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Annual Survival and Harvest Vulnerability of Elk (*Cervus canadensis*)

Maksim Sergeyev

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Annual Survival and Harvest Vulnerability of Elk (*Cervus canadensis*)

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Master of Science

Across the western United States, most populations of Rocky Mountain elk (*Cervus canadensis*) are managed through hunter harvest (Sandrey 1983). In hunted populations, human harvest is the leading source of mortality (Ballard 2000). With the exception of elk in national parks, populations are primarily managed through hunter harvest. Other sources of mortality include disease, automobile collisions, and predation from mountain lions, coyotes, wolves, and black bears (Childress 2003, Hornocker 1970). As a species of management concern and high economic value (Pickton 2008), hunted populations of elk are carefully managed to target population sizes to guarantee a sustainable supply and ensure available harvest in the future. Estimates of survival, an understanding of cause-specific mortality, and knowledge of high-risk harvest areas are essential to effective management strategies (Stussy 1994). In the first chapter, I examined habitat use of elk during the hunting season and determined habitat characteristics that best predicted vulnerability to harvest. In the second chapter, I calculated annual survival and determined cause-specific mortality of elk.

Keywords: harvest vulnerability, hunters, survival, cause-specific mortality, habitat use, elk

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CHAPTER I

Habitat Use and Harvest Vulnerability of Elk (*Cervus canadensis*): Do Elk Learn to Avoid Hunters as They Age?

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ABSTRACT

Pressure from hunting alters the behavior and habitat selection of game species. During hunting periods, animals like deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) typically select for areas further from roads and closer to tree cover, while altering the timing of their daily activities to better avoid hunters. Our objective was to determine the habitat characteristics most influential in predicting harvest risk of elk and further, to determine if elk learned to avoid hunters with age. We captured 445 elk between January 2015 and March 2017 in the Uinta-Wasatch-Cache National Forest and surrounding area of central Utah. We determined habitat selection during the hunting season using a resource selection function (RSF). Additionally, we modeled vulnerability to harvest based on habitat use within home ranges as well as based on the location of the home range on the landscape to evaluate vulnerability on a broader scale. Elk selected for areas that reduced hunter access (rugged terrain, within tree cover, on private land). Age, elevation and distance to roads were most influential in predicting harvest risk based on use within home ranges (top model accounted for 36.2% of the weight). Elevation and distance to trees were most influential in predicting risk based on centroid of home range (top model accounted for 42.1% of the weight). Vulnerability to harvest was associated with increased proximity to roads. Additionally, survival decreased with age; we found no evidence of learned hunter-avoidance by older elk.

INTRODUCTION

Selection of resources and habitats is a driving force influencing animal populations (Rosenzweig 1981). As such, a thorough understanding of the factors driving habitat selection is vital for proper management and conservation of a species (Lele 2009). Because resources are not uniformly available across the landscape, organisms will select the most beneficial habitats (Manly 2002). Selection occurs at multiple scales and has been categorized into specific orders of selection (Owen 1972). The broadest of these scales, first order selection, describes selection of a geographic range, while second order narrows the selection further to local sites (Johnson 1980). Third order selection describes usage patterns of local areas and finally, fourth order selection can describe selection for particular species in a diet. Selection of habitats may be influenced by quality of forage, risk of predation, energy trade-offs, or anthropogenic influences like development, outdoor recreation, and hunting (Conover 2001, Pierce et al. 2004, Nix et al. 2018)

Pressure from hunting (additional disturbance, increased risk of mortality) can influence behavior and habitat selection of game species. During hunting periods, game species often shift habitat use away from areas with optimal resource quality towards areas offering greater security (Proffitt et al. 2010). For example, black bears (*Ursus americanus*) and wolves (*Canis lupus*) shifted habitat use towards less accessible areas, further from roads (Conover 2001). White-tailed deer (*Odocoileus virginianus*) altered their habitat use and timing of daily activity to avoid hunters (Verdade 1996). Hunting led to reduced intraspecific competition, decreased mating opportunities, and increased group size in red deer (*Cervus elaphus*) and Dall sheep (*Ovis dalli*), likely due to the removal of dominant individuals (Verdade 1996, Singer and Zeigenfuss 2002).

Understanding the effects of harvest and anthropogenic activities on behavior, resource selection, and population dynamics is fundamental to conservation.

Rocky Mountain elk (*Cervus canadensis*), a big game species across the United States, similarly respond to hunting pressure suggesting that hunters may influence elk population dynamics beyond the direct effects of harvest-related mortality. During the hunting season, elk select for areas further from roads and often use private land as a means of refuge (Burcham et al. 1999, Conner et al. 2001, Viera et al. 2003, Proffitt et al. 2013). Daily movement rates increase and elk expend additional energy avoiding hunters (Johnson et al. 2004, Proffitt et al. 2009). Additionally, flight distances of elk increase during the hunt, while group size decrease, suggesting elk are acutely aware of the increased risk of mortality (Bender et al. 1999, Proffitt et al. 2009). Not only can hunting pressure influence distribution of elk, the distribution of elk on the landscape may influence susceptibility to harvest. Vulnerability of elk to harvest is likely influenced by hunter efficiency, characteristics of the home range, and detectability of the elk (McCorquodale et al. 2003). Detectability of the elk can vary with time of day and cover type and may decrease with age as older individuals become familiar with annual hunting pressure.

As elk age, they may learn the nuisances of hunter avoidance and reduce use of high-risk areas accordingly (Wright et al. 2006, Thurfjell et al. 2017). Bull elk had more pronounced responses to hunting pressure than cows and mature bulls exhibited greater flight distances than younger bulls, consistent with higher rates of harvest for mature bulls (Bender et al. 1999). Older cow elk reduced movement rates during the hunting period and increased use of rugged terrain (Thurfjell et al. 2017). Further, the same study showed that cows over the age of 9 or 10 were less susceptible to harvest by hunters. As long-lived, gregarious animals, elk may learn to avoid hunters by altering habitat use.

The risk of harvest for a game animal is likely influenced by a multitude of factors, including selection of habitat during the hunting season. Our objectives were to determine the habitat characteristics most influential in predicting harvest risk of elk and to determine whether elk learned to avoid hunters with age. We expected risk of harvest to be correlated with hunter accessibility and that elk in rugged, less accessible areas will be at a reduced risk. Further, we predicted older elk would reduce use of high-risk areas. Identifying the factors associated with harvest risk of elk can increase knowledge of population dynamics, advance understanding of the responses of game species to hunters, and provide additional insight into age structure of the population, thereby improving management.

METHODS

Study Area

We conducted this study in the Wasatch Mountains and surrounding area of central Utah, west of Salt Lake City (Figure 1-1). The Wasatch range, the southwestern portion of the Rocky Mountains extending approximately 400 kilometers (Britannica 1988), is characterized by rugged terrains and steep slopes, a result of past glaciation events (Brooks 2001). The mountains are comprised primarily of dolomite and limestone (Andersen and Holmgren 1969). In addition to the rugged mountain ranges, the region contains numerous valleys and plateaus, as well as a greater amount of domestic livestock grazing than surrounding portions of the Rocky Mountains (White et al. 2006). At a base elevation of approximately 1370 meters, Mount Nebo, at 3620 meters, is the highest point along the range, alongside other notable peaks like Mount Timpanogos and Mount Olympus (Cottam and Evans 1945, Halleran 1994). The region receives an average of 40 centimeters of annual precipitation, varying with elevation (Fuller 1973).

Composition of plant communities also varies with elevation and distinct ranges have been described (Madsen and Currey 1979). Elevations below 1980 meters, the Upper Sonoran Zone, are dominated by sagebrush (*Artemisia* spp) and Mexican cliffrose (*Purshia stansburyana*), while elevations between 1981 – 2440 meters, the Transition Zone, are covered by mountain brush species like Gambel oak (*Quercus gambelii*) and curl-leaf mountain mahogany (*Cercocarpus ledifolius*; USFS 1974). The Canadian Zone, 2440 - 2900 meters, is characterized by aspen (*Populus tremuloides*) and white fir (*Abies concolor*), followed by the Hudsonian Zone, composed of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Finally, primrose (*Oenothera* spp) and alpine moss populate the Arctic-Alpine Life Zone, above 3200 meters.

Elk Capture

We captured elk via helicopter net-gunning from January 2015 through March 2017 (Webb et al. 2008). Individuals were restrained using hobble straps and fit with a blindfold. We collected body measurements, blood, and fecal samples for each elk, as well as an estimate of body condition (Cook et al. 2001) and age based on dental wear. We measured loin muscle thickness and rump fat using ultrasonography. Body mass and ingesta free body fat were calculated for each individual (Cook et al. 2010). Captured individuals were then fitted with radio and GPS collars before being released. In order to balance frequency of data collected and longevity of the collars, we programmed collars to collect a GPS location every 13 hours. Mortality warnings were triggered by a lack of animal movement. When we received a mortality signal, we located the deceased animal and determined cause of death within 48 hours.

