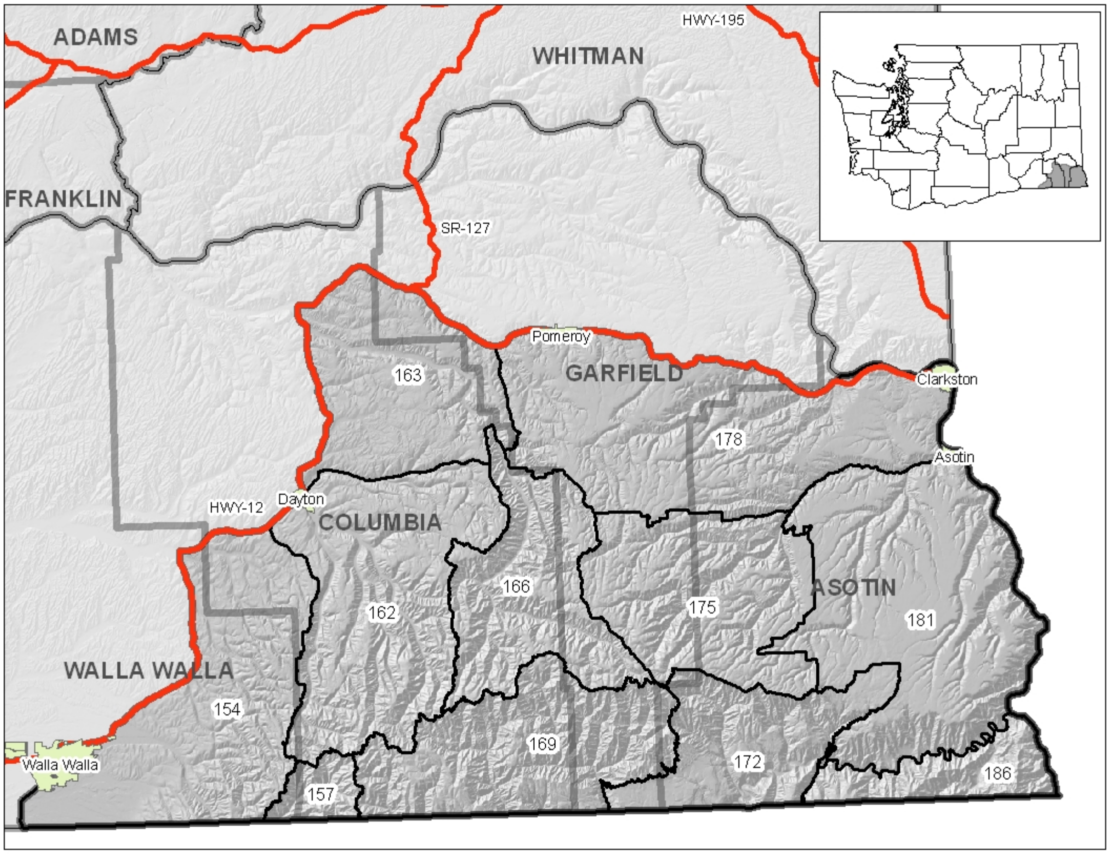


Figure 1. Game Management Units comprising the Blue Mountains Elk Herd Area in southeastern Washington.

Climatically, the Blue Mountains experience relatively cool winters with deep snowpacks in drainage headwaters, relatively mild winters at lower elevations, and hot, dry summers throughout. Precipitation averages approximately 40 cm (~15.7 in), with most falling between December and March (Fowler 2001).

Plant communities within the study area were diverse. Lower elevation foothills were relatively open communities of grass and shrublands, interspersed with developed pasture and cropland areas. These gentle, open, low-elevation foothills provided attractive winter and spring foraging conditions for elk.

Mid-elevation forests and xeric uplands sites were dominated by Ponderosa pine (*Pinus ponderosa*). Higher elevations supported extensive forests in a mosaic of openings and closed canopy stands. North-facing slopes typically supported dense, climax communities of mature conifers, mostly Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea englemannii*), or grand fir (*Abies grandis*).

Previous research indicated that the Tucannon River defined a logical subpopulation boundary for the Blue Mountains elk herd (Myers and Lyndaker 1999). Recent harvest and survey data also suggested that bull elk survival and vulnerability might differ in landscape units west vs. east of the Tucannon River (WDFW, 2000, Fowler 2001). Because of this, we initially subdivided the study area into 2 zones for some analyses, reflecting potentially higher and lower bull elk vulnerability zones. The hypothesized higher vulnerability zone (HVZ) consisted of GMUs 166 and 175, whereas GMUs 162 and 169 comprised the possibly lower vulnerability zone (LVZ). Our research design addressed potential differences in bull elk survival between the 2 vulnerability zones.

The Blue Mountains of Washington experienced 2 landscape level fire events during the course of our study, with approximately 65,000 ha (~160,000 acres) burning. The fires burned predominantly within Columbia and Garfield Counties, although Walla Walla County was impacted by the Columbia Complex Fire. Six Washington Blue Mountains elk herd GMUs were affected (GMUs 154, 162, 163, 166, 169, and 175), with approximately 90% of the Tucannon unit (GMU 166) burning during the 2 fires.

The School Fire burned approximately 21,000 ha (~52,000 acres) in the Tucannon River, Cummings Creek, Tumalum Creek, and Pataha Creek drainages in 2005. This was a high intensity fire resulting in significant loss of vegetative cover within all of these drainages. The high intensity of the burn resulted in the short-term loss of significant wildlife habitat and the direct mortality of animals, including elk. Habitat recovery from this fire will likely take decades.

The Columbia Complex Fire was a result of 3 fires merging in 2006, burning a total of 44,000 ha (~109,000 acres). The fire resulted in a mosaic of understory burns and stand replacing patches. This fire should provide short- and long-term benefits to wildlife within the management units it affected (GMUs 154, 162, 166, and 169).

METHODS

Background

Our goal was to quantify survival and model vulnerability for four demographic classes of elk, where age-class was defined by age during the current year's fall hunting season.

1. Adult bulls
2. Subadult bulls
3. Adult cows (potentially including yearlings)
4. Yearling bulls

We defined **adult bull** elk as individuals at least four-years-old. Although there is evidence that full physical and sexual maturity does not occur until approximately age five in male elk (Flook 1970), our interest was principally in adult bulls in a management context. Although hunters may select for larger, older bulls when they can, we believed that branch-antlered bulls in the Blue Mountains were large enough by age four to be perceived as adult bulls by elk hunters.

Each year, we monitored a group of **subadult bulls**, those individuals 2-3 years-old during that year's fall hunting season. Bulls in the subadult sample included winter-marked yearlings and 2-year-olds from the current marking year, as well as bulls that had recruited from previous marking years (but would not be older than 3 years by the current year's fall hunting season). For some analyses, we collapsed subadult and adult bulls into a **branch-antlered bull** class (any bull at least 2-years-old during the current year's fall hunting season). There were several reasons we included younger, branch-antlered bulls in our sample of radiomarked elk.

One issue we were concerned about was that larger, older bulls on a modest-to-high vulnerability landscape were likely to reach maturity because they used secure areas of the landscape. So, we believed it would potentially introduce a bias to our survival and vulnerability analysis if we monitored only larger, mature adult bulls (≥ 5-yr-old) (*i.e.*, such a sample would potentially already have been screened to select animals using higher security areas).

Subadult bulls, like this 3-yr-old, were radiomarked each winter and monitored, as were adult bulls, as part of the mortality study.

We were also concerned that we would not be able to find and radiomark enough ≥4-yr-old bulls to comprise a marked sample in the hypothesized HVZ, based on preliminary reconnaissance. Lastly, we expected some of our marked yearling bulls to survive the spike-only general season, and wanted to be able to continue to collect data from these bulls (*i.e.*, allow them to recruit upwards in age-class sample). Our goal was to allocate radiomarks among the branch-antlered bull subsample such that relatively balanced numbers of fully mature and younger adult bulls would be monitored annually.

Our goal of estimating survival for yearling bulls added unique complications to the study. Because our intent was to measure survival of bulls during the hunting season in which they were yearlings, winter marking was not appropriate (*i.e.*, wintering yearlings had already survived the fall hunting season). To obtain estimates of survival associated with 1-year-old bulls, we opted to mark our sample of yearling bulls during late spring (*i.e.*, at age 10-11 months, after velvet growth had started), before the hunting season and before summer temperatures increased capture-related mortality risks.

Our study was initially conceptualized as a 3-year study, but in spring 2006 we obtained additional support to continue monitoring radiomarked elk for an additional year. However, this extension was implemented too late to add a radiomarked cohort of 11-month-old bulls in the spring of 2006.

Elk Marking

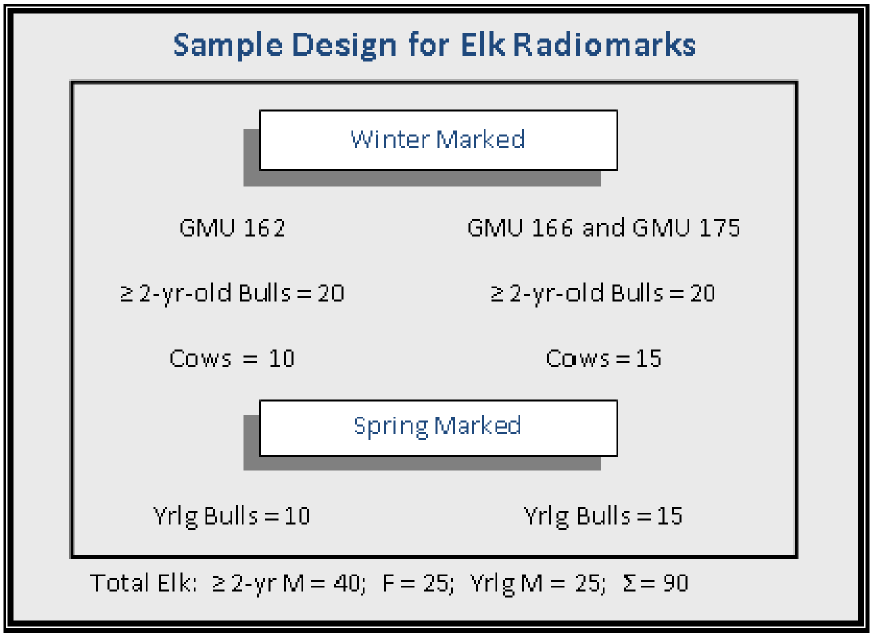
We captured elk by darting them with carfentanil citrate and xylazine hydrochloride from a *Bell 206 B3 Jet Ranger* helicopter. We darted adults and hard-antlered yearlings during February, 2003-2005 and ~11-month-old bull calves in May, 2003-2005. During May captures of bull calves, we occasionally darted an adult bull to add to the sample size of radiomarked branch-antlered bulls.

We hobbled and blindfolded elk we captured, fitted them with transmitters (described below), removed a canine tooth for estimating age via cementum annuli analysis (if they were clearly at least 24 months old), and gave them prophylactic injections of penicillin, vitamins B and E, selenium, and a clostridial vaccine.

Immobilized 11-month-old bull elk in the Washington Blue Mountains.

We conducted capture operations in GMUs 162, 166, and 175. Our basic design was predicated on an annual total marked elk sample = 90 elk, with radiomarks allocated to branch-antlered bulls, yearling bulls, and adult cows in the 2 study area subunits (zones) as per the scheme defined in Table 2.

This design defined the initial marking goal, as well as the goal for elk to be monitored each year. After the first marking year (February and May 2003), additional elk were marked annually in 2004 and 2005 to try to achieve and/or maintain this design.


Sample Design for Elk Radiomarks

Winter Marked

GMU 162	GMU 166 and GMU 175
≥ 2-yr-old Bulls = 20	≥ 2-yr-old Bulls = 20
Cows = 10	Cows = 15

Spring Marked

GMU 162	GMU 166 and GMU 175
Yrlg Bulls = 10	Yrlg Bulls = 15

Total Elk: ≥ 2-yr M = 40; F = 25; Yrlg M = 25; Σ = 90

Table 2. Annual Radiomarked Elk Design

Using the fate of a marked animal sample to infer the contribution of human harvest to population-level mortality, assumes that the marks do not influence hunter behavior. Bias could result from increased probability of harvest (*e.g.*, because of enhanced detection of a marked animal) or decreased probability of harvest (*e.g.*, because of the fear that killing a marked animal is illegal or disapproved of). To minimize this bias, WDFW researchers previously developed rumen implantable radio transmitters that facilitated radiomarking elk with no outward evidence of research handling (Fig. 2) (Smith et al. 1994).

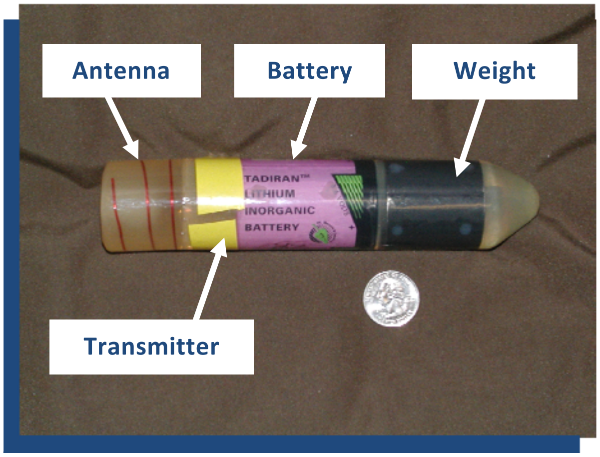


Figure 2. Rumen radio transmitter for elk

Hunters have rarely detected these rumen implants during field dressing. In theory, rumen radios also enhance the ability of researchers to detect illegal harvest, because poachers who may be inclined to destroy an obvious transmitter cannot destroy a rumen radio they are unaware of. Rumen implants also can yield unbiased information relative to kill site locations, because elk are usually field-dressed where they are killed and rumen implants often remain at the site of field-dressing.

We initially intended to instrument elk with only rumen-implanted VHF radio transmitters (Smith et al. 1994). However, we experienced substantial and unexpected problems with signal reception range after deploying rumen radios during our first capture, in February 2003, and we opted to double-mark elk during all subsequent captures using both a rumen VHF radio and a standard VHF neck radiocollar.