Analysis

We calculated separate home ranges for every hunting season that each elk lived through. We created 95% minimum convex polygons (MCPs) using locations during the hunting season (late August through January 31st; McCorquodale 2003, Middleton et al. 2013, Cole et al. 2015). We excluded animals with less than 50 locations during the hunting season to avoid biased estimates of home ranges (Sakai and Noon 1997, Van Dyke et al. 1998). We analyzed selection preferences during the hunting season using a resource selection function (RSF) to provide an understanding of habitat selection and distribution of individuals (Boyce et al. 2002). Based on known locations of use from collared individuals, relative probabilities of use can be estimated with an RSF (Hebblewhite et al. 2005, Lele and Keim 2006). To examine habitat use during the hunting season, we evaluated 27 candidate models of habitat selection based on all elk locations collected using an AICc model selection process for logistic regression models in program R (Akaike 1973, RCoreTeam 2013). To examine differences in selection between day (i.e., when elk are susceptible to harvest) and night, we used interaction terms between habitat variables and a binary variable to denote the time as either day (1) or night (0).

We evaluated elk habitat use and its effect on harvest vulnerability at two scales: habitat use within home ranges (McCorquodale et al. 2003) and at a broader scale based on the overall location of the home range on the landscape using the centroid of each home range (Cole et al. 2015). We modeled risk of harvest by hunters using logistic regression with 1 corresponding to survival and 0 representing harvest (McCorquodale et al. 2003). We included variables for distance to roads, aspect, elevation, slope, terrain ruggedness, distance to tree cover, and distance to private land (McCorquodale et al. 2003, Viera et al. 2003). We evaluated vulnerability to harvest based on use within the home range by averaging data from all locations within the home

range and considered each hunting season from every elk as an individual observation (Hayes et al. 2002). We excluded locations that occurred outside of hunting hours, as there was no risk of harvest mortality during these hours. We used linear mixed effects regression models to examine habitat characteristics as fixed effects while accounting for random temporal variation and dependence of the locations using animal ID as a random effect (Hebblewhite and Merrill 2008). We evaluated 20 candidate models of harvest vulnerability using an AICc selection process in program R (Akaike 1973; R Core Team 2013). To evaluate if elk learned to avoid hunters as they aged, we examined the effect of age on vulnerability. Additionally, we evaluated harvest risk based on the location of the home range on the broader landscape using the centroid of each home range (Cole et al. 2015). We obtained measurements of the aforementioned habitat characteristics for the centroid of each home range. We evaluated the same set of 20 candidate models to compare influential habitat characteristics between the two scales. Using the top model, we developed a map of risk of hunter harvest across the study area (Kauffman et al. 2007).

RESULTS

Between January of 2015 and March of 2017, we captured and collared 445 elk. We restricted the analysis to locations during the hunting season and removed any elk with less than 50 locations, at which point 255 animals remained. We created separate home ranges for each hunting season during which an animal had locations, totaling 358 home ranges. We evaluated habitat selection in the context of harvest vulnerability within home ranges and on a broader scale to evaluate position of home range on the landscape. We evaluated harvest risk at two

scales in order to determine vulnerability based on use within an animals home range as well as based on the overall location of the home range on the broader landscape.

Out of 27 candidate models of habitat use, the top model accounted for 83.6% of the weight compared to 16.4% for the second most supported model (Table 1-1). Habitat use of elk during the hunting season was influenced by aspect, elevation, ruggedness, slope, and distance to private land, trees, roads, day vs night, and an interaction between time of day and ruggedness, distance to private land, and distance to trees (Table 1-2). According to the interaction terms in the model, elk selected for rugged terrain, closer to private land and tree cover during the day compared to nighttime. Overall, elk selected for areas that were high in elevation and far from roads and tree cover. Steep slopes and rugged terrain were correlated with decreased use.

We determined habitat factors that had the greatest support for predicting risk of harvest and found differing results between the two scales examined. We restricted the model set to locations collected during hunting hours (30 minutes prior to sunrise – 30 minutes past sunset) as animals were at no risk of harvest outside this period. Within each animal's home range, harvest vulnerability was most influenced by distance to roads, elevation, and age of the animal (top model accounted for 36.2% of the weight, Table 1-3). We did not average top models because no additional statistically significant variables were present in remaining models. According to our top model, harvest risk increased with proximity to roads ($p = 0.056$, Table 1-4, Figure 1-2). Additionally, survival was lower at higher elevations (Figure 1-3) and for older animals (Figure 1-4). We examined learned hunter-avoidance by older elk using interactions terms between age and distance to roads, distance to trees, distance to private land, and elevation. We found no evidence for learned hunter-avoidance by older animals.

Based on overall location of the home range on the landscape, vulnerability to harvest was most influenced by elevation and distance to trees (top model accounted for 42.1% of the weight, Table 1-5). The top model included an interaction between elevation and distance to trees ($p = 0.028$, Table 1-6) suggesting that at higher elevations, distance to trees became more influential in predicting harvest risk. As we were unable to model age across the landscape, the top model based on home range characteristics was used to create a heatmap of harvest vulnerability across the study area (Figure 1-5) to illustrate high-risk areas. Our results predict high vulnerability in the northwest (Currant Creek/Wasatch front) and southwest portions (Nebo Mountains) of the study area, as well as throughout the Uinta Mountains near the center of the study site. Additionally, we predict low vulnerability in the southeastern portion (Uinta basin).

DISCUSSION

Elk altered habitat selection during hunting hours, selecting for areas that limited hunter access. Habitat selection was influenced by all seven of the habitat variables measured (elevation, slope, ruggedness, aspect, distance to roads, distance to trees, and distance to private land). During hunting hours, elk selected for rugged terrain, closer to tree cover and private land. Overall, elk selected for land that was at high elevations, far from roads and further from tree cover. Additionally, we found preference for flatter, less rugged terrain. Models of habitat selection by elk typically incorporate variables describing vegetation and cover, road density, land ownership, topographical complexity, and various measures of hunter effort or access (Unsworth et al. 1998, McCorquodale et al. 2003, Cleveland et al. 2012). Similarly, our models incorporated distance to trees, distance to roads, distance to private land, slope, ruggedness, elevation, and aspect. We predicted elk would select for terrain with reduced hunter access,

specifically steep, rugged terrain, within forested cover, and on private land. Based on our top model, elk altered their selection preferences during hunting hours, increasing use of areas with limited hunter access (rugged terrain, close to private land and tree cover), supporting our predictions. We also found preference for flatter, less rugged areas further from tree cover, contrary to our expectations, however during the winter elk may select flatter grasslands for forage (Proffitt et al. 2010), possibly explaining the use of flatter, open areas. During the hunting season, elk selected for rugged areas with lower road density, closer to tree cover, consistent with other populations of elk (Hayes et al. 2002, McCorquodale et al. 2003). Additionally, we found a preference for private land, consistent with prior studies of hunted populations of elk (Burcham et al. 1999, Viera et al. 2003, Proffitt et al. 2013).

Within an animal's home range, harvest vulnerability was best predicted by distance to roads, age of the individual, and elevation. Elk had increased survival further from roads. Survival decreased with increasing elevation. This was likely due to public land generally occurring at higher elevations than private land within our study area; as hunting primarily occurred on public land, this may explain the decreased survival at higher elevations. Vulnerability of elk to harvest is often correlated with road density or proximity to roads (Millspaugh et al. 2000, Hayes et al. 2002, McCorquodale et al. 2003, Cleveland et al. 2012). Our results support the idea that harvest risk increases with proximity to roads. Additionally, survival decreased with age. We tested the idea of elk learning to avoid hunters using logistic models that included interactions terms between age and distance to roads, distance to trees, distance to private land, and elevation. However, as none of these models were among the top supported models, we found no evidence of learned behavior in regard to hunter-avoidance by older elk. In contrast, our results suggest older elk had a greater likelihood of harvest. There has been past evidence to suggest elk learn to avoid hunters with age. Mature bull elk in Michigan

had greater flight distances than yearling bulls, in a population where mature bulls were harvested at five times the rate of yearling bulls (Bender et al. 1999). Older cow elk increased use of rugged terrain closer to roads (Thurfjell et al. 2017). Further, in the same study they concluded that hunter avoidance of elk improved with age through natural selection and learning. Additional work may show patterns of hunter avoidance by elk in central Utah; however, our results provided no evidence to support this hypothesis.

Based on the centroid of the home range, risk of harvest was best predicted by distance to trees, elevation, and an interaction between the two. The interaction term was positive, suggesting that at higher elevations, survival was higher with increasing distance to trees, somewhat contradictory to our expectations. However, overlap between elk and hunters was highest in forested areas and lower in uncovered areas (Millspaugh et al. 2000), possibly explaining why we found lower harvest risk away from forest cover. Additionally, elk decreased use of forested areas during the hunting season (Cleveland et al. 2012, Thurfjell et al. 2017), consistent with our results that survival increased as distance to trees increased.

Elk altered habitat use during hunting hours, increasing use of areas with limited hunter access (rugged terrain, within tree cover and closer to private land). Additionally, elk selected for areas far from roads and high in elevation. Based on the centroid of the home range, vulnerability to harvest was influenced by elevation and distance to trees. Age, elevation and distance to roads were the best predictors of harvest risk based on habitat use within the home range. Much is known about resource selection during the hunting season, however, less research has focused on harvest vulnerability and such studies typically examine risk based on use within the home range, while our study compared vulnerability based on habitat use within home ranges and on the overall location of the home range. Further, our study benefitted from a large sample size and

repetition across multiple years. However, some limitations should be taken into consideration as well. Similar studies have incorporated some measure of hunter density or hunter effort (Millspaugh et al. 2000), which was not included in our set of variables. Other habitat variables, such as topographical complexity, that were not measured may have also been influential in predicting vulnerability to harvest. Our study supports the idea that elk select for areas with limited hunter access and highlights habitat characteristics that best predict harvest risk of elk in central Utah. These results can provide further insight into the responses of game species to hunting pressure and can be used to inform future management policies.

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FIGURES

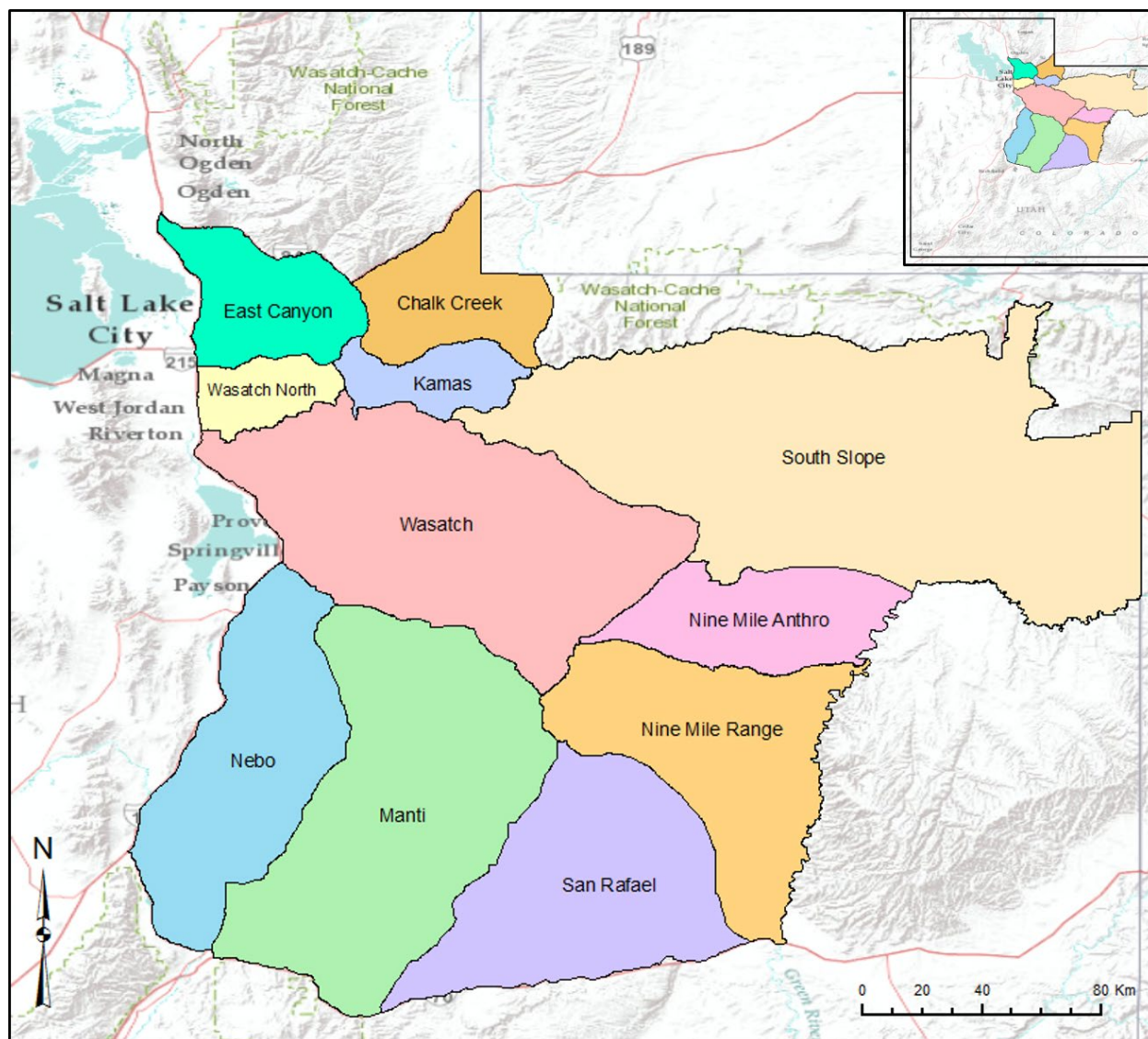


Figure 1-1. Our study area was the Wasatch and surrounding management units of central Utah. Colored polygons denote the separate management units.

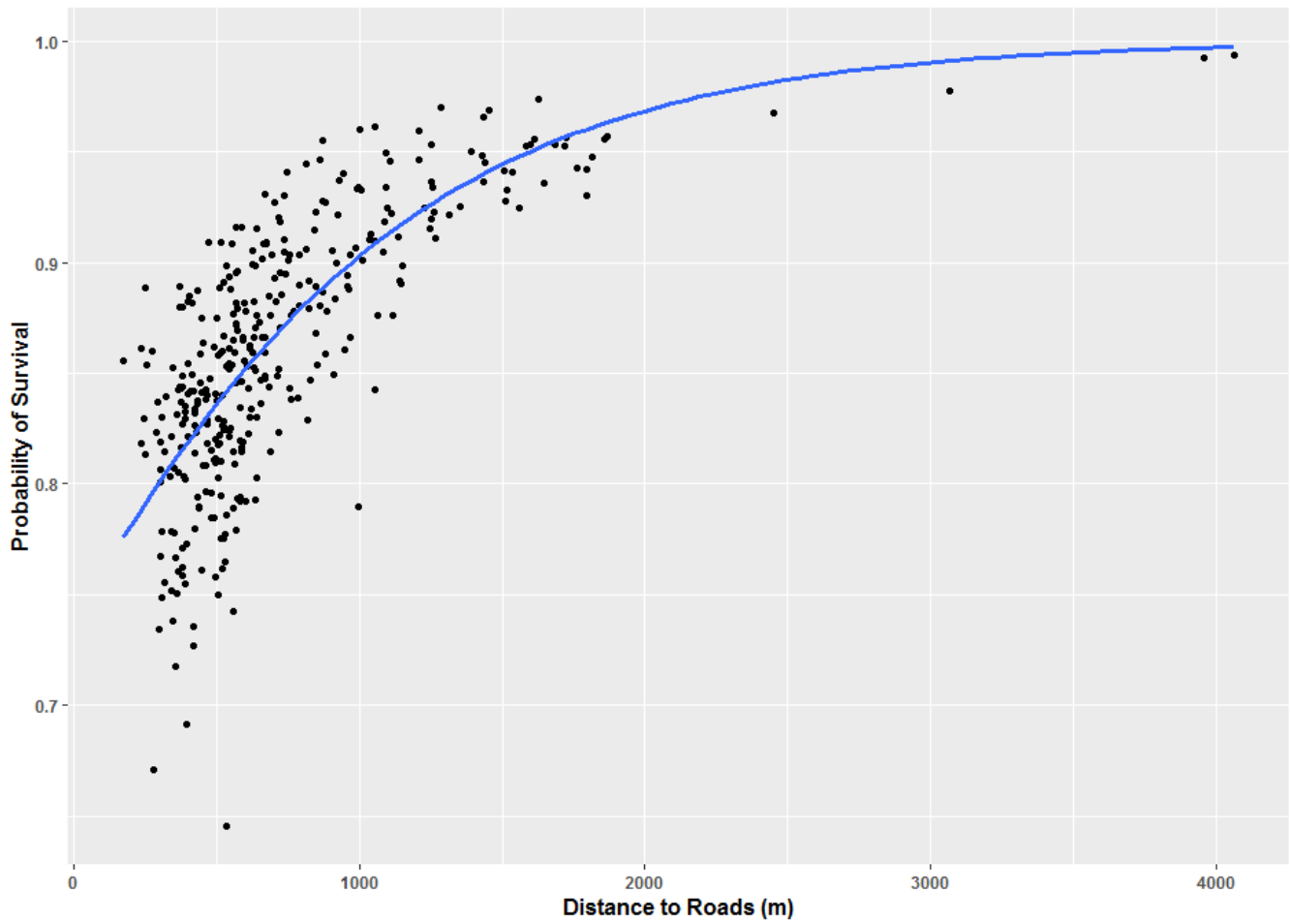


Figure 1-2. Predictive model of harvest vulnerability based on distance to roads, according to the top model from AICc selection. Top model included age, distance to roads, and elevation.