Our signal reception issues with the rumen radios deployed in February 2003 were eventually diagnosed as a manufacturing error wherein the vendor had mistakenly constructed the implants with 2-stage boards instead of 3-stage boards. All rumen implants we used after February 2003 contained 3-stage boards and performed better. Nonetheless, we continued the practice of double-marking study animals throughout the course of the study. On very rare occasions, we marked an elk with only a neck radio due to difficulty with an implanting procedure or the need to reverse an animal quickly to prevent critical hyperthermia.

Figure 3. Blue Mountains bull elk wearing low visibility neck radiocollar.

The neck radiocollars we used were constructed with brown conveyor belting that was designed to make the collars inconspicuous (Fig. 3); we believed these collars would be difficult for hunters to detect and have no effect on their selection of target animals. The collars we deployed on ~11-month-old bull calves were fitted with folded and sewn, elasticized cloth spacers designed to periodically expand as the bull grew and eventually rot through and release the collar (Fig. 4). Based on the design and materials, we expected bulls to shed the break-away collars after 1-2 years.

Figure 4. Eleven-month-old Blue Mountains bull elk wearing neck radiocollar fitted with expandable and degradable, elasticized cloth spacer to facilitate neck growth as the bull ages and eventual collar breakaway after 12-24 months.

We presumed that the benefit of the clandestine rumen radios was still in effect with the double-marking strategy (*i.e.*, if a poacher was inclined to destroy the visible neck collar, we believed they would be unaware of the rumen radio and not destroy it). We did not publicize our use of rumen radios while the study was ongoing. All VHF radios had batteries rated for 4 years and were equipped with motion-sensing circuitry that functioned as a mortality sensor.

To implant elk with rumen radios, we reversed the carfentanil portion of the immobilization cocktail with naltrexone hydrochloride, which re-established a gag reflex in immobilized elk. The presence of a gag reflex reduced risks of implants entering the trachea during the implanting procedures. We then liberally lubricated the rumen radios with surgical lube and petroleum jelly and guided them gently down the elk's esophagus with a specially designed implanting tube made from ½", flexible PVC pipe.

Once the implants had reached the rumen, we used a special release mechanism to free them from the implanting pole. After we had placed rumen radios, secured the neck radiocollars, and completed all other procedures, we injected elk with yohimbine hydrochloride to reverse the xylazine portion of the immobilizing cocktail and quickly removed the animal's hobbles and unfastened their blindfolds. Elk were usually alert and ambulatory in ½-5 minutes after receiving the yohimbine injection.

Monitoring

We monitored the fate and movements of radiomarked elk by tracking them regularly from a Cessna 182 fixed-wing aircraft using procedures generally described by Gilmer et al. (1981). Because we expected elk mortalities to occur principally in late summer to fall, and in late winter, the frequency of our monitoring flights varied seasonally. We attempted to conduct 2 monitoring flights per month during Dec-Jul and 2-3 flights per week during Aug-November. Inclement weather during winter and spring and other constraints (*e.g.*, airspace restrictions associated with wildland firefighting in late summer 2005 and 2006) occasionally impacted our flight schedule.

Because we had more radiomarked elk to monitor than we could pinpoint to geographic location during a flight, we attempted to obtain accurate geographic locations for ~30% of the radiomarked elk during each flight. These locations were geo-referenced with a Geographic Positioning System receiver aboard the airplane. We rotated the elk to be tracked each flight to maintain relatively even effort across elk.

During our tracking flights, we also monitored for telemetry detections of elk not scheduled for precise locating. These detections were spatially referenced only to general areas within the study area. Combining the precise locations and the coarser detections served as the basis for also monitoring radiomarked elk for mortality. Because of problems with early rumen radios and occasional long-range dispersal, we had extended loss of contact with some radiomarked elk. We included such elk regularly on the scan list in an attempt to re-establish contact.

Elk Mortality Investigations

We initiated a process leading to a mortality site investigation whenever mortality signals were detected during monitoring flights, usually visiting these sites within 48 hours of the detection. During ground visits, we homed to radios in mortality mode and initially looked for evidence (*e.g.*, hair, blood, entrails) that these sites were actual death sites.

If we confirmed a mortality site, we attempted to attribute death to a proximate, and if different, an ultimate cause (*e.g.*, predation of an animal in emaciated condition reflected different proximate and ultimate causes). We used specific criteria to serve as corroborating evidence of proximate death causes (Table 3). These *a priori* criteria were needed to assign probable death causes for causes that could be assumed to be unreported (*i.e.*, winterkill, predation, wounding loss, poaching) or under-reported (*i.e.*, tribal hunting).

Table 3. Potential Mortality Sources and Diagnostic Criteria.

Mortality Source	Corroborating Evidence
Predation	Puncture wounds on head and/or neck or evidence of subcutaneous bleeding at wound sites, no evidence of human activity
Legal state hunter	Legal animal during an open non-tribal season, complete recovery
Legal tribal kill	Outside of non-tribal season, legal animal during legal tribal season, and complete recovery
Illegal non-tribal kill	non-legal animal or outside of legal season and incomplete recovery or legal animal during open season with incomplete recovery
Illegal tribal kill	During closed tribal season or a non-legal animal under tribal regulation, and complete recovery or other evidence of tribal hunting activity (e.g., witness reports)
Wounding Loss	Evidence of human kill, no recovery (illegal kill if outside of legal season or non-legal animal)
Winterkill	No evidence of human activity, poor physical condition or fat-depleted bone marrow, no evidence of predation
Unknown	Inconclusive evidence of mortality cause

Attributing sources of unreported, human-caused mortality presented challenges. Because legal tribal seasons occurred outside the timeframe of non-tribal seasons, it was possible to confuse legal tribal kills with illegal non-tribal kills. Elsewhere in Washington, tribal hunters tended to make complete recoveries of consumable portions of elk carcasses, whereas non-tribal poachers tended to take only selected portions of the animal (*e.g.*, antlers from trophy bulls, high-grade cuts of meat only) (J. Smith, *pers. comm.*). So, we used the level of recovery as an *a priori* diagnostic criterion for distinguishing probable legal tribal kills from illegal non-tribal kills. We always sought other corroborating evidence of the type of human-caused mortality when possible (*e.g.*, witness or enforcement reports, other physical evidence).

Estimating Survival

We estimated annual survival using *maximum likelihood* methods implemented in Program MARK (White and Burnham 1999). We created encounter histories for each radiomarked elk using the *known fate* data type. Telemetry data are generally well-suited for *known-fate* analyses. Censoring animals will not bias estimates of survival and associated variances if censoring is uninformative (*i.e.*, not systematically related to censoring causes). However, *known fate* models were developed under the assumption that the fate of most animals is known. Because of issues related to poor performance of first-year rumen radios, we had numerous instances of elk that were either permanently right-censored at some point or whose fate was periodically unknown for several weeks to months.

Because censoring was most common for elk marked with rumen radios known to be performing poorly, we believed that such censoring was not likely systematically related to probability of death. In light of our censor issue, we estimated survival using 3 alternate datasets. The first dataset (**Data A**) included all elk we radiomarked for which we had some level of initial continuous contact (*i.e.*, at least 2 months of regular detections post-marking). We created another dataset (**Data B**) by dropping all elk marked the first winter from the analysis (*i.e.*, these individuals were never considered among the radiomarked elk). This dataset consisted almost entirely of elk bearing 2 radiomarks. We created a final dataset (**Data C**) by permanently right-censoring all elk marked the first winter (*i.e.*, prior to initiating double-marking) after 1 year. We opted to create this dataset because it was apparent that for several elk marked with only the defective rumen radios, we had regular contact for several months, before permanently losing contact during the second year of the study.

We coded individual elk encounter histories using 30 groups. Each elk was assigned to a demographic class: yearling bull, 2-yr-old bull, 3-yr-old bull, adult bull (>3-yr-old), and adult cow (≥1-yr-old), and each demographic class was further apportioned to marking cohorts (*i.e.*, marked in 2003, 2004, or 2005) and a vulnerability zone (*i.e.*, low and high vulnerability zones). The 30 groups coded represented the cross-classification of 5 demographic classes × 3 cohorts × 2 zones. Even though our research design defined subadult bulls as 2-3-yr-old bulls, we coded subadult bulls separately as 2 or 3-yr-old bulls to facilitate allowing bulls to recruit upward in demographic class as they matured and because some subadult bulls were marked as 2-yr-olds (*i.e.*, would be subadults for 2 years) and some as 3-yr-olds (*i.e.*, recruited to be adults after 1 year).

To maximize the information on survival embodied in the datasets, given censoring, we coded the elk encounter histories using 2-month intervals. We estimated annual survival as the product of 6, 2-month intervals, and we estimated the variance of annual survival using the *Delta* method (Seber 1982). We estimated 95% confidence intervals on annual survival by backtransforming an algebraic manipulation of 2-month confidence intervals from the logit to the probability scale using MARK-derived estimates of *Beta* (*i.e.,* logit) parameters and their variances. We used a survival year defined as May 1–Apr 30, which largely reflected seasonal patterns of deaths and was a good fit to our annual marking schedule. We explored alternative hypotheses about Blue Mountains elk survival by comparing 9 *a priori* models with different parameterizations.

This candidate model set included models of varying complexity that embodied different age-class effects among bulls, landscape vulnerability zone effects for bulls (*i.e.*, high vulnerability vs. low vulnerability zones), and a simple year effect on branch-antlered bull survival. The different model parameterizations we explored are depicted in Table 4. We evaluated the same candidate model set with all 3 encounter history datasets described above (Data A, B, C).

We used an information-theoretic approach to model selection. Using features in Program MARK, for each candidate model, we calculated a model likelihood, Akaike's Information Criterion adjusted for small samples sizes (AIC_c) (Burnham and Anderson 2002), and Akaike model weights (w_i).

We based our inference principally on a *best models* subset of the candidate model set (*i.e.,* a confidence model set), defined by the top models comprising ~90% of the available Akaike model weight.

Table 4. Candidate survival models for elk in the Blue Mountains of Washington, 2003-2006.

Parenthetical elements denote levels of survival variation invoked by model parameterizations: (.) = no zone, or year variation; (zone) = zone variation, but no year variation; (2006 vs. other) = a simple year effect that allowed survival specific to 2 periods (2006 vs. all other years equal), but no zone variation. Zone variation modeled bull survival specific to 2 zones: *Low Vulnerability Zone* (LVZ = GMU 162, 169) and *High Vulnerability Zone* (HVZ = GMU 166, 175).

CANDIDATE SURVIVAL MODELS
Ylg ♂ (.), B-A ♂ (.), Ad ♀ (.)
Ylg ♂ (.), Sub-Ad ♂ (.), Ad ♂ (.), Ad ♀ (.)
Ylg ♂ (.), B-A ♂ (zone), Ad ♀ (.)
Ylg ♂ (.), Sub-Ad ♂ (.), Ad ♂ (zone), Ad ♀ (.)
Ylg ♂ (zone), B-A ♂ (zone), Ad ♀ (.)
Ylg ♂ (.), Sub-Ad ♂ (zone), Ad ♂ (zone), Ad ♀ (.)
Ylg ♂ (zone), Sub-Ad ♂ (zone), Ad ♂ (zone), Ad ♀ (.)
Ylg ♂ (.), B-A ♂ (2006 vs. others), Ad ♀(.)
Ylg ♂ (.), B-A ♂ (2006 vs. others, zone), Ad ♀ (.)

Estimating Cause-specific Mortality

Our overall objectives included quantifying sources of elk mortality, particularly sources of human-caused mortality. We considered estimating the contribution to overall mortality rates of each specific type of hunting-related mortality (*e.g.*, wounding loss, tribal kills, state-licensed archery kill, state-licensed muzzleloader kill, *etc.*), but we obtained data for several sources (*e.g.*, state-licensed muzzleloader kill) that were too sparse to justify this.

We quantified the following types of mortality:

- Natural non-predation
- Predation
- Tribal hunting
- State-licensed hunting
- Illegal hunting
- Wounding loss

However, we collapsed some categories prior to estimating actual rates for mortality causes because of the rarity of some death causes in our final dataset.

We estimated cause-specific mortality functions using a *nonparametric cumulative incidence function estimator* (NCIFE) (Lunn and McNeil 1995, Heisey and Patterson 2006) to estimate annual cause-specific mortality rates (M_k = mortality rate due to cause k) in a competing risks context. We modified ***S-plus*** code provided in Heisey and Patterson (2006) for this analysis and considered 3 competing sources ($k = 3$) of mortality: 1) *state-licensed hunting and wounding*, 2) *tribal hunting*, and 3) *all other sources of mortality combined.*

The mortality data for some sources (*e.g.*, tribal hunting, illegal harvest, predation) were sparse when spread across age/sex classes of elk. Because our principal interest in cause-specific mortality was to judge the qualitative contributions (*i.e.*, substantive vs. trivial) of non-tribal and tribal hunting mortality to cumulative hunting mortality and the relative contribution of hunting mortality to all sources of mortality, we derived NCIFE's for our dataset by pooling sex/age classes.

Geographic Database

Modeling the relationship between elk harvest risks and landscape features required digital data reflecting environmental and management features of the analysis area. We assimilated landscape data reflecting various management, ecological, and physiographic features of our study area from a variety of sources. We used a digital elevation model (DEM) as the principal source data for modeling topographic features; DEM data had a resolution of 30 m^2 (~36 yd^2).

We created a raster dataset indexing topographic complexity using a Vector Ruggedness Measure (VRM) (Sappington et al. 2005). Conceptually, topographic complexity represented localized variability in aspect; the VRM of cell x in the raster dataset was modeled by the variation among vectors perpendicular to the aspect of each 30 m^2 cell in a 3 × 3 cell window centered on cell x. Thus, a moving 3 x 3 window was used to populate each cell of our study area with a VRM index value. The unitless VRM index theoretically ranged from 0.0-1.0 (Sappington et al. 2005).

We used a raster dataset reflecting forest vegetation attributes to derive a vegetation structure/composition classification for our study area. The initial forest vegetation dataset was based on gradient nearest neighbor (GNN) imputation using stand data from a variety of sources (Ohmann and Gregory 2002, Wimberly et al. 2003); GNN stand attribute data also had a resolution of 30 m^2. We derived a simplified habitat classification using tree size and canopy closure classes (for forested habitats) and National Land Cover Data classes (for nonforested habitats) available in the GNN dataset (Table 5). We also obtained digital data for the road network and land ownership in our study area (source data: *Washington Dept. of Natural Resources*).

Table 5. Habitat classification scheme used in landscape mediated vulnerability modeling for Blue Mountains elk in Washington, 2003-2006.