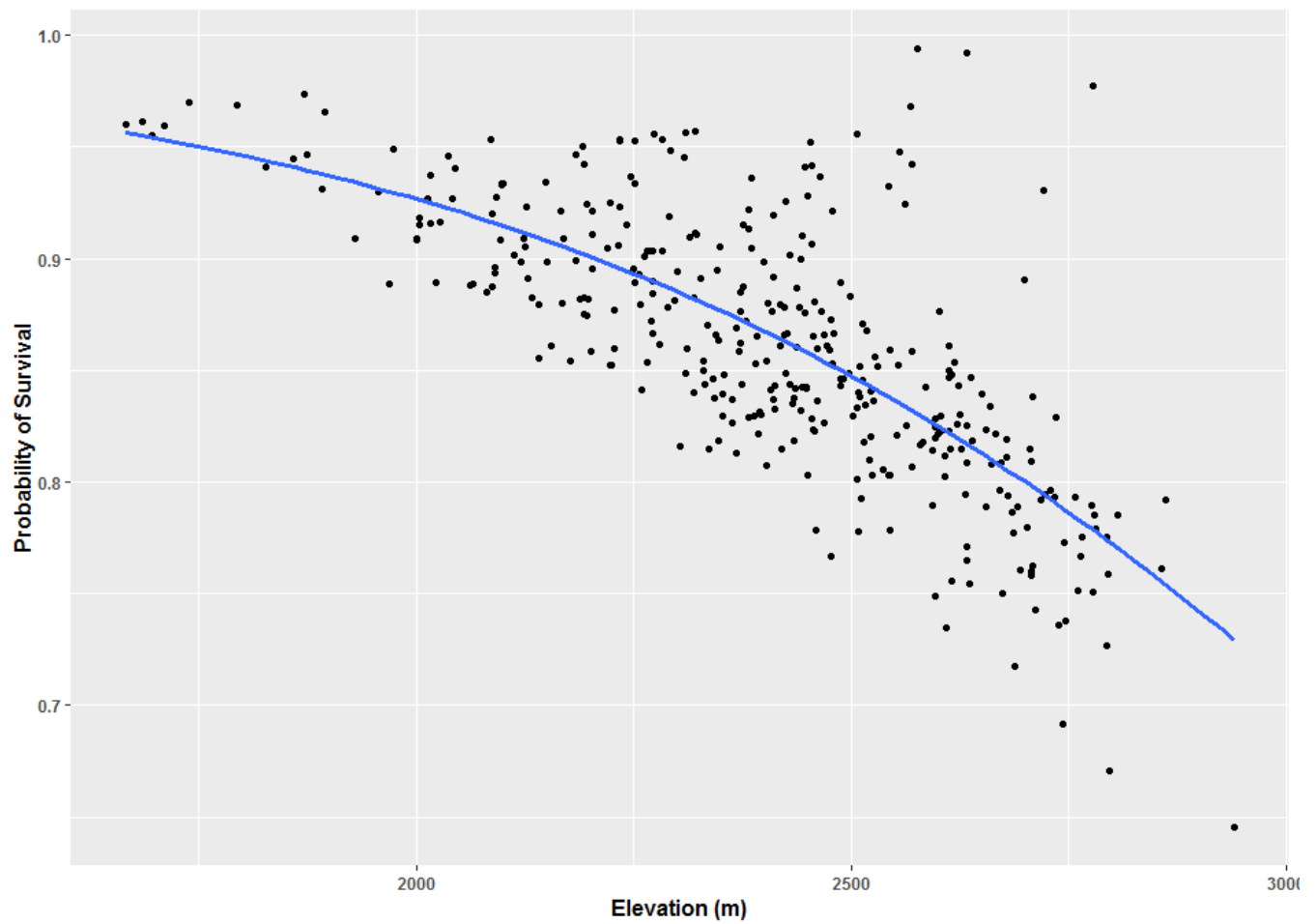


Figure 1-3. Predictive model of harvest vulnerability based on elevation, according to the top model from AICc selection. Top model included age, distance to roads, and elevation.

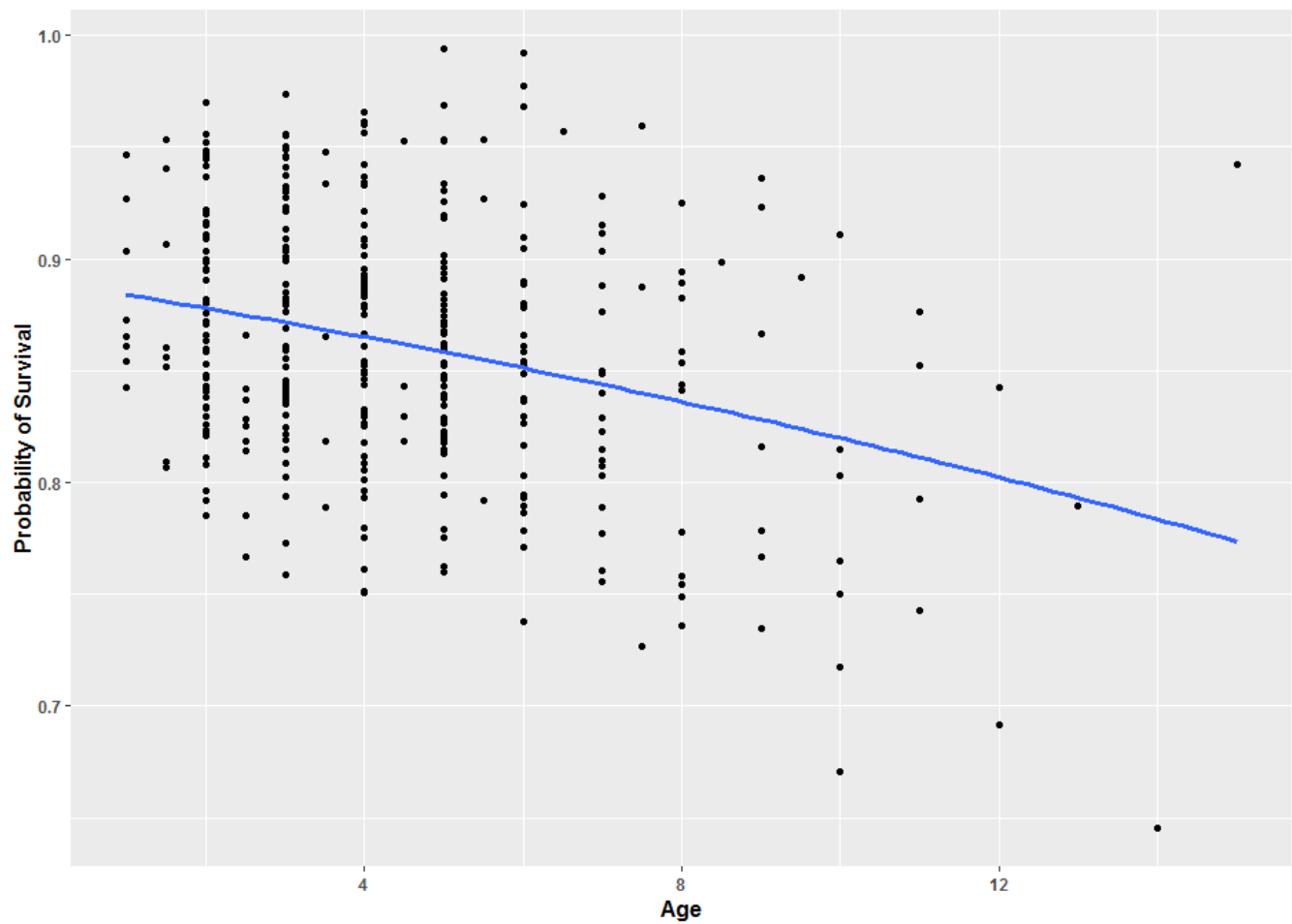


Figure 1-4. Predictive model of harvest vulnerability based on age, according to the top model from AICc selection. Top model included age, distance to roads, and elevation.

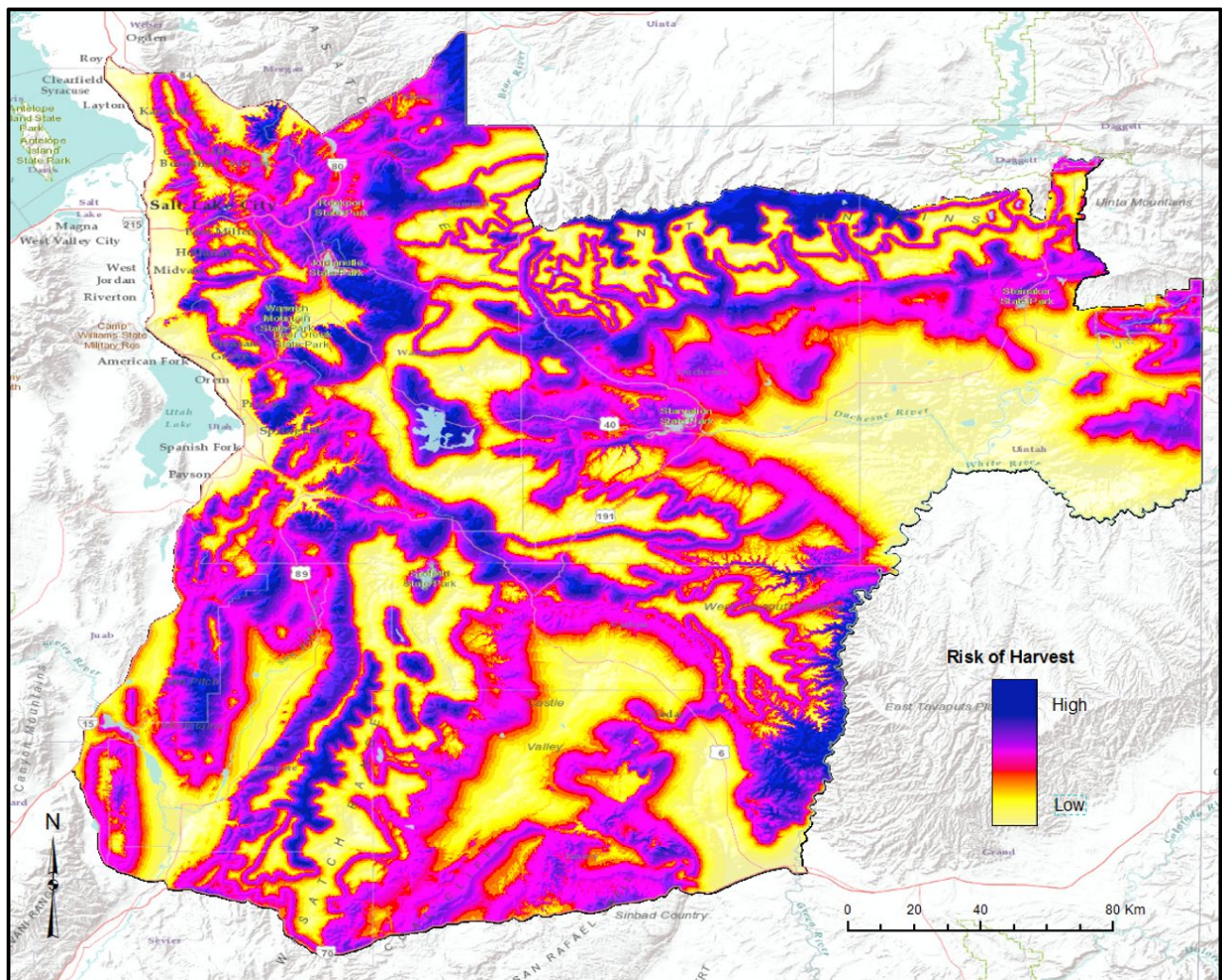


Figure 1-5. Heat map of elk harvest vulnerability based on the location of the home range on the landscape, modeled as a function of elevation, distance to trees, and an interaction between the two.

TABLES

Table 1-1. AICc model selection results for 27 candidate models of habitat use. Top model included aspect, elevation, ruggedness, slope, distance to trees, distance to roads, and distance to trees, accounting for 83.6% of the total weight. We included Animal ID as a random effect in every model.

	d.f.	AICc	Δ AICc	Weight
Aspect + Elevation + Day*Ruggedness + Slope + DistTrees + DistRoads + Day + DistPriv + Day*DistPriv + Day*DistTrees	13	191845.2	0.00	0.836
Aspect + Elevation + Ruggedness + Slope + DistTrees + DistRoads + Day + DistPriv + Day*DistPriv + Day*DistTrees	12	191848.5	3.26	0.164
Aspect + Elevation + Ruggedness + Slope + DistTrees + DistRoads + Day + DistPriv + Day*DistPriv	11	192073.3	228.10	0.000
Aspect + Elevation + Ruggedness + Slope + DistTrees + DistRoads + DistPriv+ Day + Day*DistTrees	11	192214.2	368.97	0.000
Null	1	193528.7	1683.48	0.000

Table 1-2. Output from top model (based on AICc) of habitat selection of elk during the hunting season.

	Estimate	Std. Error	p – Value
Intercept	-0.0045	0.0073	0.533
Aspect	0.0634	0.0054	< 0.001
Elevation	0.0394	0.0066	< 0.001
Day	0.0133	0.0109	0.221
Ruggedness	-0.0448	0.0077	< 0.001
Slope	-0.1368	0.0062	< 0.001
DistTrees	0.0992	0.0084	< 0.001
DistRoads	0.0881	0.0059	< 0.001
DistPriv	0.0078	0.0080	0.331
Day*Ruggedness	0.0251	0.0109	0.022
Day*DistPriv	-0.2163	0.0113	< 0.001
Day*DistTrees	-0.1663	0.0111	< 0.001

Table 1-3. AICc model selection results for 20 candidate models of survival based on habitat use. We included Animal ID as a random effect in every model. Models with greater than five percent of the cumulative weight are listed below. Top model included age, distance to roads, and elevation, accounting for 36.2% of the total weight.

	d.f.	AICc	Δ AICc	Weight
Age + DistRoads + Elevation	5	283.4	0.00	0.362
DistRoads + Elevation + Age + DistPriv	6	284.7	1.37	0.195
Age + Elevation + DistRoads + Ruggedness	6	285.5	2.07	0.129
Elevation + DistRoads + Aspect + Slope + Age + DistPriv	8	286.1	2.45	0.096
Age + Elevation	4	286.3	3.21	0.084
Null	1	295.1	11.71	0.001

Table 1-4. Output from top model (based on AICc) of harvest vulnerability of elk based on habitat use.

	Estimate	Std. Error	p – Value
Intercept	1.937	0.172	< 0.001
Age	-0.114	0.151	0.451
DistRoads	0.465	0.243	0.056
Elevation	-0.305	0.179	0.089

Table 1-5. AICc model selection results for 20 candidate models of survival based on overall location of the home range on the landscape. We included Animal ID as a random effect in every model. Models with greater than two percent of the cumulative weight are listed below. Top model included elevation, distance to trees, and an interaction term, accounting for 42.1% of the total weight.

	d.f.	AICc	Δ AICc	Weight
Elevation + DistTrees + Elevation*DistTrees	5	239.0	0.00	0.421
Elevation + Ruggedness	4	242.1	3.15	0.087
Age + Elevation	4	242.3	3.33	0.080
Age*DistRoads + Age + DistRoads	5	242.5	3.52	0.072
Age*Elevation + Age + Elevation	5	242.8	3.87	0.061
Age + DistRoads + Elevation	5	243.7	4.71	0.040
Age + DistTrees + DistPriv	5	243.8	4.79	0.038
Age*DistTrees + Age + DistTrees	5	243.8	4.81	0.038
DistPriv + DistTrees	4	244.3	5.33	0.029
Age*DistPriv + Age + DistPriv	5	244.4	5.38	0.029
Age + Elevation + DistPriv	5	244.4	5.38	0.029
Slope + Aspect + Ruggedness + DistTrees	6	244.6	5.61	0.025
Elevation + DistTrees + Ruggedness + DistRoads	6	244.9	5.95	0.021
Null	1	295.1	56.16	0.000

Table 1-6. Output from top model (based on AICc) of harvest vulnerability of elk based on based on overall location of the home range on the landscape.

	Estimate	Std. Error	p – Value
Intercept	10.784	1.447	< 0.001
Elevation	0.430	0.811	0.596
DistTrees	0.507	0.804	0.528
Elevation*DistTrees	1.228	0.560	0.028

CHAPTER II

Effect of Body Size and Condition on Survival and Cause-Specific Mortality of Elk (*Cervus canadensis*)

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ABSTRACT

The size of an animal population fluctuates with number of births, rate of immigration, rate of emigration, and number of deaths. For many ungulate populations, adult female survival is the most important factor influencing population growth. As a result, removal of healthy adult females can greatly influence population dynamics. Increased understanding of survival and causes of mortality for adult females is fundamental for conservation and management. The objectives of our study were to quantify survival rates of female elk (*Cervus canadensis*) and determine cause-specific mortality. We predicted that hunter harvest would be the leading cause of mortality. Further, we predicted that hunters would harvest animals that were more prime-aged and in better condition than elk predated by mountain lions. From 2015 to 2017, we captured 452 female elk via helicopter net gunning in central Utah. Individuals were fitted with a GPS-transmitting collar that collected a location every 13 hours. When a mortality warning was received, we located collared individuals and determined cause of death within 48 hours whenever possible. We estimated survival using Kaplan-Meier estimates and Cox Proportional Hazard models within an AICc model selection framework to identify covariates that influenced survival. Our best model was consistent survival across years with mean survival of 78.3% (SE = 3.5%) including harvest and 95.5% (SE = 1.6%) without human harvest. In decreasing order of importance, elk mortality occurred from hunter harvest (21.2%), mountain lion predation (3.7%),

depredation removal (0.5%), automobile collision (0.3%), disease (0.3%), complications during calving (0.3%), and those characterized as undetermined (1.3%). Based on the top model, neck circumference, body length, and loin fat were negatively associated with survival suggesting that larger animals in good condition had lower survival. However, individuals lost to cougar predation were younger and in worse body condition than the average animal. It appears that hunters are removing individuals that likely have a greater effect on population dynamics than other predators.