Data were derived by reclassifying vegetation attributes available in the GNN raster dataset (Ohmann and Gregory 2002). Tree size classes were defined by diameter at breast height (dbh), coded in cm (38 cm ≈ 15 in).

Class	% Canopy Closure	Tree Size	Habitat
Opening	<10%	all	Meadow, Grassland, steppe
Young, open forest	10-39%	<38 cm dbh	Forest
Young, semi-closed forest	40-69%	<38 cm dbh	Forest
Young, closed forest	70+%	<38 cm dbh	Forest
Older, open forest	10-39%	38+ cm dbh	Forest
Older, semi-closed forest	40-69%	38+ cm dbh	Forest
Older, closed forest	70+%	38+ cm dbh	Forest
Pasture/Agriculture	0%	na	Pasture/Field/Crop
Other	na	na	All Else

Vulnerability Factors

For our analyses we identified, *a priori*, several landscape-oriented covariates that could logically be hypothesized to affect the chances of an elk being harvested, assuming they were *at risk* (Table 6). These features reflected landscape attributes that we believed might influence hunter effort (*e.g.*, ease of access, difficulty of terrain) or the detectability of an elk (*e.g.*, concealing cover, predictability of elk use).

Table 6. Factors used to model potential landscape influences on elk vulnerability to harvest.

Factor	Covariate	Units
Distance to nearest road	RDDIST	decameters = m/10
Road density	RDDENS	km/km^2
Terrain Ruggedness	VRM	unitless (0.0-1.0)
Topographic diversity	TDIV	unitless index
Slope	SLP	degrees
Closed (≥70% cc) forest	CLFOR	proportion of landscape unit
Moderate (≥40% cc) forest	MDFOR	proportion of landscape unit
Public ownership	OWN	proportion of landscape unit
Elk use density	LOC	number of elk relocations

We previously described the derivation of the VRM index (above; see Sappington et al. 2005); we considered 2 basic VRM covariates: the index of the center cell in the circular landscape sampling frame and the mean VRM for all cells in the frame. We also derived an additional, simplified VRM summary statistic for each circular landscape sampling frame by calculating a Shannon-Wiener diversity index (Ricklefs 1979) based on deciles of the VRM index values, where:

$$\boldsymbol{H} = -\sum p_i \ln(p_i),$$

and p_i = proportion of the sampling frame in decile $\boldsymbol{i}$, and TDIV = $e^{\boldsymbol{H}}$. This covariate indexed both the range of VRM values in the sampling frame, and their relative proportionality.

We also used univariate *t*-tests and binary logistic regression (Hosmer and Lemeshow 1989) to quantify and model factors mediating systematic effects on the relative vulnerability of elk to human harvest. We based these analyses on landscape-oriented features surrounding live elk relocations and known death locations (limited to human-caused deaths). For logistic regression modeling we coded a dichotomous outcome variable reflecting site type (0 = live elk relocation; 1 = death site). Because we were interested in landscape, rather than point features, we defined 2 relatively fine scales of landscape analysis by buffering live elk relocations and elk death sites with 250-m (820-ft) and 450-m (1,476-ft) radii circles, centered on the actual elk site.

Because most of the environmental GIS data we were working with were raster data, we then converted the 250-m and 450-m radii circular polygons to 30-m × 30-m raster approximations of these circles, yielding landscape sampling frames of approximately 19.53-ha (~48.2 ac) (250-m radius) and 63.29-ha (~156.3 ac) (450-m radius), centered on the respective elk sites.

Our analytic strategy to quantify landscape feature effects on elk vulnerability to harvest invoked the concept of sampling *risk* factors. That is, we fundamentally assumed that samples of landscape features associated with live elk use must represent samples where elk could have been harvested (*i.e.*, the site could be assumed to have potentially been a dead elk site). Clearly, regulatory structures are important determinants of harvest risk, assuming legal harvest is a dominant source of mortality.

We did not believe it was appropriate to sample landscape data surrounding live elk relocations, where there was an assumable low probability (*i.e.*, zero or near zero) of the elk being harvested at the site. Our study began following considerable enforcement emphasis to substantially reduce illegal harvest. Previous research in Washington had also demonstrated that illegal harvest and legal tribal harvest predominantly occurred in the fall, relatively close to the timing of legal state-sanctioned elk hunting seasons (Smith et al. 1994).

During our study, legal opportunity for state-licensed hunters to harvest branch-antlered bulls and cow elk was very limited. Most legal, state-licensed hunting was directed towards spike bull elk by general season regulations. Because branch-antlered bulls and cows largely represented non-legal animals, at least to a dominant mortality source, we did not believe it was appropriate to assume telemetry relocations of branch-antlered bulls and cow elk represented *at risk* sites, even in the fall. Therefore, we limited our analyses of factors affecting harvest vulnerability to an assumable *at risk* sample of elk relocations: yearling bull elk relocations obtained between August 30 and November 15.

We employed 2 separate analytic strategies for the logistic regression modeling. One strategy invoked an unmatched *case vs. control* design, wherein we did not allow the landscape sampling frames to overlap. The rationale for this approach was based on our objective to define landscape features that had explanatory power to discriminate between places where radiomarked elk died (cases), and where we detected elk use but not a death (controls), despite elk being at risk.

We assumed that no landscape unit was so vulnerable that any elk that used the unit was sure to die. But we believed that any harvest-related elk death in a landscape unit suggested some level of harvest vulnerability associated with that landscape unit. We thus defined live elk sites as those circular landscape sampling frames that had no overlap with the sampling frame of any kill site.

We drew our sample sites for this analysis by selecting the potential population of *at risk* elk sites, then eliminating live elk sites that overlapped with death sites at the same scale of analysis. Because we wanted this analysis to be based upon independent samples, we also eliminated overlapping sites within the live elk relocation and the death site subsamples by deleting randomly selected sampling frames where overlap occurred. This produced a final sample of at risk live elk relocations and death sites with no sampling frame overlap within or between the subsamples.

We conducted a second logistic regression analysis by drawing a sample of *at risk* live elk relocations and death sites wherein we relaxed the requirement for geographic independence of the circular landscape sampling frames, both within and between the *status-based* subsamples. We thus used all circular sampling frames that met the criteria for *at risk* sites (defined by elk age/sex class and date, as above).

We anticipated a modest sample size, at best, of dead yearling bull sites during fall. For this reason, we only considered main effects covariates in our vulnerability factors analyses. We did not believe our sample size would warrant exploration of interactions among covariates, although some logical ones could be hypothesized (*e.g.*, road × topography, road × cover interactions). We based our statistical inference on critical values of Student's t-distribution associated with a significance level of $P \leq 0.10$ for parametric univariate tests and model-specific, chi-square test statistics and goodness-of-fit tests for logistic regression models. We used SAS 9.1 (SAS Institute, Inc., 2002) and/or SPSS 11.0 (SPSS, Inc., 2001) software for all statistical procedures.

RESULTS

Elk Marking

We radiomarked 190 elk in the Washington Blue Mountains between February 2003 and May 2005. We marked 82 bulls (37, 20, and 25 during February 2003, 2004, and 2005, respectively) and 39 cows (23, 6, and 10 during February 2003, 2004, and 2005) during winter capture sessions. We also radiomarked 65 velvet-spike bulls during spring marking (24, 23, and 18 bulls during May 2003, 2004, and 2005); we also marked 4 branch-antlered velvet bulls in May 2004 and 2005 (2 each year).

The mean age of known-age branch-antlered bulls at the age they entered the study was 4.75 years, and the oldest bull at the age it entered the study was 16 years (Fig. 5). Forty-two of 77 (54.5%) branch-antlered bulls radiomarked entered the study at ages 2-3 years, 19 of 77 (24.7%) entered as 4-7 yr-olds, and 16 of 77 (20.8%) entered as adults at least 8-yrs-old (Fig. 5). Thus, slightly less than half (45.5%) of the branch-antlered bull sample entered as adult bulls under the criterion of adult bulls = bulls ≥ 4 yrs-old.

Adult elk were captured for radiomarking by helicopter darting in mid-winter.

The mean age of known-age cow elk at the age they entered the study was 7.3 years, and the

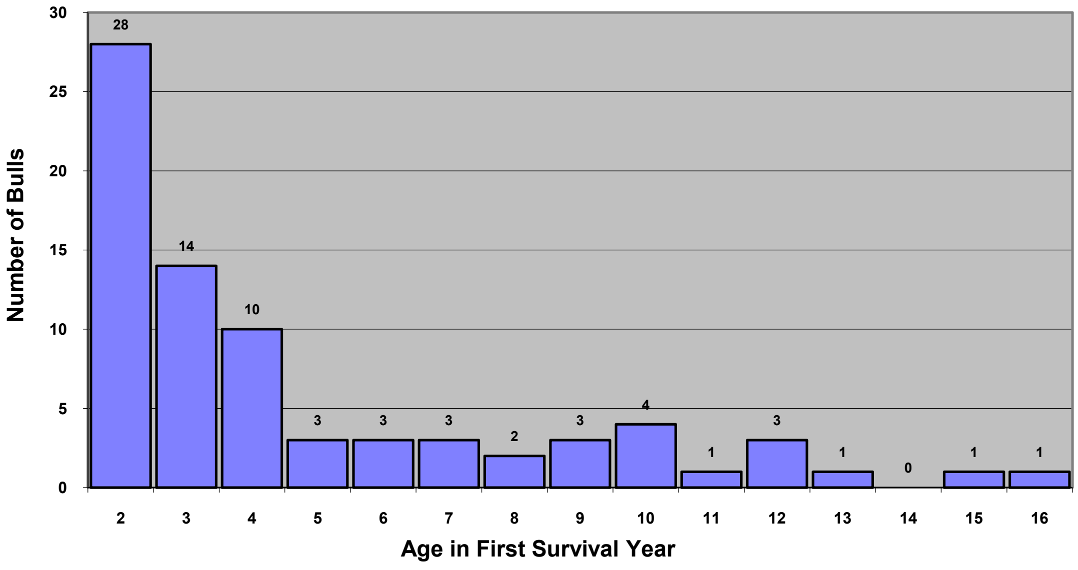


Figure 5. The distribution of ages of known-age, branch-antlered bull elk upon first entering the study in the Washington Blue Mountains, 2003-2005 (n = 77).

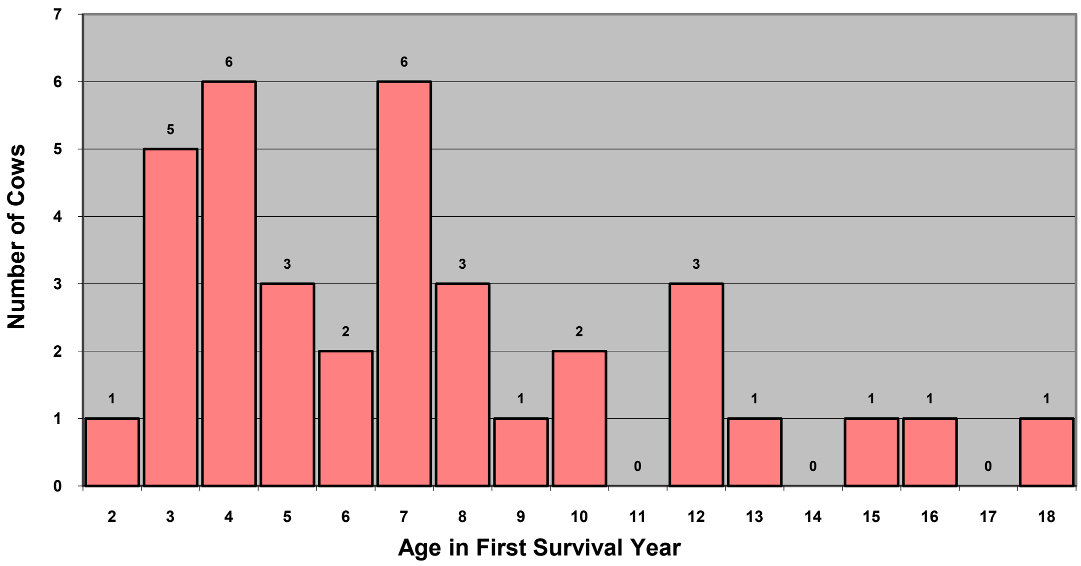


Figure 6. The distribution of ages of known-age, cow elk upon first entering the study in the Washington Blue Mountains, 2003-2005 (n = 36).

oldest cow at the age it entered the study was 18 years (Fig. 6). Nine of 36 (25.0%) known-age cows were ≥ 10 yrs-old when they entered the study and the other 27 (75.0%) were age 2-9 years in the first survival year they were monitored.

Because of censoring issues, particularly in 2003, not all radiomarked elk provided usable data. The numbers of radiomarked elk we actually monitored effectively for movement, survival, and mortality-source data across the study area zones ($N = 2$) during 2003-2006 are shown in Table 7. Radiomarked elk monitored each year included new elk marked in that year, plus surviving elk from previous years, for which we still had radio contact.

Table 7. Sample sizes of radiomarked elk monitored across demographic classes, hypothesized vulnerability zones (HVZ = high vulnerability zone [i.e., GMUs 166, 175]; LVZ = low vulnerability zone [i.e., GMUs 162, 169]), and years in the Washington Blue Mountains, 2003-2006.

HVZ	**2003**	**2004**	**2005**	**2006**
Yg Males	12	16	12	0[d]
SubAd Males[a]	6	13	22	12
Adult Males[b]	1	5	7	14
TOTAL BA Males[c]	7	18	30	26
Adult Females	9	13	12	5
TOTAL HVZ ELK	28	47	53	31
LVZ	**2003**	**2004**	**2005**	**2006**
Yg Males	12	4	5	0 [d]
SubAd Males[a]	5	9	8	3
Adult Males[b]	17	17	18	15
TOTAL BA Males[c]	22	26	26	18
Adult Females	12	10	9	5
TOTAL LVZ ELK	46	40	40	23
ALL ELK	74	87	93	54

[a] Subadult males = 2-yr-old and 3-yr-old bulls.
[b] Adult males = ≥ 4-yr-old bulls.
[c] Branch-antlered (*i.e.,* BA) males = ≥ 2-yr-old bulls.
[d] No yearling bulls were marked in 2006.

Because of censored individuals, we fell short of our marking design goals in 2003 for HVZ branch-antlered bulls, cows, and yearling bulls, and total marked elk monitored (Table 7; compare to Table 2). We met marking design goals for total branch-antlered bulls in 2004-2006, but were slightly below the goal for the HVZ subsample in 2004 (-2) and the LVZ subsample in 2006 (-2). We were slightly below marked cow elk design goals for total cows in all 4 years and for HVZ cows in all 4 years.