INTRODUCTION

Effective management of a species requires a thorough knowledge of the vital rates that influence population dynamics (Murray and Patterson 2006, Bender et al. 2008). The size of an animal population is influenced by four factors: the number of births, the rate of immigration, rate of emigration, and the number of deaths (Doss et al. 2013). As individuals die or permanently emigrate, the population will decline and, conversely, as new individuals are born or immigrate, the population increases (O'Hara et al. 2009). Understanding rates of immigration and emigration can provide an understanding of directional movement and source-sink dynamics occurring in the population (Peery et al. 2006). However, natality and mortality are the primary components of population growth and as such, understanding survival rates provides insight to recruitment, sex ratios, and the overall size of the population (Murray 1997, Webb et al. 2011).

Estimating survival rate is an essential component of population biology and conservation of large mammals (Evans et al. 2006, Murray 2006). Survival of individuals can be influenced by a combination of ecological, environmental, genetic, and demographic factors

(Murray and Patterson 2006). For populations of ungulates, adult female survival is often the most significant parameter influencing growth (Grovenburg et al. 2011, Webb et al. 2011). While adult survival typically remains constant for long-lived ungulates, small changes in survival rate can have pronounced effects on population growth (Brodie et al. 2013). For game species in North America, survival of adults can be determined largely by hunter harvest and populations are typically managed by adjusting survival of adult females (Monello et al. 2014).

Across the western portion of the United States, Rocky Mountain elk (*Cervus elaphus*) are a big game species of high ecological and economic value (Brodie et al. 2013). Various factors influence survival of elk including density, age, sex, and climate (Sauer and Boyce 1983, McCorquodale et al. 2011). Mortality of elk typically results from human hunters, predation, road kill, and to a lesser degree, other natural causes (Ballard et al. 2000, McCorquodale et al. 2011). In areas where rates of predation are low, harvest by humans is often the leading cause of mortality of elk (Webb et al. 2011).

Hunter harvest has the potential to influence population dynamics of ungulates differently than predation by large carnivores (Kunkel et al. 1999, Mech et al. 2001). Predators such as wolves (*Canis lupus*), mountain lions (*Puma concolor*), and grizzly bears (*Ursus arctos*) often preferentially target elk calves or individuals that are old, weak, or diseased (Gunther and Renkin 1990, Wright et al. 2006, Zager and Beecham 2006, Rearden et al. 2011,). Elk killed by wolves and cougars also had lower marrow fat content, suggesting weaker animals in poor condition (Kunkel et al. 1999, Mech et al. 2001, Wright et al. 2006). In contrast, hunters targeted large, prime-aged elk (2-9 years), removing those individuals that may have the greatest impact on population growth (Boyd et al. 1994, Kunkel et al. 1999, Wright et al. 2006).

Prior studies focusing on adult survival and differences in cause-specific mortality often examine differences in age, while less research has focused on the influence of condition and size-related attributes, aside from a few studies that measured fat content. Birth mass and condition have been evaluated in the context of calf survival (Smith and Anderson 1998, Bender et al. 2002). Additionally, effect of fat content on survival of adult elk has been examined (Bender et al. 2008) however, most models of elk survival simply focus on the effect of landscape features, such as road density and tree cover (Cole et al. 1997, McCorquodale et al. 2003, White et al. 2010, Proffitt et al. 2013). As such, the effects of body size combined with fat content on adult survival and cause-specific mortality are less understood.

Throughout the western United States and Canada, elk often inhabit areas with complex carnivore communities (Griffin et al. 2011). Across the northern extent of their range, survival of elk is influenced by predation from mountain lions, coyotes, bears, and wolves (Bender et al. 2002, Evans et al. 2006, Barber-Meyer et al. 2008, Foley et al. 2015). The majority of research on elk survival and cause-specific mortality has occurred in areas where large carnivore communities are still present, despite a large portion of elk range in North America lacking wolves or grizzly bears (Wright et al. 2006, White et al. 2010). Though the southern range of elk lacks gray wolves and grizzly bears, rates of mountain lion predation are higher and areas are being recolonized by Mexican wolves (*Canis lupus baileyi*; Ballard et al. 2000). While predation of elk by mountain lions occurs in the central portion of their range, rates of predation are low (Griffin et al. 2011). Further, the abundance of mule deer (*Odocoileus hemionus*) may result in predators such as mountain lions and coyotes preferring deer over elk as they are likely easier to predate (Kunkel et al. 1999). As such, managing populations of elk relies almost entirely on hunter harvest. Low rates of predation, combined with higher rates of hunting may influence elk

survival differently than in some of the previously mentioned studies, particularly as hunting may affect population dynamics differently than predation (Mech et al. 2001).

Our objectives were to estimate survival rates of female elk and determine cause-specific mortality in a region that is lacking a complex predator community (i.e., no grizzly bears or wolves). Specifically, we determined the body size and condition attributes that influenced survival. In addition, we determined whether differences in age, size, and condition existed between elk harvested by hunters and those taken by other predators. We predicted that hunter harvest would be the leading cause of mortality. Further, we predicted that hunters would harvest animals that are more prime-aged and in better condition than elk taken by other predators. If hunters are indeed removing prime-aged animals in better condition, their impact on population growth could be more pronounced than that of other predation. Identifying differences in selection preferences between humans and other predators can improve management strategies and provide additional insight into factors driving population dynamics.

METHODS

Study Area

We conducted this study in the Wasatch Mountains and surrounding area of central Utah, west of Salt Lake City (Figure 2-1). The Wasatch range, the southwestern portion of the Rocky Mountains extending approximately 400 kilometers (Britannica 1988), is characterized by rugged terrains and steep slopes, a result of past glaciation events (Brooks 2001). The mountains are comprised primarily of dolomite and limestone (Andersen and Holmgren 1969). In addition to the rugged mountain ranges, the region contains numerous valleys and plateaus, as well as a

greater amount of livestock grazing than surrounding portions of the Rocky Mountains (White et al. 2006). From a base elevation of approximately 1370 meters (Cottam and Evans 1945), Mount Nebo, at 3620 meters, is the highest point along the range, alongside other notable peaks like Mount Timpanogos and Mount Olympus (Halleran 1994). The region receives an average of 40.6 centimeters of annual precipitation, varying with elevation (Fuller 1973). Composition of plant communities also varies with elevation and distinct ranges have been described (Madsen and Currey 1979). Elevations below 1980 meters, the Upper Sonoran Zone, are dominated by sagebrush (*Artemisia* spp) and Mexican cliffrose (*Purshia stansburyana*), while elevations between 1981 – 2440 meters, the Transition Zone, are covered by mountain brush species like Gambel oak (*Quercus gambelii*) and curl-leaf mountain mahogany (*Cercocarpus ledifolis*; USFS 1974). The Canadian Zone, 2440 - 2900 meters, is characterized by aspen (*Populus tremuloides*) and white fir (*Abies concolor*), followed by the Hudsonian Zone, composed of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Finally, primrose (*Oenothera* spp) and alpine moss populate the Arctic-Alpine Life Zone, above 3200 meters.

Elk Capture

Elk were captured via helicopter net-gunning from January of 2015 through March of 2017 (Webb et al. 2008). Individuals were restrained using hobble straps and fit with a blindfold. Body measurements, blood, and fecal samples were collected for each elk, as well as an estimate of body condition score (Cook et al. 2001) and age of the individual. We measured loin muscle thickness and rump fat using ultrasonography. Body mass and ingesta free body fat were calculated using formulas from Cook et al. (2010). Captured individuals were fitted with radio and GPS transmitting collar before being released. In order to balance frequency of data

collected and longevity of the collars, we collected GPS locations every 13 hours. Mortality warnings were triggered by a lack of animal movement. When we received a mortality signal, we attempted to locate the deceased animal and determine cause of death within 48 hours.

Analysis

Using known time and cause of death for each collared individual, we estimated annual survival using the Kaplan-Meier method in program R (Kaplan and Meier 1958, RCoreTeam 2013). A Kaplan-Meier analysis allows for a flexible, non-parametric approach that easily accounts for individuals censored throughout the study or added later, using adjustments for staggered entry (Pollock et al. 1989). Survival times were considered left-censored, as the time of death occurred at some point between the last living location and the first deceased location. Elk lost due to broken collars or collar failure were also censored (Stussy et al. 1994). We evaluated the effect of age, condition, and body size on survival and cause-specific mortality, statistically using ANOVAs and visually using density plots.