We achieved marked LVZ cow design goals in 2003 and 2004, and we were only 1 cow below goal in 2005 (Table 2). We were slightly below marked elk design goals for total yearling bulls in 2004 (-2) and more substantially low in 2005 (-7). We met LVZ marked yearling bull goals only in 2003, partly due to elk movement (see next paragraph). We were slightly below HVZ marked yearling bull goals in 2003 (-2) and 2005 (-3), but met the goal in 2004. No new elk were marked in 2006, so no yearling bulls were available for monitoring.

Attrition of radiocollared elk led to a small marked cow sample in 2006, in the absence of new elk marking. Branch-antlered bulls monitored in 2006 met the total and HVZ bull goals. The 54 total marked elk monitored in 2006 was substantially lower than the annual marked elk goal of 90, but this was due mostly to the absence of a radiomarked yearling bull cohort that year.

We marked elk in both zones of the study area, but we keyed their zone coding, relative to survival analyses, to the zone they principally used from mid-summer through fall/winter migration each year. As such, our design goals were vulnerable to compromise by elk moving from their zone of marking to the other zone. This happened notably for marked yearling bulls in 2004 and 2005, where a number of young bulls marked in May in the LVZ, ended up using the HVZ GMUs for summer-fall range (Table 7), somewhat compromising the design.

Telemetry Data

We obtained 3,095 radiomarked elk relocations georeferenced to specific coordinates between May 2003 and April 2007. Of the 3,095 fixes, 3,025 (97.7%) were obtained from a fixed-wing aircraft. Of the fixed-wing relocations, 1,267 (41.9%) were based on visual contact with radiomarked elk. We estimated the mean error of non-visual aerial relocations at 186.0 m (~610 ft), based on test tracking of 60 known-position transmitters.

Of the 60 test relocations obtained from a fixed-wing, 17 (28.3%) were biased by less than 100 m (328 ft), 25 (41.7%) were biased by at least 200 m (656 ft), and 8 (13.3%) were biased by at least 300 m (984 ft). Estimated bias reflected both error in judging the transmitter location and GPS system error.

Survival

Across the 9 candidate survival models (Table 4), the ~90% confidence model set consisted of the 5 best-supported models for all 3 datasets (Table 8). The top 4 models were common across datasets. These models assumed no zone effect on survival for yearling bulls or adult cows.

The top 3 models for Data A and B (the 1st, 2nd, and 4th best models for Data C) assumed equal survival for subadult and adult branch-antlered bulls; these 3 models differed in model constraints on branch-antlered bull survival (only a year effect on survival [2003-2005 vs. 2006]; no year or zone variation; zone variation only). In general, the simplest models (3 and 4-parameter models) were among the best-supported models; the most parameterized models (6 and 7 parameters) had little support (w_i = 0.01-0.07).

Two simple models (the first 2 models in Table 8) accounted for a substantial amount of the available model weight across all 3 datasets (Data A = 0.63; Data B = 0.57; Data C = 0.55). These 2 models assumed no zone effects for any age/sex classes and assumed equal survival for younger and older branch-antlered bulls; one model invoked survival variation for branch-antlered bulls between the 2003-2005 period and 2006.

Table 8. Ranks of candidate survival models based on Akaike model weights (w_i) for the 3 datasets analyzed. Data A=all marked elk; Data B=2003 February-marked adults omitted; Data C=2003 February-marked adults censored after 1 yr. Models highlighted in each dataset represent an approximate 90% confidence model set (i.e., cumulatively account for ~90% of the available Akaike model weight).

Model	**k**[a]	**Data A**	**w_i**	**Data B**	**w_i**	**Data C**	**w_i**
Ylg ♂ (.), B-A ♂ (2006 vs. others), Ad ♀(.)	4	1	0.41	2	0.20	2	0.25
Ylg ♂ (.), B-A ♂ (.), Ad ♀ (.)	3	2	0.22	1	0.37	1	0.30
Ylg ♂ (.), B-A ♂ (zone), Ad ♀ (.)	4	3	0.11	3	0.13	4	0.13
Ylg ♂ (.), Sub-Ad ♂ (.), Ad ♂ (.), Ad ♀ (.)	4	4	0.09	4	0.13	3	0.14
Ylg ♂ (.), B-A ♂ (2006 vs. others, zone), Ad ♀ (.)	6	5	0.07	7	0.03	7	0.04
Ylg ♂ (zone), B-A ♂ (zone), Ad ♀ (.)	5	6	0.05	5	0.06	5	0.06
Ylg ♂ (.), Sub-Ad ♂ (.), Ad ♂ (zone), Ad ♀ (.)	5	7	0.04	6	0.05	6	0.05
Yg ♂ (.), Sub-Ad ♂ (zone), Ad ♂ (zone), Ad ♀ (.)	6	8	0.02	8	0.01	8	0.02
Yg ♂ (zone), Sub-Ad ♂ (zone), Ad ♂ (zone), Ad ♀ (.)	7	9	0.01	9	0.01	9	0.01

[a] Number of survival parameters in model.

The 3 encounter history datasets differed only in respect to the treatment of elk radiomarked in February 2003, exclusively with rumen radios, and all these elk would have been ≥2 yr-olds during the first year of survival monitoring (May 2003-Apr 2004). Therefore, yearling survival bull survival estimates we obtained did not differ across datasets, as all these elk were marked after February 2003.

We estimated yearling bull survival at 0.41 (95% *CI* = 0.29-0.53), in models assuming no zone effect (Table 9). In models assuming a zone effect on survival, we estimated yearling bull survival at 0.45 for LVZ bulls and 0.38 for HVZ, but 95% confidence intervals overlapped broadly for zone-specific estimates (0.27-0.62 and 0.23-0.54 for LVZ and HVZ, respectively) (Table 9). In models that differed only relative to whether yearling bull survival was modeled with and without a zone effect, the model with no zone effect always ranked higher.

Table 9. Maximum likelihood estimates of survival parameters (and 95% confidence intervals) in the 9 candidate survival models for radiomarked Blue Mountains elk, 2003-2006. Data A=all marked elk; Data B=2003 February-marked adults omitted; Data C=2003 February-marked adults censored after 1 year.

Parameter	Data A	Data B	Data C
Yearling ♂ (.) [a]	0.41 (0.29-0.53)	0.41 (0.29-0.53)	0.41 (0.29-0.53)
Yearling ♂ (HVZ) [b]	0.38 (0.23-0.54)	0.38 (0.23-0.54)	0.38 (0.23-0.54)
Yearling ♂ (LVZ) [c]	0.45 (0.27-0.62)	0.45 (0.27-0.62)	0.45 (0.27-0.62)
SubAd ♂ (.)	0.81 (0.71-0.89)	0.81 (0.69-0.89)	0.81 (0.70-0.88)
SubAd ♂ (HVZ)	0.80 (0.66-0.89)	0.81 (0.65-0.90)	0.80 (0.66-0.89)
SubAd ♂ (LVZ)	0.83 (0.64-0.93)	0.81 (0.57-0.92)	0.82 (0.63-0.92)
Adult ♂ (.)	0.84 (0.74-0.90)	0.81 (0.67-0.89)	0.85 (0.74-0.92)
Adult ♂ (HVZ)	0.79 (0.58-0.91)	0.82 (0.59-0.93)	0.83 (0.61-0.93)
Adult ♂ (LVZ)	0.86 (0.74-0.92)	0.80 (0.57-0.92)	0.86 (0.72-0.94)
B-A [d] **♂ (.)**	0.83 (0.76-0.88)	0.81 (0.72-0.87)	0.83 (0.76-0.88)
B-A ♂ (HVZ)	0.80 (0.69-0.88)	0.81 (0.69-0.89)	0.81 (0.70-0.89)
B-A ♂ (LVZ)	0.85 (0.76-0.91)	0.80 (0.67-0.89)	0.85 (0.74-0.91)
B-A ♂ (03-05)	0.86 (0.78-0.91)	0.83 (0.73-0.90)	0.85 (0.77-0.91)
B-A ♂ (06)	0.73 (0.57-0.84)	0.76 (0.59-0.87)	0.76 (0.59-0.87)
B-A ♂ (03-05, HVZ)	0.83 (0.69-0.91)	0.85 (0.70-0.93)	0.85 (0.71-0.92)
B-A ♂ (06, HVZ)	0.74 (0.51-0.87)	0.74 (0.51-0.87)	0.74 (0.51-0.87)
B-A ♂ (03-05, LVZ)	0.88 (0.78-0.93)	0.81 (0.64-0.90)	0.86 (0.74-0.93)
B-A ♂ (06, LVZ)	0.72 (0.46-0.87)	0.79 (0.49-0.93)	0.79 (0.49-0.93)
Adult ♀ (.)	0.80 (0.64-0.93)	0.84 (0.67-0.93)	0.82 (0.69-0.90)

[a] (.) survival model assumed no zone or year variation for the parameter.

[b] (HVZ) survival parameter estimate specific to the hypothesized high vulnerability zone (GMU 166, 175).

[c] (LVZ) survival parameter estimate specific to the hypothesized low vulnerability zone (GMU 162, 169).

[d] B-A ♂ = branch-antlered bull. Parameter constrained survival to be equal for subadult and adult bulls.

For branch-antlered bulls, the relationships among point estimates of survival were consistent with the hypothesized zone effect (*i.e.*, survival was estimated to be lower for HVZ bulls than for LVZ bulls) for Data A and Data C, but not for Data B (Table 9). This was true whether branch-antlered bull survival was modeled with a single zone-specific parameter or with parameters that were specific to subadult and adult bulls in each zone. However, 95% confidence intervals on these zone-specific survival parameters for branch-antlered bulls overlapped broadly, and the magnitudes of the differences in point estimates were typically modest (0.02-0.07).

In general, branch-antlered bull survival estimates were high (only 1 estimate <0.80 in models without a year effect), rivaling estimates of adult cow survival. Annual survival rates we estimated for bulls at least 2-yrs-old were lower in 2006 compared to 2003-2005 for all 3 datasets, although 95% confidence intervals on estimated survival were relatively wide for 2006 estimates.

We did not include models in our candidate model set invoking annual variation in yearling bull survival. We did not believe our data were sufficient to effectively model such fine-scale variation; parameter estimates in such models tend to confound sampling error with process variation (Burnham and Anderson 2002). We did, however, derive *maximum likelihood* estimates of yearling bull annual survival across years as a simple data exploration step.

Assuming no zone variation, we estimated yearling bull annual survival at 0.37±0.10 (±SE) in 2003, at 0.38±0.10 in 2004, and at 0.51±0.12 in 2005. Year-specific estimates of yearling bull survival allowing for zone variation were: LVZ = 0.48±0.14 (2003), 0.47±0.16 (2004), and 0.37±0.18 (2005), and HVZ = 0.26±0.12 (2003), 0.33±0.12 (2004), and 0.60±0.15.

Because of relatively large standard errors, the coefficients of variation (CV) ranged 24-26% for yearling bull annual survival estimates without zone variation and 25-50% for estimates allowing both zone and year variation. Based on model likelihoods allowing annual variation in yearling bull survival, but constraining branch-antlered bull and cow survival (*i.e.,* B-A ♂ (.), Adult ♀ (.) models), these models would not have competed well against the 9 models in the candidate model set.

The precision of the survival estimates in our candidate models, as indexed by the CV, were reasonably good (*i.e.,* most CVs < 10%) (Table 10). Yearling bull survival estimates were the least precise, with CVs ranging ~15-21%. Survival estimates for elk >1-yr-old had CVs of 3.6-7.7%, in models without zone-specific parameters, and 4.5-11.0% in models with zone-specific parameters.

In general, parameter estimates were most precise for Data A and Data C models; Data B was the most rarified dataset and produced estimates with slightly higher CVs (Table 10).

Table 10. Coefficients of variation (%) (CV = SE(S) × 100 / S) for survival parameters in the 9 candidate survival models for radiomarked Blue Mountains elk, 2003-2006. Data A = all marked elk; Data B = 2003 February-marked adults omitted; Data C = 2003 February-marked adults censored after 1 yr.

Parameter	Data A	Data B	Data C
Yearling ♂ (.) [a]	14.79	14.79	14.79
Yearling ♂ (HVZ) [b]	20.70	20.70	20.70
Yearling ♂ (LVZ) [c]	20.98	20.98	20.98
SubAd ♂ (.)	5.52	6.13	5.64
SubAd ♂ (HVZ)	7.27	7.54	7.36
SubAd ♂ (LVZ)	8.41	10.53	8.74
Adult ♂ (.)	4.73	6.78	5.13
Adult ♂ (HVZ)	10.36	9.92	9.45
Adult ♂ (LVZ)	5.21	9.25	6.05
B-A [d] **♂ (.)**	3.60	4.55	3.83
B-A ♂ (HVZ)	5.96	6.01	5.82
B-A ♂ (LVZ)	4.45	6.95	5.02
B-A ♂ (03-05)	3.68	5.12	4.07
B-A ♂ (06)	9.46	9.16	9.16
B-A ♂ (03-05, HVZ)	6.58	6.47	6.29
B-A ♂ (06, HVZ)	12.35	12.35	12.35
B-A ♂ (03-05, LVZ)	4.35	8.12	5.32
B-A ♂ (06, LVZ)	14.67	13.41	13.41
Adult ♀ (.)	5.94	7.65	6.49

[a] (.) survival model assumed no zone or year variation for the parameter.

[b] (HVZ) survival parameter estimate specific to the hypothesized high vulnerability zone (GMU 166, 175).

[c] (LVZ) survival parameter estimate specific to the hypothesized low vulnerability zone (GMU 162, 169).

[d] B-A ♂ = branch-antlered bull. Parameter constrained survival to be equal for subadult and adult bulls.

Mortality Sources

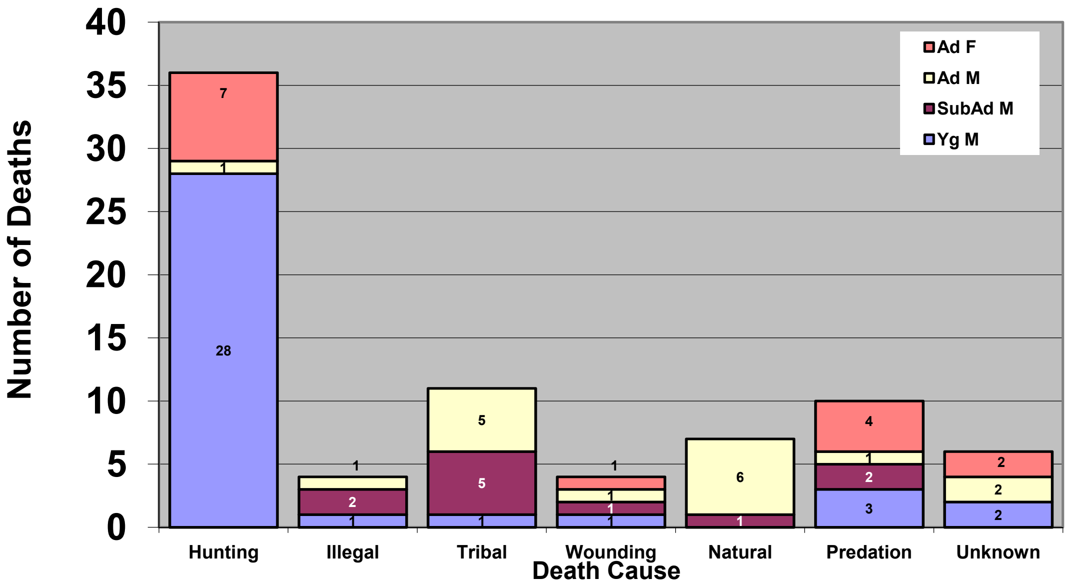


Figure 7. Sources of mortality for radiomarked elk by demographic class in the Washington Blue Mountains, 2003-2006 (years pooled).

We recorded the known deaths of 78 radiomarked elk during our 4-year study, and we had evidence of proximate causes for 72 deaths. Deaths due to legal, state-licensed hunting were most common ($n = 36$ hunter-retrieved, 4 wounding losses), and the majority of these hunter-killed elk were yearling bulls killed during general, spike-only seasons (Fig. 7). Of 28 yearling bull kills attributed to state-licensed hunters, we had direct reports from hunters or other unequivocal evidence of a state-licensed hunter kill for 23 kills (82.1%). The other 5 were classified based on the *a priori* cause-of-death criteria defined in Table 3. The 1 state hunter kill of an adult bull was reported by the hunter.

Hunting kills by state-licensed hunters predominated among adult cow deaths ($n = 7$ recovered kills among 14 deaths). Three of the cow elk killed by state-licensed hunters were taken in elk damage areas. We had specific evidence of a state hunter kill for 5 of 7 of the cow elk kills attributed to state-licensed hunting; the other 2 cow kills assumed to represent state hunter kills were classified based on timing and location. Most subadult bull deaths were due to tribal hunting ($n = 5$), and most mature adult bulls (≥ 4 yr-olds) died as a result of natural causes ($n = 6$) and tribal hunting ($n = 5$). Of the 10 branch-antlered bull kills we attributed to tribal hunting, 1 was reported by a tribal hunter, 3 were cases where the radiotransmitters were retrieved from tribal communities, 1 was reported by a tribal wildlife enforcement officer, 1 was classified based on a vehicle seen at the kill site and later linked to a tribal hunter, and 4 were based on the *a priori* criteria in Table 3.

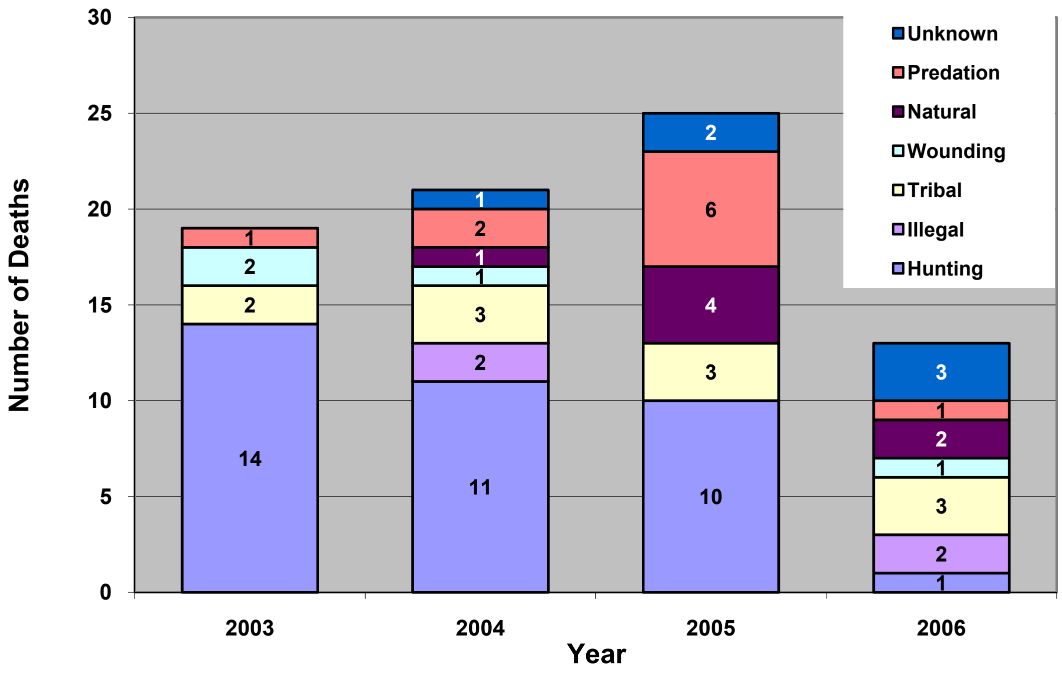


Figure 8. Sources of mortality for radiomarked elk across years, 2003-2006 (demographic classes pooled).

Among the non-predation, natural causes of adult bull deaths were 2 bulls that were killed in a large wildfire (Aug 2006), 2 apparent deaths from rut fight injuries, a bull that succumbed to a neck neoplasm, and a bull that died of malnutrition in January 2006.

Predators killed radiomarked elk of all sex/age classes, and predation was the third most common mortality source. We documented only 4 illegal kills of radiomarked elk (1 adult bull, 2 subadult bulls, and 1 yearling bull) during 2003-2006. All 4 of the illegal kills were classified on the basis of circumstantial evidence consistent with the criteria in Table 3.

Across years, we recorded 19 radiomarked elk deaths in 2003, 21 in 2004, 25 in 2005, and 13 in 2006 (Fig. 8). Hunting deaths by state-licensed hunters predominated in all years but 2006. The drop in hunting deaths associated with state-sanctioned seasons in 2006 was clearly due to the absence of a radiomarked yearling bull cohort the last year of the study. Tribal hunting deaths were relatively constant across years (*n* = 2-3 annually), and all occurred in the HVZ subarea. Predation and other natural deaths were most common (*n* = 10) in the 2005 survival year (*i.e.*, May 2005-Apr 2006).

Across years, we recorded 26 total known-cause deaths among radiomarked branch-antlered bulls. We recorded 3 deaths in 2003, 3 in 2004, 7 in 2005, and 13 in 2006 (Fig. 9). Tribal kills predominated in 2003 and 2004. Across years, the dominant sources of mortality were tribal hunting and natural causes; each cause accounted for 10 total deaths. Few branch-antlered bulls died as a result of legal state-licensed hunting, wounding loss, or illegal kills. Deaths of radiomarked branch-antlered bulls were nearly

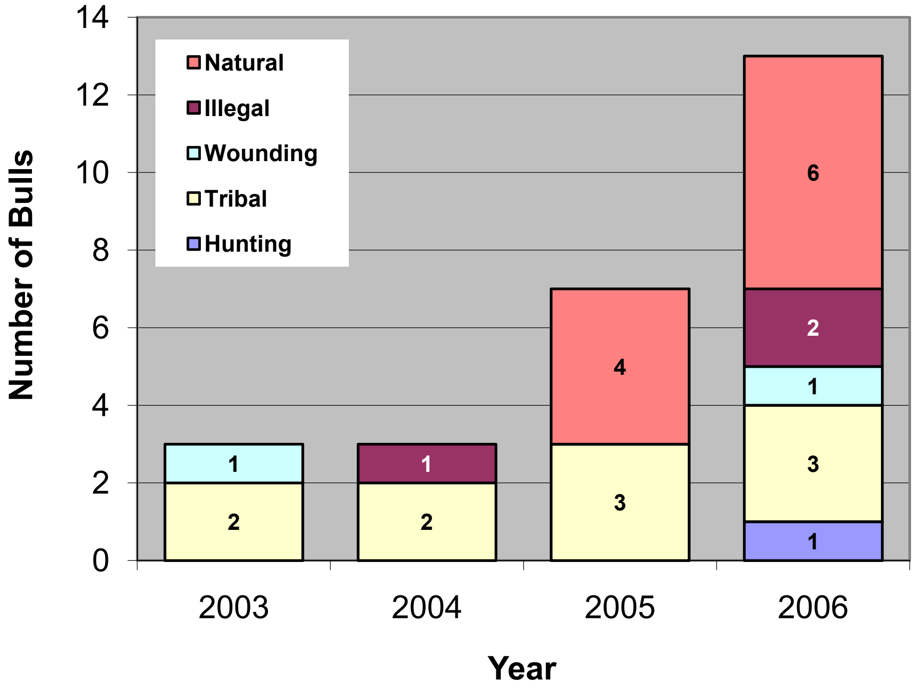


Figure 9. Sources of mortality for radiomarked branch-antlered bulls across years, 2003-2006 (n = 26).

twice as high in 2006 than in any other year. Deaths recorded in 2006 were nearly evenly split between natural causes (*n* = 6) and human-caused deaths (*n* = 7).

Pooling mortality data across years, we detected elk deaths in every month (Fig. 10). Most mortality occurred in the fall, with 50 of 77 known month deaths (64.9%) occurring during Sep-Nov, and 60 of 77 deaths (77.9%) occurring during Aug-Dec. Considering the subsample of human-caused deaths, 46 of 53 deaths (86.8%) with precise month assignments occurred during Sep-Nov, and 49 of 53 (92.5%) occurred during Aug-Dec (Fig. 11). Ten of 11 tribal kills (90.9%) occurred during Sep-Oct, and the 4 illegal kills we detected occurred in February, June, October, and December (1 each month).

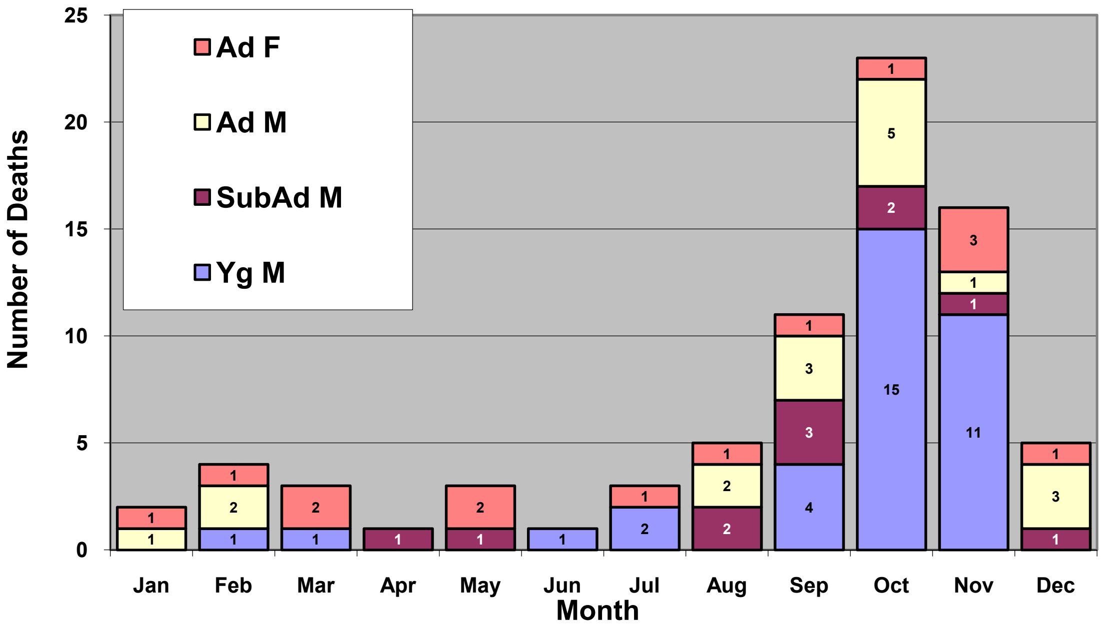


Figure 10. Monthly distribution of radiomarked elk deaths due to all causes (all years pooled).

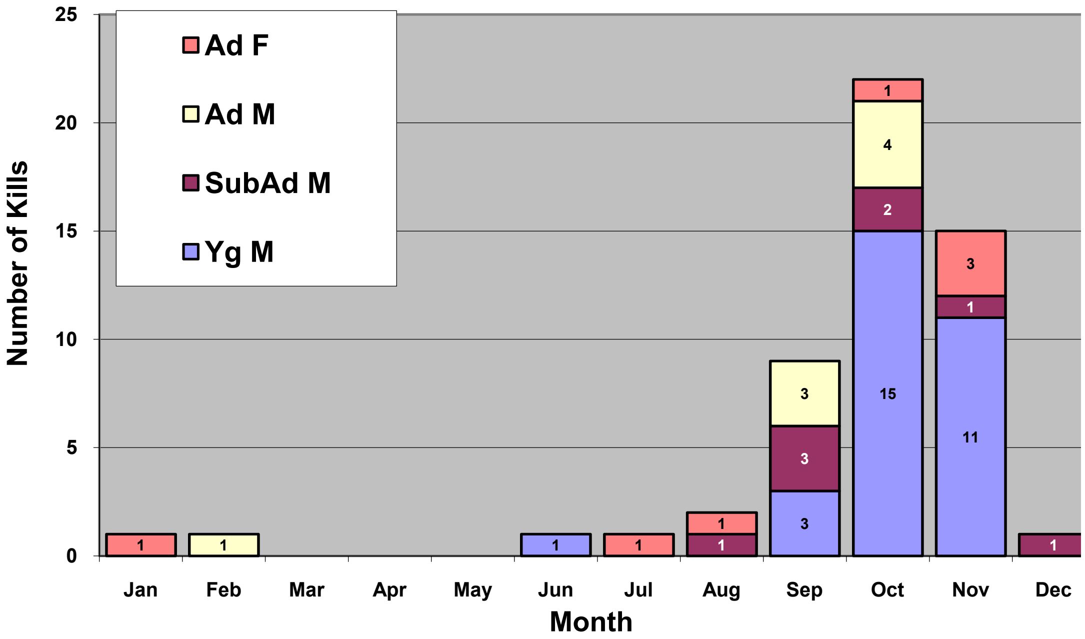


Figure 11. Monthly distribution of human-caused, radiomarked elk deaths (all years pooled).