Cox Proportional Hazard (CPH) models are a commonly used technique for survival analysis that allow for estimates of survival functions for each individual, based on the covariates (Cox 1972, Lin 1986). We used CPH regression models to examine variables associated with body size and condition to model the likelihood of survival. We determined the most influential factors associated with elk survival and susceptibility to specific causes of mortality. We used an AICc model selection process to determine the best-supported model (Akaike 1973).

RESULTS

We captured 376 female elk between January of 2015 and February of 2017. From February 2015 through January 2018, 111 elk died. Eleven elk were lost due to capture related injuries or capture myopathy (2.9%). After removing non-functioning collars (N=17 or 4.5%) and elk lost to capture-related mortalities, 348 elk were used for the analyses of survival. Two additional mortalities from mountain lion predation occurred during 2018. These elk were included in statistical models to increase sample size of elk preyed by lions.

Survival of elk remained consistent throughout the study, with mean survival of 78.3% (SE = 0.035%) including hunter harvest and 95.5% (SE = 0.017%) excluding harvest (Table 2-1, Figure 2-2). Mortality resulted from human hunting, mountain lion predation, vehicle collisions, and other natural causes like disease or complications with calving. In decreasing order of importance, elk mortality occurred from hunter harvest (21.2%), mountain lion predation (3.7%), depredation removal (0.5%), automobile collision (0.3%), disease (0.3%), complications during calving (0.3%), and those characterized as undetermined (1.3%; values represent percentage out of the entire collared herd; Figure 2-3). Hunter harvest accounted for 80 out of the 100 total mortalities, by far the leading source of mortality. As such, elk mortality rarely occurred outside of the hunting season.

Out of 26 candidate models examining the influence of condition and size on survival, our top model accounted for 43.1% of the total weight, compared to the second model holding 16.5% of the weight with a $\Delta AICc$ value of 1.91 (Table 2-2). We modeled survival as a function of neck circumference and body length using a Cox Proportional Hazard model (Table 2-3). Neck circumference and body length were both significant predictors of survival ($p = 0.008$; $p = 0.056$ respectively; Figures 2-4 and 2-5). Hazard ratios showed neck circumference and body

length were negatively associated with survival, suggesting larger animals had lower survival. We chose not to average models because the only statistically significant predictors in the top weighted models were neck circumference and body length, the same two variables in the top model.

The influence of age, condition, and body size were evaluated graphically and using ANOVAs. Distribution of rump fat, loin thickness, and age appeared to differ between elk harvested by hunters and those predated by mountain lions (Figure 2-6). There were significant differences in loin thickness ($p = 0.003$) and neck circumference ($p = 0.084$) between harvested elk and those lost to predation, but not age or measurements of condition such as rump fat and IFFB (Table 2-4).

DISCUSSION

Annual survival of elk was high; 78% including hunter harvest and over 95% excluding harvest. Elk typically experience high adult survival and typically mortality results from predation or hunter harvest. Our estimates of survival were consistent with survival estimates for elk in Colorado, Wyoming, and Washington (76% - 83%; McCorquodale et al. 2003, Bender et al. 2006, Evans et al. 2006, McCorquodale et al. 2011, Webb et al. 2011). Survival of elk in Arizona was estimated at 89% (Ballard et al. 2000), higher than our study; however, survival of elk in the region not subjected to harvest was 97%, consistent with our results and similar to other studies of survival when harvest was excluded (91%; Webb et al. 2011). Differences in areas lacking complex carnivore communities are likely due to differences in management objectives and harvest rates.

There was a significant effect of body condition and size on survival. Body length and circumference of the neck were the most influential predictors of survival. Both variables were negatively associated with survival, suggesting larger animals had lower survival (Table 2-4). This is consistent with previous studies that found hunters targeted larger animals whenever possible (Wright et al. 2006). Past studies have documented the effect of condition and size on calf survival. However, the relationship between body measurements and adult survival remains largely untested (Smith and Anderson 1998, Barber-Meyer et al. 2008, Griffin et al. 2011). Measurements of condition, such as IFBF and rump fat, were not correlated with survival in our study. In areas where nutritional quality was not a limiting factor, survival was independent of IFBF and condition (Halbritter and Bender 2011). However, elk in areas with limited nutritional quality did exhibit higher survival with increased IFBF (Bender et al. 2008, Webb et al. 2011). When examining the effect of age on survival, we detected no relationship. Prior research on the effect of age on elk survival offers some contrasting results. Webb et al. (2011) found survival to be independent of age, consistent with our study. Survival of elk in Wyoming varied greatly for juveniles based on density and climate, however, remained consistently high for adults (Sauer and Boyce 1983). Survival was negatively associated with age for elk in Washington (McCorquodale et al. 2011), however, elk in southern Canada had higher survival with age and were virtually unharvestable past age 9 possibly due to learned behavioral adaptations (Thurfjell et al. 2017). Our data do not support a pattern of behavioral adaptation with age.

When comparing elk harvested by hunters to those predated by mountain lions, we found a difference in loin muscle thickness and neck circumference (Table 2-4). Overall, elk lost to mountain lion predation were smaller and in worse body condition than harvested elk and the entire collared herd. Though not statistically significant, density plots and ANOVA results suggest trends in other body measurements and age of individuals that are consistent with our

expected differences and may be of biological significance. Additionally, elk harvested by hunters appeared to be in above average condition and size and slightly above average in age, approximately five years old. These results are consistent with the current understanding of differences in selection of elk by hunters versus large carnivores (Kunkel et al. 1999, Wright et al. 2006). Wolves, bears, and mountain lions predated primarily calves or old individuals (Gunther and Renkin 1990, Zager and Beecham 2006, Rearden et al. 2011). Additionally, elk lost to predation were often in poor nutritional condition with less fat (Gunther and Renkin 1990, Kunkel et al. 1999, Mech et al. 2001). Similarly, we found that elk lost to predation were in worse body condition and younger than average while hunters harvested elk that were above average age and condition.

Results of this study provide additional evidence of differential selection by hunters and large carnivores. Mountain lions appeared to predate elk that were generally more vulnerable to predation (e.g., smaller or in worse condition). Younger elk may be more naïve and therefore more susceptible to ambush from a mountain lion. Hunter harvest removed large individuals in good condition that likely have high reproductive value and contribute the most to population growth. In areas where populations of game species are above objective or targeted size, this effect may be inconsequential or even desirable. However, in smaller populations that may be more vulnerable to shifts in sex-age structure, the effects of harvest may manifest in reduced reproduction and population growth. These effects may become particularly pronounced in areas with low rates of predation from carnivores. Understanding survival and cause-specific mortality of a population allows for informed, accurate management plans. Whenever possible, management of game species should attempt to account for rates of predation. If vital rates are of concern, allocation of hunting permits can be adjusted by age or sex class to achieve management goals.