Estimates of cause-specific mortality rates suggested differences in both risks *due-to-cause* and the timing of risks throughout the year (Fig. 12). In contrast to the major hunting-related risks, risks from other causes were relatively constant across the year. Most of the deaths in this category were from natural sources, and individual natural mortality sources were often associated with different periods (*e.g.*, nutritional deprivation typically was limited to mid-to-late winter, rut injury deaths and the fire-related deaths we detected occurred in late summer and fall).

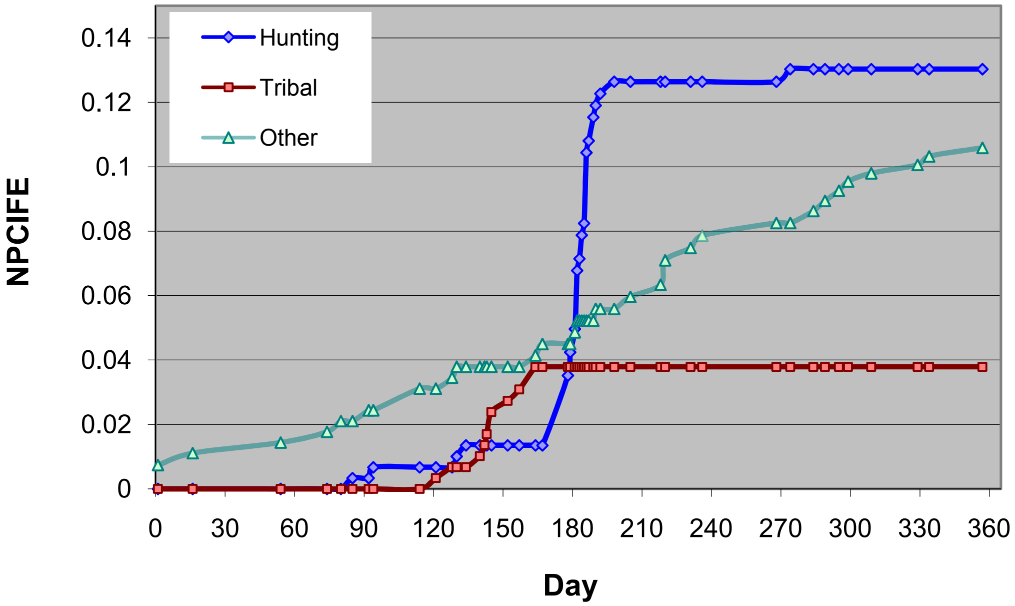


Figure 12. Cause-specific mortality functions derived using the Nonparametric Cumulative Incidence Function Estimator (NPCIFE) for 3 mortality sources: 1) Hunting = legal state-sanctioned hunting kills and wounding losses; 2) Tribal = tribal hunting kills, and 3) Non-harvest = deaths due to non-hunting sources of mortality. Day 1 = 1 May, Day 180 = 27 Oct, Day 365 = 30 Apr.

Risk of death due to state-sanctioned recreational hunting was the highest risk to marked elk in our study (collectively). This risk predictably increased slowly in early fall, rose dramatically in late October, and largely ended by the second week of November, following the pattern of legal hunting seasons. Risk from tribal hunting was the lowest of the 3 risks we estimated rates for, with a total approximate risk ratio relative to state-licensed recreational hunting of 0.29, based on estimates of annual risk (Table 11). Risk due to tribal hunting appeared to begin about the last week of August, rose rapidly during September, and largely disappeared after mid-October. The risk due to tribal hunting peaked earlier than the risk due to state-licensed recreational hunting.

Table 11. Estimates of annual Cause-specific mortality rates for 3 mortality sources on Blue Mountains elk, 2003-2006 (all age/sex classes combined). Mortality sources affecting radiomarked elk were treated as competing risks using the nonparametric cumulative incidence function estimator (NPCIFE).

Cause	NPCIFE Estimate	Lower 95% *CI*	Upper 95% *CI*
State Hunting	0.130	0.095	0.165
Tribal Hunting	0.038	0.018	0.058
Other	0.106	0.071	0.141

Vulnerability Factors

The criteria we used for defining potentially *at risk* samples of elk use (live elk relocations and death sites) resulted in modest sample sizes for the vulnerability factors analysis (*i.e.*, 102 live elk sites and 25 death sites for the case vs. control design and 216 live elk sites and 27 death sites for the sampling with replacement design). Among the landscape and elk use metrics we considered as potentially influencing elk harvest risks, we found that means differed between live and dead elk sites only for road-related metrics (Tables 12, 13).

Dead elk sites were located closer to roads than were live elk sites, and road densities were higher near dead elk sites relative to live elk sites, at both scales of analysis. Mean values for topographic complexity and diversity, and relative amounts of closed canopy habitats and public land were similar between dead elk and live elk sites.

Not only were means for non-road metrics not statistically different for live vs. dead elk sites, but point estimates of the means were qualitatively counter-intuitive for several metrics (*e.g.*, higher topographic complexity and diversity, more moderately closed canopy forest, less public ownership for dead elk sites relative to live elk sites).

The differences between live and dead yearling bull elk sites in the fall relative to distance-to-roads were also clearly apparent in scattergrams of the data (Figure 13). Death sites occurred at distances-to-roads characteristic of the lower end of distances-to-roads detected for live elk relocations. Due to considerations outlined in the Methods section, we did not attempt to statistically contrast distance-to-road metrics for live and dead elk sites for other demographic classes of radiomarked elk or for any elk site outside of our date range criteria.

We did, however calculate descriptive statistics for the dead elk sites (human-caused deaths only) not included in our vulnerability factors analyses. The means (SE) for RDDIST were 35.77 (11.06) and 12.72 (4.61) decameters for illegal kill (n = 4) and tribal kill sites (n = 6) not included in our vulnerability factors analyses, respectively. These were qualitatively similar (*i.e.*, close to roads) to means for dead elk sites in our vulnerability factors analyses.

Table 12. Results of univariate t-tests comparing means for live elk radiolocations (n = 102) and harvest-related dead locations (n=25) under the case vs. control design. Some covariates reflect point samples and some reflect means derived from circular landscape sampling frames consisting of a 250-m or 450-m radius circle centered on the live or dead elk site. See Table 5 for details on covariates.

Covariate	$Mean_{live}$	$Mean_{dead}$	t	*P*-value
RDDIST	74.71	28.38	3.82	<0.001
$RDDENS_{250}$	1.10	1.94	-1.83	0.08
$RDDENS_{450}$	1.15	1.88	-2.17	0.03
VRM_{point}	0.008	0.009	-0.59	0.56
$VRM_{250mean}$	0.007	0.008	-0.38	0.71
$VRM_{450mean}$	0.007	0.007	0.05	0.96
$TDIV_{250}$	2.96	3.07	-0.32	0.75
$TDIV_{450}$	3.14	3.13	0.02	0.98
SLP	18.35	16.55	0.80	0.42
$CLFOR_{250}$	0.13	0.12	0.18	0.85
$CLFOR_{450}$	0.12	0.11	0.36	0.72
$MDFOR_{250}$	0.49	0.54	-0.86	0.39
$MDFOR_{450}$	0.47	0.50	-0.44	0.66
OWN_{250}	0.79	0.64	1.44	0.16
OWN_{450}	0.79	0.64	1.43	0.16
LOC_{250}	1.43	1.28	0.26	0.79
LOC_{450}	3.07	4.20	-1.02	0.31

Table 13. Results of univariate t-tests comparing means for live elk radiolocations (n = 216) and harvest-related dead locations (n = 27) allowing sampling with replacement. Some covariates reflect point samples and some reflect means derived from circular landscape sampling frames consisting of a 250-m or 450-m radius circle centered on the live or dead elk site. See Table 6 for details on covariates.

Covariate	$Mean_{live}$	$Mean_{dead}$	t	*P*-value
RDDIST	64.14	26.66	4.90	<0.001
$RDDENS_{250}$	1.18	2.02	-2.01	0.05
$RDDENS_{450}$	1.18	1.93	-2.50	0.01
VRM_{point}	0.008	0.010	-1.12	0.27
$VRM_{250mean}$	0.007	0.008	-0.58	0.56
$VRM_{450mean}$	0.007	0.008	-0.11	0.91
$TDIV_{250}$	2.99	3.12	-0.43	0.67
$TDIV_{450}$	3.14	3.19	-0.15	0.88
SLP	18.87	16.81	0.99	0.32
$CLFOR_{250}$	0.14	0.12	0.60	0.55
$CLFOR_{450}$	0.11	0.10	0.39	0.70
$MDFOR_{250}$	0.49	0.54	-1.02	0.31
$MDFOR_{450}$	0.46	0.49	-0.44	0.66
OWN_{250}	0.72	0.59	1.27	0.22
OWN_{450}	0.72	0.59	1.27	0.21
LOC_{250}	1.77	1.22	1.00	0.32
LOC_{450}	3.91	4.37	-0.44	0.66

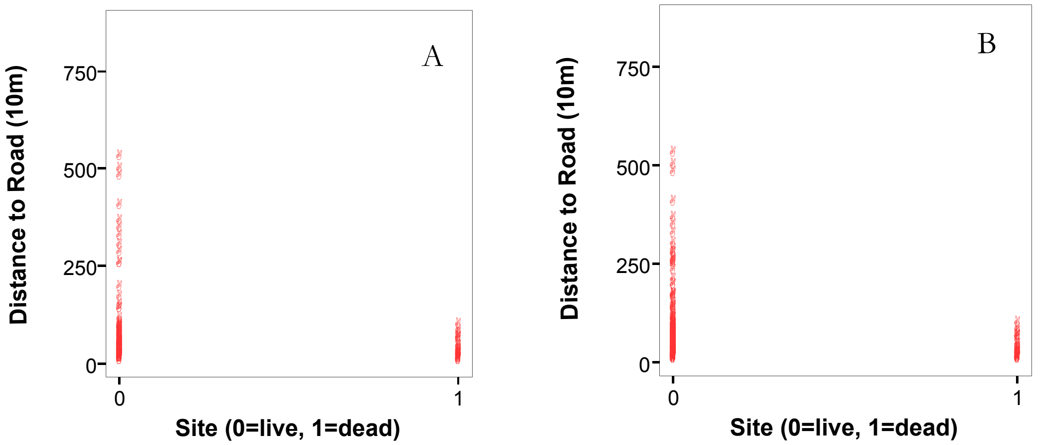


Figure 13. Scattergrams for Distance-to-road (decameters) for fall relocations of live yearling bull elk and death sites for harvested yearling bulls (A = Case vs. Control design [n = 25, 102]; B = all sites meeting sample selection criteria for age/sex class and date [n = 27, 216]).

The distance-to-road metric and the road density metrics at both scales were related to the outcome variable in univariate logistic regression analyses under both analytic designs (Table 14). Based on Hosmer-Lemeshow goodness-of-fit test statistics, all models fit the data adequately. Based on results from tests of the equality of means, we did not consider any univariate logistic regression models for non-road covariates. Due to high correlations among all road metric covariates (Kendall's $|\tau| \geq 0.70$), we also did not evaluate any multivariate logistic models.

Table 14. Results for univariate logistic regression models relating road metrics to the binary outcome (0 = live, 1 = dead) for the case-control design (n = 127) and sampling with replacement design (n = 243).

Model	-2LL[a]	X^2	df	P-value	G-O-F[b]
Case-Control Design					
RDDIST	118.62	7.36	1	0.007	0.16
RDDENS$_{250}$	121.99	4.00	1	0.05	0.99
RDDENS$_{450}$	121.66	4.32	1	0.04	0.31
W/ Replacement					
RDDIST	160.57	8.96	1	0.003	0.90
RDDENS$_{250}$	164.81	4.72	1	0.03	0.94
RDDENS$_{450}$	163.98	5.55	1	0.02	0.44

[a] −2 log likelihood for the model.
[b] Hosmer-Lemeshow goodness-of-fit test *P*-value.

Coefficient estimates from univariate logistic regression modeling indicated logical relationships between the outcome variable and road metric covariates: the odds of a site being a dead elk site increased with proximity to roads and with increasing road density, under both analytic designs and at both scales (Table 15). With each increase of 10 meters (32.8 ft) further from a road, the odds of a sample elk site being a dead elk site was estimated to be ~0.99; a 100 meter (328 ft) increase in the distance to a road would imply a reduction in the odds of a site being a dead elk site of ~0.88 (i.e., $e^{10 \times -0.013}$).

This implied a real, but modest effect of proximity to roads as a vulnerability factor. The odds ratio for the road density metrics implied an increase in the odds of a sample site being a dead elk site of ~1.3 with each increase of 1 km of road per km^2 (~1.6 mi/mi^2) (Table 15).

Table 15. Coefficient estimates from univariate logistic regression modeling of road metrics vs. binary outcome (0 = live, 1 = dead) for the case-control design (n = 127) and sampling with replacement design (n = 243).

Covariate	**B**	**SE(B)**	**df**	***P*-value**	**Odds Ratio**	**Odds Ratio 90% *CI***
Case-Control						
RDDIST	-0.013	0.007	1	0.07	0.987	0.986-0.988
$RDDENS_{250}$	0.230	0.114	1	0.04	1.259	1.241-1.277
$RDDENS_{450}$	0.291	0.139	1	0.04	1.337	1.314-1.361
W/ Replacement						
RDDIST	-0.015	0.007	1	0.03	0.985	0.984-0.986
$RDDENS_{250}$	0.224	0.100	1	0.03	1.252	1.236-1.267
$RDDENS_{450}$	0.298	0.124	1	0.02	1.347	1.326-1.368

Although road metrics were related to the odds of an elk site being a dead elk site, they were not good absolute predictors of the outcome. Probabilities of a sample site being a dead elk site under the RDDIST models, with the covariate set equal to zero distance (*i.e.*, maximal *distance-to-road* effect), are defined by the model intercepts and would be estimated at 0.30 (*SE* = 0.31) and 0.18 (*SE* = 0.28), for the case-control and sampling with replacement designs, respectively.

For the RDDENS covariates, predicted probabilities at a road density of 1.0 km per km^2 would range 0.10-0.18, and predicted probability of an event (*i.e.*, site is a dead elk site) would not rise above 0.50 until the road density exceeded 6.0 km per km^2 (~9.6 mi/mi^2) for the model with the greatest predicted effect (450-m scale, case-control design).

DISCUSSION

Our work was principally motivated by questions about unreported sources of human-caused elk mortality in the Washington Blue Mountains. In particular, the WDFW, the public, and the NPT and CTUIR all shared concerns about levels of illegal hunting mortality on the adult bull subpopulation, based on enforcement reports during 2001-2003. Documented poaching losses of this magnitude were considered problematic, especially given that such illegal kills are always under-reported.

WDFW elk managers and the public had also been unable to characterize the potential contribution of legal tribal hunting to recent, cumulative human-caused elk mortality in this population, due to the absence of harvest reporting by the 2 tribes with treaty hunting rights in the Washington Blue Mountains.

At the same time we were planning and implementing our investigation, enforcement efforts had been intensified to identify and prosecute elk poachers, and several successful prosecutions occurred. Concurrently, legal state-sanctioned take of branch-antlered bull elk was reduced, due to uncertainty about current mortality rates.

Survival

The use of rumen-implanted radiotransmitters seemed initially like a good fit to the questions we were attempting to address. In practice, it proved difficult to monitor elk in our study through the use of these radios alone. Their typical reception range was much more limited than characteristic of neck radiocollars, even for the best implants, and our efforts were substantially complicated by the vendor manufacturing error in the first batch of rumen radios we deployed. Collectively, these issues created unanticipated levels of censored radios, which were particularly problematic for elk marked during our first capture session in February 2003.

We dealt with the censor issue in our analyses principally by creating 3 alternate datasets, wherein 1 was the full dataset and 2 consisted of different levels of data rarification relative to elk marked with the most problematic implant radios. This strategy potentially invoked the question, if the survival analyses across datasets did not yield convergent results, as to which dataset was best and supported the most reliable inference? The results of final survival model selection were similar across datasets, but clearly not identical.

Because several models made up the ~90% confidence model set across datasets, it is not appropriate to make inference based only on a single top model, and the following discussion includes allowance for model selection uncertainty. We would note that this is not an unusual situation, nor does it preclude making sense of the survival models analysis (Burnham and Anderson 2002).

The most basic questions embodied in our survival model parameterizations were:

- Was there evidence of differences in annual survival between subadult and adult bulls?
- Was there evidence of survival rate differences reflecting different levels of harvest vulnerability east and west of the Tucannon River?

Survival modeling suggested relatively similar risks of mortality for radiomarked subadult and mature adult bulls during 2003-06.

The highest model weight for any model that allowed different survival rates for subadult (2-3-yr-olds) and adult (≥ 4 yr-olds) bulls was 0.14; this model was the 4th rated model for Data A and Data B models; it was the 3rd best model among Data C models. This suggested relatively minimal evidence of differences in survival of radiomarked young and older branch-antlered bulls during our study; models that assumed no difference in survival among these 2 age groupings had more support in the data. Further, for models that differed only relative to whether branch-antlered bull survival was modeled with a single parameter or 2, age-class parameters, the simpler model always ranked higher.

There was some evidence for a vulnerability zone effect on bull survival, but it was equivocal. The highest ranked model that invoked zone variation in survival was the 4-parameter model with zone-specific parameters for branch-antlered bulls (≥ 2-yr-olds), but no zone differences for yearling bulls. This model ranked 3rd for Data A and Data B (w_i = 0.11-0.13); it ranked 4th for Data C (w_i = 0.13).

Another way of looking at the results of the survival analyses to assess support for the hypothesized zone effect, is to contrast models that differed only relative to whether they modeled a zone effect or not [e.g., model Ylg ♂ (.), B-A ♂ (.), Ad ♀ (.) vs. model Ylg ♂ (.), B-A ♂ (zone), Ad ♂ (.)]. In all such contrasts among our candidate models, the model assuming no zone effect ranked higher than the one that invoked zone-specific survival. Our formal model selection criteria invoked the principle of parsimony, wherein simpler models generally are favored unless additional parameters greatly improve the likelihood of the observed data, and the estimates for all model parameters are relatively precise.

Thus, although in most cases point estimates of zone-specific survival were lower for HVZ bulls (of all ages), parsing out the encounter history data between the 2 zones resulted in relatively lower-precision parameter estimates. The absolute magnitudes of differences in zone-specific survival estimates were also typically modest.

These 2 factors predictably precluded the zone-specific models from competing well in a multi-model inference framework. However, based on the consistency in the qualitative relationships among zone-specific survival estimates for bulls (i.e., usually lower survival for the HVZ bulls), we are reluctant to conclude that the hypothesized zone effect on survival does not exist. Particularly in light of adult sex ratio data stemming from annual management surveys, but also due to the inclusion of model Ylg ♂ (.), B-A ♂ (zone), Ad ♀ (.) among the confidence model sets. Also, all 11 of the tribal kills occurred in the HVZ. But, we acknowledge that our data provided only modest support for an area-mediated effect on bull survival.

The demographic class with the lowest annual survival among our radiomarked elk was yearling bulls. This was a logical outcome given that most general season harvest was directed at this class by regulation. Included among our survival models were models that either had a single parameter for yearling bull survival, or 2 zone-specific parameters.

The actual parameter estimates for yearling bulls were consistent with the hypothesized zone effect on survival (*i.e.*, HVZ yearling survival was substantially lower than LVZ yearling survival). However, losses of yearling bulls from our radiomarked cohorts demonstrated considerable annual variation, and because these samples did not accumulate over time (*i.e.*, each cohort could only be used to model yearling bull survival for a single year), precision of the yearling bull survival estimates was relatively low. For this reason, models that had a single yearling bull survival parameter always ranked higher than those that allowed zone-specific survival estimates.

Our ability to model yearling bull survival with zone-specific parameterizations was also complicated by movements of radiomarked yearling bulls between marking in spring and hunting seasons in the fall, resulting in very small sample sizes for 1 zone in some years.

One interesting result we obtained was the relatively competitive performance of the 4-parameter model that had single survival parameters for yearling bulls and adult cows, but modeled branch-antlered bull survival using different parameters for the 2003-2005 period vs. 2006. This model ranked 1st for Data A and 2nd for Data B and Data C (w_i = 0.20-0.41), despite 1 of the branch-antlered bull survival parameters being estimated from a single year's data. This result suggested that bull survival differed during the 2 time periods embodied in the model parameterization.

The period-specific bull survival parameter estimates from this model were substantively different (0.07-0.13) across all 3 datasets, indicating lower branch-antlered bull survival in 2006 for all datasets. Although this result was consistent with an increased quota for *any bull* permits during 2006, cause-of-death data indicated that mortality differences between the 2 periods was mostly due to high natural mortality among radiomarked branch-antlered bulls in 2006. So, although our survival modeling provided support for a difference in branch-antlered bull survival in 2003-2005 vs. 2006, that result seemingly had little to do with increased *any bull* permits near the end of our study.

Overall, the simplest models among our candidate model set were the best supported; the top 4 models for each dataset consisted of all of the 3 and 4 parameter models. The top 4 models provided support for similar survival across young and older branch-antlered bulls, modest evidence of a zone effect on survival for branch-antlered bulls only, and suggested a decrease in survival for branch-antlered bulls in 2006 relative to 2003-2005.

Based on the actual parameter estimates, survival of radiomarked subadult (2-3 yr-olds) and adult bulls (≥ 4yr-olds) during our study was high, rivaling that of adult cows (≥ 0.80). Survival this high for male elk has generally been atypical in hunted populations. In an earlier study of elk mortality across 3 populations in Washington, Smith et al. (1994) estimated bull survival at 0.49 (Mt. St. Helens herd), 0.34 (Colockum herd), and 0.23 (Olympic herd). McCorquodale et al. (2003) estimated annual adult bull survival at 0.65 during 1992-1999 in a population harvested by both tribal and state-licensed hunters along the east slopes of the Washington Cascades.

In a study of bull elk mortality in north-central Idaho, Unsworth and Kuck (1991) estimated annual branch-antlered bull survival at 0.41 in a roaded study area and 0.78 in a roadless area, and Hurley and Sargeant (1991) estimated subadult bull survival at 0.40 and adult bull survival at 0.60 in a managed elk population in western Montana. Prior to our investigation, Myers et al. (1999b) estimated mean annual adult bull survival at 0.74 in the Washington Blue Mountains from a modest sample of radiomarked bulls.

Although spike-only general season management has been in place in the Washington Blue Mountains since 1989 and has been employed to some degree in Oregon, Idaho, and Montana as well, we could find only 1 published study of yearling bull survival under this management scheme, based on fates of radiomarked bulls. Vore and DeSimone (1991) calculated naïve survival (*i.e.*, n_{dying} / n_{total}) for all radiomarked yearling bulls under a spike-only general season in the Elkhorn Mountains of Montana at 0.38, and at 0.29 for legal spikes (*i.e.*, 1 × 1, 1 × 2).

Yearling bull survival has been estimated under other bull harvesting schemes. Beiderbeck at al. (2001) estimated yearling bull survival using harvest data and regression techniques at ~0.30-0.40 under *any bull* regulations in western Oregon. Hurley and Sargeant (1991) estimated yearling bull survival from radiomarked elk at 0.59 in a western Montana area managed under *any bull* regulations. Unsworth and Kuck (1991) estimated yearling bull survival at 0.44 and 0.79 in a roaded and roadless area of north-central Idaho under any bull management.

We estimated annual survival for radiomarked yearling bulls in our study at 0.41 under our best-supported survival models. Statistically plausible survival rates for yearling bulls in our study were about ~0.30-0.50, not attempting to model annual variation in true survival. Spike only general seasons direct most legal hunting mortality towards the yearling cohorts in the bull subpopulation; yearling survival should be lower under this management scheme than under *any bull* regulations. The yearling mortality rate (*i.e.*, $1 - S$) we documented for the Washington Blue Mountains was clearly not excessive, suggesting moderate general season hunting pressure and relatively good recruitment of bulls annually into the branch-antlered bull subpopulation.

We estimated annual survival of radiomarked cow elk at approximately 0.80-0.84 during our study. Gaillard et al. (1998) summarized population dynamics for a variety of large herbivores in attempting to define the most variable and influential vital rates in these populations, and they provided reference values for adult cow elk survival of 0.89-0.92 from long-term studies. Our estimated survival for adult cows was lower than this, but was very similar to a previous estimate for the Washington Blue Mountains (S = 0.80, 95% CI = 0.70-0.88) provided by Myers et al. (1999*b*). Stussy et al. (1994) estimated annual adult cow elk survival was 0.92 in the Oregon Cascades, and McCorquodale et al. (2003) estimated adult cow survival at 0.83 for a Washington Cascades elk population. Smith et al. (1994) estimated adult cow elk survival at 0.87, 0.86, and 0.82 for Washington elk in the Colockum, Olympic, and Mt. St. Helens herds. Ballard et al. (2000) provided a meta-analysis estimate of annual survival for adult cow elk in hunted populations in Arizona of 0.90.

Mortality Causes

The dominant source of mortality for our radiomarked elk was intentional kills by people, accounting for ~76% of all known-cause mortalities. Harvest associated with legal, state-sanctioned hunting accounted for 55.5% of all known-cause mortalities and 72.7% of all human-caused mortalities. This was remarkably similar to results obtained during a previous study of Blue Mountains elk in Washington, where legal, state-sanctioned hunting accounted for 55.5% of all known-cause deaths and 71.4% of all human-caused deaths (Myers et al. 1999b).

In the previous Blue Mountains study most hunting deaths were of radiomarked cow elk, whereas in our study most marked elk were bulls, as were most hunting deaths. Collectively, these proportions were not appreciably different than results obtained in another Washington study using radiomarked elk from 3 other herds (Smith et al. 1994). In that study, conducted during 1988-92, ~82% of all known-cause mortalities were human kills; legal, state-sanctioned hunting in that study accounted for 61.2% of all mortalities and 74.8% of all human-caused deaths.

In our study, state-licensed hunters predominantly killed yearling bulls due to general season regulations (72.5% of all state-sanctioned kills). Bull elk hunting during the Smith et al. (1994) study was under a mix of *any bull* and *branch-antlered bull only* general season regulations across their 3 study areas; less than 20% of all state hunter kills and ~25% of state hunter bull kills were yearling bulls in their study.

Tribal hunting during our study accounted for ~15% of all known-cause deaths and was the second most common mortality cause. In an earlier study, tribal hunting accounted for ~11% of all known-cause marked elk deaths and removed about 1/5 as many elk as did legal, state-sanctioned hunting in the Washington Blue Mountains (Myers et al. 1999b).

In our study tribal kills were a little more than 1/4 the magnitude of legal, state hunter kills. Elsewhere in Washington where tribal hunting occurred, Smith et al. (1994) found that tribal kills accounted for ~7% of all known-cause elk deaths and were about 1/6 the magnitude of legal, state hunter kills. It is important to note that the *proportion* of all deaths attributable to tribal hunting (or any other cause) is not an estimate of the probability of elk dying due to that cause; these proportions are based only on the number of elk dying, not on numbers of elk at risk (information on the latter would be required to estimate *probability* of mortality).

During our study, tribal hunters predominantly killed adult and subadult bulls from our marked elk sample. We estimated risk (*i.e.*, probability of death) to branch-antlered bulls from tribal hunting by censoring all other causes of death under a known-fate model; estimated annual risk (*i.e.*, the probability that a radiomarked branch-antlered bull was killed by a tribal hunter) was 0.056 (95% *CI* = 0.029-0.096).

In recent years, the reported state-sanctioned general season elk harvest in the GMUs representing the Blue Mountains elk herd area has been approximately 140-165 elk. Based on our results, tribal harvest would be expected to have removed approximately 35-45 total elk annually during the same period if estimated on the basis of the magnitude of tribal kills relative to state hunter kills.

Based on our results, a substantive number of the elk killed by tribal hunting may have been branch-antlered bulls. Based on our estimate of tribal hunting risk *specific to radiomarked branch-antlered bulls* (0.056; see previous paragraph) and the average number of branch-antlered + yearling bulls counted in late winter surveys (*i.e.*, the next hunting season's branch-antlered bulls), 2004-2007 (~495), tribal harvest would have been expected to remove approximately ~28 branch-antlered bulls annually (14-47 bulls based on 95% *CI* of the risk estimate). These coarse approximations are relatively congruent.

Off-reservation tribal kills are a legal source of hunting mortality, but in the Washington Blue Mountains, off-reservation tribal harvest has never been formally accounted for in harvest management, despite that it appears to contribute in a nontrivial way to cumulative human-caused mortality. Tribes have been reluctant to report off-reservation hunting kills presumably because of cultural and political sensitivities (McCorquodale 1997, 1999).

Despite documentation of high levels of illegal elk harvest in the Washington Blue Mountains just prior to our work, we detected only minimal losses (*n* = 4) of radiomarked elk to illegal harvest. Illegal kills represented only ~5% of all known-cause deaths and ~7% of all human-caused deaths. We detected only a single illegal kill of a trophy-class mature bull.

During the earlier Blue Mountains elk study, illegal elk kills represented ~11% of all known-cause deaths and ~14% of all human-caused deaths (Myers et al. 1999b). All illegal kills during the earlier study were of adult cows, but only a few radiomarked bulls were monitored in that effort. Elsewhere in Washington, Smith et al. (1994) found that illegal kills represented ~15% of all known-cause mortalities and ~19% of all human-caused elk deaths.

In a study of elk mortality in the south-central Cascades of Washington, illegal kills represented ~7% of all known-cause deaths and ~8% of all human-caused deaths (McCorquodale et al. 2003). In an Idaho study, illegal kills comprised ~5% of human-caused bull elk deaths (Unsworth et al. 1993).

Our results suggested recent enforcement efforts in the Washington Blue Mountains had been successful in reducing levels of illegal harvest occurring just prior to our investigation. The apparent reduction in illegal take of adult bulls, as measured by radiomarked elk deaths, was consistent with WDFW Enforcement's perceptions during our study: there was a substantial drop in field reports of suspicious elk carcasses during 2003-2006. This attested to the effectiveness of collaborative enforcement by both WDFW and the Oregon State Police in the Blue Mountains.

Our inference assumes we had relatively unbiased data relative to causes of death. Because we had to classify some kills on the basis of *a priori* defined circumstantial evidence (Table 3), it is possible we misclassified some death causes. For example, it was clearly possible to confuse legal tribal kills and nontribal poaching. In general, we often had additional corroborating evidence, especially for legal state hunter and tribal kills. We would note that if we made errors, we could not assume they were systematic (*e.g.*, tribal kills and nontribal poaching events could have as easily been underclassified as overclassified). Based on the information we had, we believe we made defensible calls on causes of deaths and that the estimates derived from these data were the best estimates we could derive. We suspect misclassifications of death causes were minor and believe such errors would not have substantively changed our basic inference about mortality agents.

Timing of Elk Deaths

Although we detected elk deaths in every month of the year, most deaths were concentrated in the late summer and fall. Human-caused deaths predominantly occurred in a 3-month period (Sep-Nov), corresponding to the timing of state-sanctioned recreational elk hunting seasons. This was consistent with findings from elsewhere in Washington, including western Washington (Smith et al. 1994), and the east slopes of the Cascades (Smith et al. 1994, McCorquodale et al. 2003).

Tribal hunting by the CTUIR was restricted to Aug-Dec by tribal regulations, but NPT hunting was not limited to the fall by tribal regulations. Still, most tribal kills that we detected occurred during September-October. Our analysis of cause-specific mortality risks suggested considerable overlap in the timing of risk due to tribal and state-sanctioned hunting, but tribal hunting risks appeared to start and end slightly earlier than hunting risks associated with state-sanctioned seasons.

In western Washington, tribal harvest of radiomarked elk occurred during August-December; 6 of 8 (75%) tribal kills recorded occurred during Nov-Dec (Smith et al. 1994). In a study of elk mortality along the east slopes of the Cascades, where the study area included a sizeable tract of tribal reservation and where tribal harvest was a substantial mortality source, McCorquodale et al. (2003) also found tribal elk kills principally occurred during the fall.

Our sample size of illegal kills was small, with no apparent seasonal pattern. The only mature bull poached was killed in February. The other illegal kills occurred in June, October, and December. It is difficult to draw conclusions about the timing of illegal hunting activity on the basis of such a small sample.

In an earlier study of elk poaching mortality elsewhere in Washington, illegal kills predominantly occurred in the fall, close to the timing of legal elk seasons (Smith et al. 1994). The authors of that work believed that legal hunting seasons provided *cover* of sorts for elk poachers; people may be less likely to be suspicious of and report activity by poachers if there is a possibility their activity could be legal, based on a current open elk season.

Vulnerability Factors

We explored several landscape factors with logical implications for the vulnerability of elk to human harvest. We detected an effect of road covariates on risks of hunting mortality to the yearling bulls used in our analyses. We did not detect any meaningful relationships between the vulnerability of yearling bulls to harvest and habitat class, ownership, or topographic covariates. Our results were very similar at both landscape scales and for both analytic strategies (case control vs. sampling with replacement).

Landscape factors have previously been linked to harvest mortality risks elsewhere. Unsworth et al. (1993) found that harvest mortality risks to elk in northcentral Idaho were lower in areas with highly dissected or broken terrain, presumably due to the extra effort hunters had to expend to access such areas. Likewise, McCorquodale et al. (2003) found that topographic complexity affected elk vulnerability to human-caused mortality in the Cascades of Washington; risks were lower with increasing topographic complexity.

Additionally, McCorquodale et al. (2003) found that risks increased as the percent of an elk's summer-fall home range consisting of managed forest increased. Hayes et al. (2002) did not find that landscape factors, apart from road effects, were useful in predicting bull elk vulnerability to hunting mortality in northern Idaho, similar to what we found for elk in the Washington Blue Mountains. Weber (1998) found a higher proportion of elk kill sites, relative to live elk relocations, were in areas where cover had been reduced by logging in western Montana. Hurley and Sargeant (1991) and Lyon and Canfield (1991) found elk habitat use reflected increased use of larger, nonfragmented tracts of forest cover during hunting seasons, compared to just prior, but these authors did not try to formally address the consequences of cover use to elk survival.

Despite the relatively sparse data we felt justified in using to address the question of landscape-mediated vulnerability, we detected a statistical relationship between elk hunting mortality risks and road effects; yearling bulls were at higher risk in areas closer to roads and where local road densities were higher. Our data also suggested other hunting-related mortality (*i.e.*, deaths of other sex/age classes and deaths not meeting our timing criteria for inclusion in the vulnerability factors analysis) tended to occur near roads.

Lyon and Burcham (1998) found that elk hunters on a western Montana landscape generally hunted near roads; only 3 of 99 hunters carrying GPS units while hunting ventured further than 1 km (0.62 mi) from a road. The average distance to the nearest road while hunting was 267 m (~300 yd). Novice hunters spent ~40% of their hunting time on roads; more experienced hunters spent about 27% of their hunting time on roads.

Using questionnaires mailed in by elk hunters in Idaho, Yuan et al. (1991) found that 16% of unsuccessful hunters and 8% of successful hunters reported road hunting as their primary hunting strategy. In a separate study from Idaho, Gratson and Whitman (2000*a*) estimated elk hunter density was 4 times greater in a highly roaded area (1.5 km/km^2) (2.4 mi/mi^2) compared to a managed access area (0.56 km/km^2) (0.90 mi/mi^2) and more than 3 times greater than in an unroaded area.

In a Montana study, Hurley and Sargeant (1991) found that 43% of the elk harvested in Elk Management Unit 10 were taken in areas with open roads, even though such areas represented only ~25% of the unit. It is notable that although many elk hunters hunt elk on or near roads and although total elk harvest is typically highest in roaded portions of the landscape, individual hunter success rates are commonly much lower for hunters near roads (Yuan et al. 1991, Cooper et al. 2002).

A substantial body of literature has documented the effect of roads on elk vulnerability to hunting mortality. In the Clearwater drainage of Idaho, Unsworth and Kuck (1991) estimated bull elk in roaded habitats were more than twice as likely to be killed by hunters than bulls in areas with few roads. Leptich and Zager (1991) found that road density was systematically related to elk harvest mortality in another area of Idaho; estimated mortality in high road density areas was nearly twice that in areas with few roads and almost 40% higher than in areas with limited road access.

Youmans (1991) found a positive relationship between landscape road miles and bull elk kill rate on the Bitterroot National Forest of western Montana, 1953-89; the trend in harvest of mature bulls decreased markedly through the time series as total road miles increased. Hayes et al. (2002) found total road density was positively related to hunting season elk mortality in northern Idaho, and Unsworth et al. (1993) found that the probability of hunting season elk mortality increased with increasing road density. McCorquodale et al. (2003) modeled elk harvest risks in the Cascades of Washington and found that road density was a principal predictor of the risk of harvest mortality. Cole et al. (1997) found the Roosevelt elk survival in western Oregon increased after a reduction in open road densities.

Contrasting fall relocations of yearling bulls with kill sites, we found that kill sites were systematically closer to roads, and, not surprisingly, that road densities near kill sites were higher than typical of areas near live yearling bull relocations. Weber (1998) similarly analyzed landscape features near fall live elk relocations and elk kill sites and found that elk kill sites were about 1,000 m (~1,100 yds) closer to open roads than were live elk relocations. McCorquodale (2000) also modeled the characteristics of landscape features near fall live elk relocations and kill sites and found that kills sites were generally closer to roads and in areas with higher road densities than typical of live elk relocations. The final predictive model developed by McCorquodale (2000) included variables for road density, percent of forest reserves, and percent of mature closed canopy forest, and the model did reasonably well at differentiating live elk relocations from kill sites (76% correctly classified).

Although we found that road variables were related to the probability that an elk site was a kill site, our simple models were not good absolute predictors of yearling bull vulnerability to harvest. This was similar to the findings of Hayes et al. (2002) who also developed models to predict harvest risks of elk based on landscape features. Their models had low predictive power in an absolute sense. Our results, and those of Hayes et al. (2002), should not be that surprising.

Elk vulnerability would generally have to be very high for simple models to correctly predict the fate of an elk using a particular landscape element. Clearly, although elk vulnerability to hunting mortality is increased near roads, not every elk that ventures near a road is killed. Factors such as topography (Edge and Marcum 1991), regulations (Beiderbeck et al. 2001), hunter density and distribution (Vales et al. 1991, Millspaugh et al. 2000), available cover (McCorquodale 2000), elk group size and density (Vales et al. 1991), time of day, weather (Yuan et al. 1991), etc. influence the vulnerability of elk to harvest, even when roads are a dominant mediator of risk (Hillis et al. 1991, Cooper et al. 2002).

Despite that road densities alone do not predict the fate of elk during fall hunting seasons, our results and those of others (Leptich and Zager 1991, Cole et al. 1997, Youmans 1991, McCorquodale et al. 2003, Hayes et al. 2002, Rumble et al. 2005), clearly suggest that road management is likely to be one of the most effective ways to manage elk vulnerability to human-caused mortality (Vales et al. 1991, Lyon et al. 1998). Reducing the density of roads, both open and closed, especially where cover is limited and/or topography is gentle, should predictably increase elk security. This may be a particularly important management tool to maintain general season elk hunting opportunity on landscapes where elk hunting recreation is high. Similarly, managing road access in areas near human population centers may reduce risks of illegal harvest of elk (Smith et al. 1994).

Gratson and Whitman (2000*b*) surveyed elk hunter attitudes towards managed road access to hunting areas and found that more than 60% supported or would be tolerant of reduced open road densities. Support was lower among hunters who mostly hunted highly roaded areas, those who had hunted ≥20 years, and those who hunted closest to home. In another survey of Idaho elk hunters, those expressing strong opposition to road closures as a management tool were far fewer than those strongly favorable towards road access management (10% vs. 67%) (McLaughlin et al. 1989). Public education is a key element to gaining support for new road management initiatives (Moroz 1991).

MANAGEMENT IMPLICATIONS

Radiomarked elk provided a means of directly estimating survival and identifying mortality factors in the Washington Blue Mountains from 2003-2006.

Our study was partly motivated by concerns about levels of illegal killing of elk. The initiation of our work coincided with the end of intensive enforcement efforts that successfully identified and dismantled 2 organized elk poaching rings. Our results suggested that those efforts were extremely successful in reducing the levels of illegal elk killing in the 2003-2006 period. This suggests that the background level of small-scale individual poacher activity was relatively small, but clearly still occurred during our study. Recent history and our results suggest that continued aggressive enforcement may be key to keeping illegal harvests of elk in the Washington Blue Mountains low.

Our results also confirmed that tribal harvest of elk from this population is relatively low, compared to recreational state-managed harvest (*i.e.,* about 1/4 of legal harvest by state hunters). However, the level of tribal harvest we detected was not a trivial source of mortality.

We believe management of the Washington Blue Mountains elk herd could be more effective, and management would be more informed, if the CTUIR and NPT collected and reported off-reservation tribal harvest. We also believe this would increase the confidence of the public in the collaborative management paradigm for this important elk herd.

Our results provided the first direct estimate of yearling bull elk survival rates under the spike only general season strategy for state-sanctioned hunting in Washington. These results suggested moderate recruitment of yearling bulls into the subadult bull class. Based on the best survival models, about 3-5 yearling bulls out of every 10 survived to recruit as 2-yr-old branch-antlered bulls, despite the popularity of hunting elk in the Washington Blue Mountains. Although current regulations direct most legal harvest mortality to the yearling bull class, the strategy appears effective at maintaining open general season recreation, acceptable annual escapement of yearling bulls, and sustainable hunting for mature bulls.

During our study, the survival of branch-antlered bulls was relatively high (~80-85%), rivaling that of adult cows. This rate of bull survival is high compared to most managed elk populations. Any bull permitting levels just prior to our study had been reduced due to uncertainty about the impacts of illegal kills. Clearly, under rates of illegal harvest typical of our study, the harvest of branch-antlered bulls could be higher with little risk to desirable bull:cow ratios or the maintenance of substantial numbers of older age-class bulls. Annual survival rates for adult bull elk of ~0.60-65 have been sufficient to meet biologically defensible management goals (Bender and Miller 1999, McCorquodale et al. 2003).

Our findings provide defensible estimates of key vital rates that should be useful for modeling elk population dynamics in the Washington Blue Mountains. Such modeling could be used to address questions about current elk population trajectories and demographics, as well as model likely outcomes under alternative management scenarios.

Our results add to the substantial body of literature that affirms that the probability of elk surviving hunting seasons is related to the density of open roads and the availability of security areas distant from roads. This strongly suggests that managing open road densities remains one of the best management tools for limiting vulnerability of elk to human-caused mortality, especially during fall, but our data did not allow us to identify optimal values or critical thresholds for open road densities.

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