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FIGURES

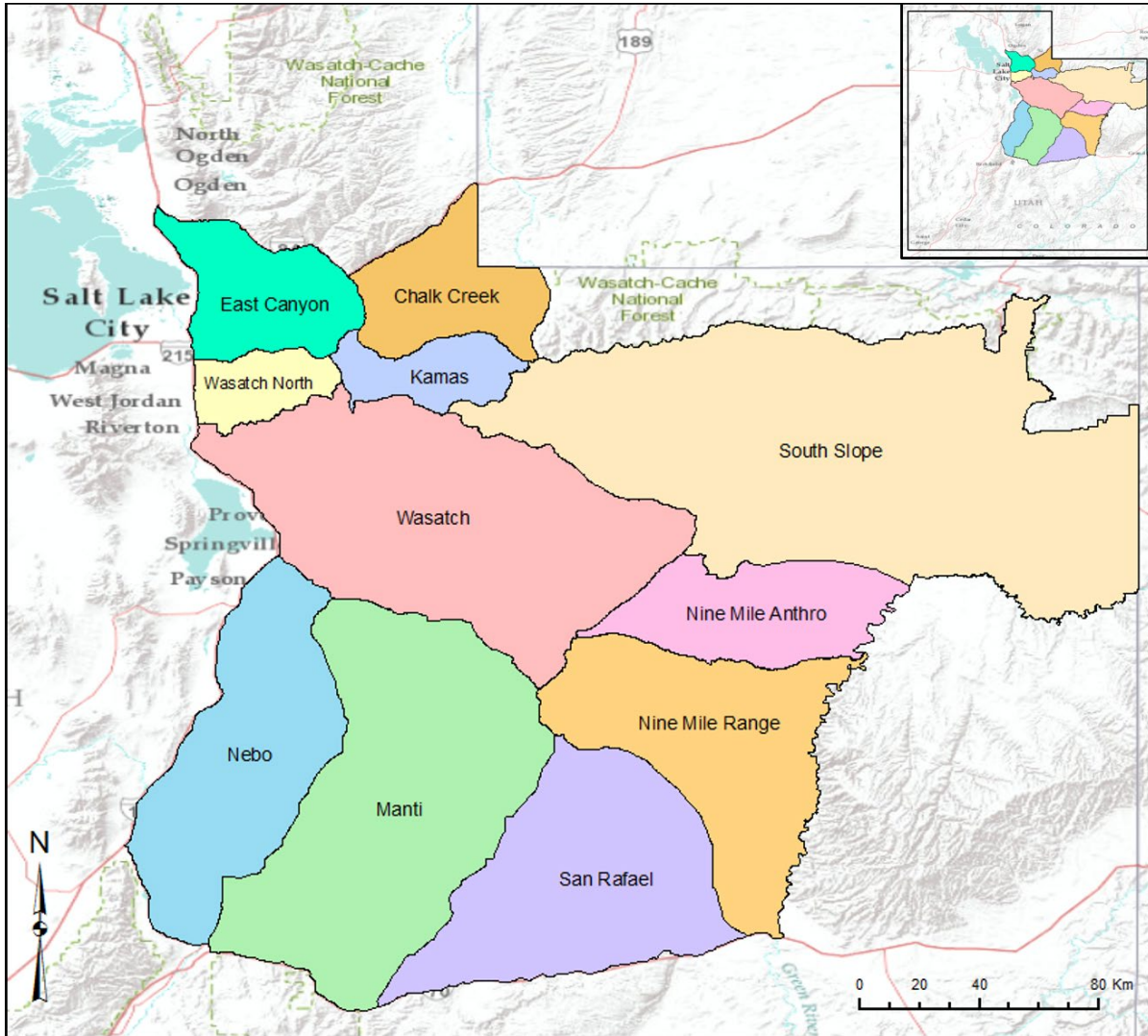


Figure 2-1. Our study area was the Wasatch and surrounding management units of central Utah. Colored polygons denote the separate management units.

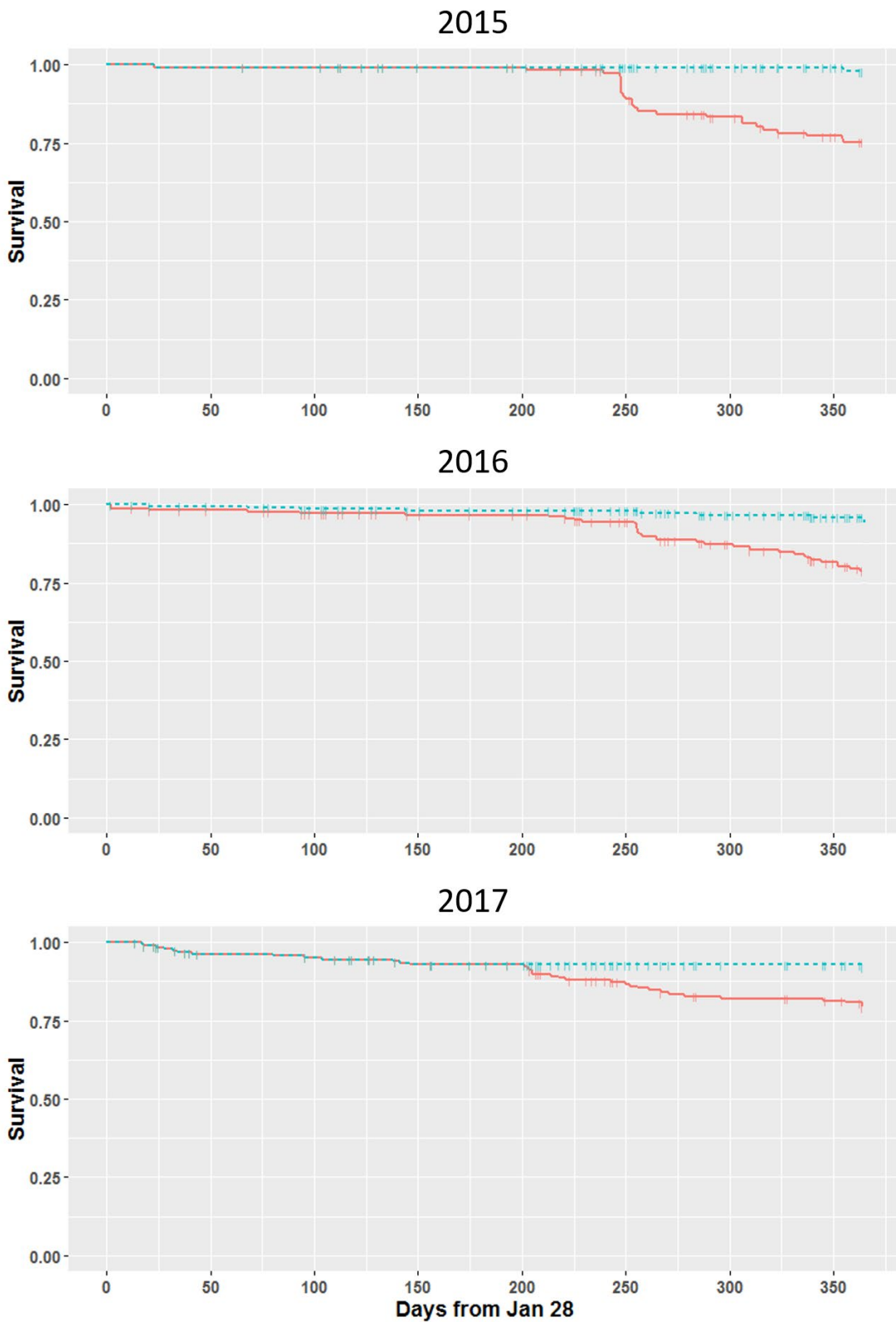


Figure 2-2. Annual survival of collared elk during a three-year span. The solid line denotes all mortalities included, the dashed line excludes hunter related mortalities.

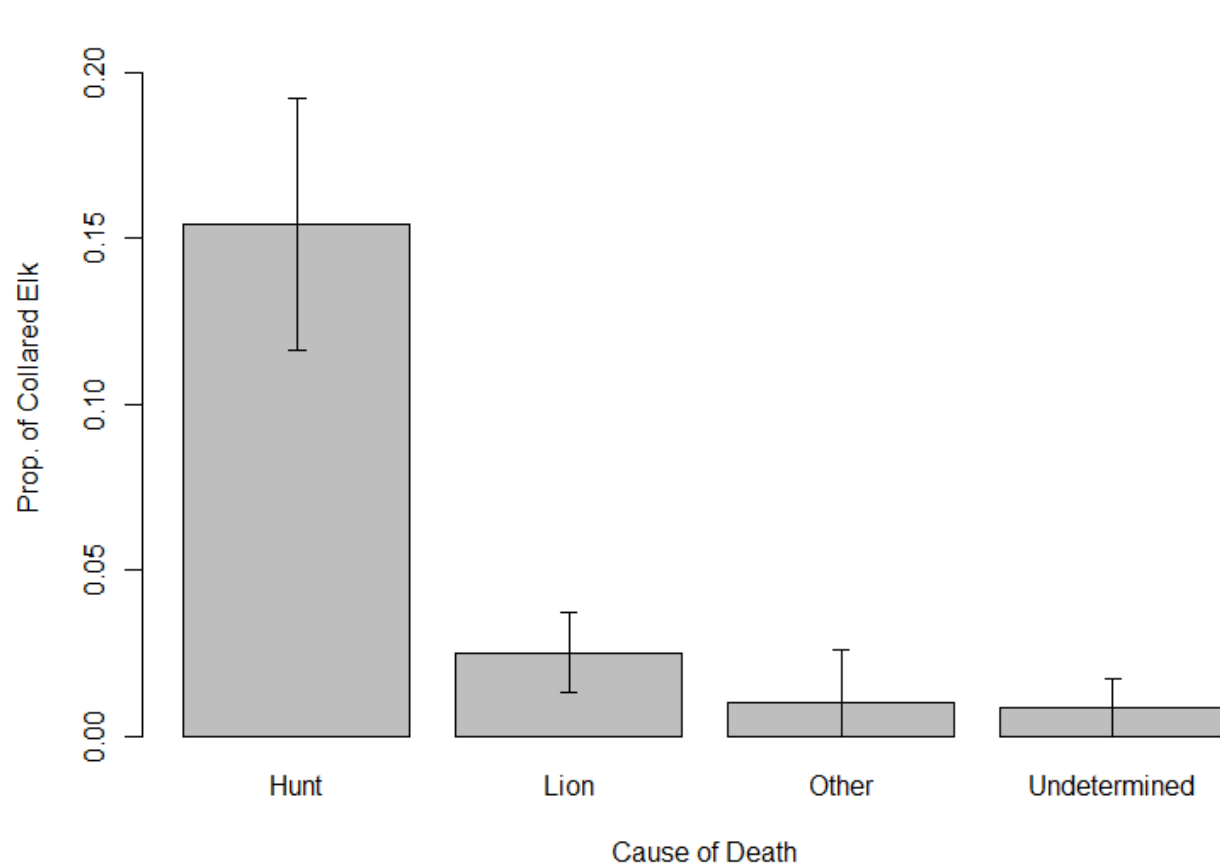


Figure 2-3. Number of mortalities by source during the entire three-year span. Other sources of mortality included automobile collisions, disease, and one elk that died during calving.

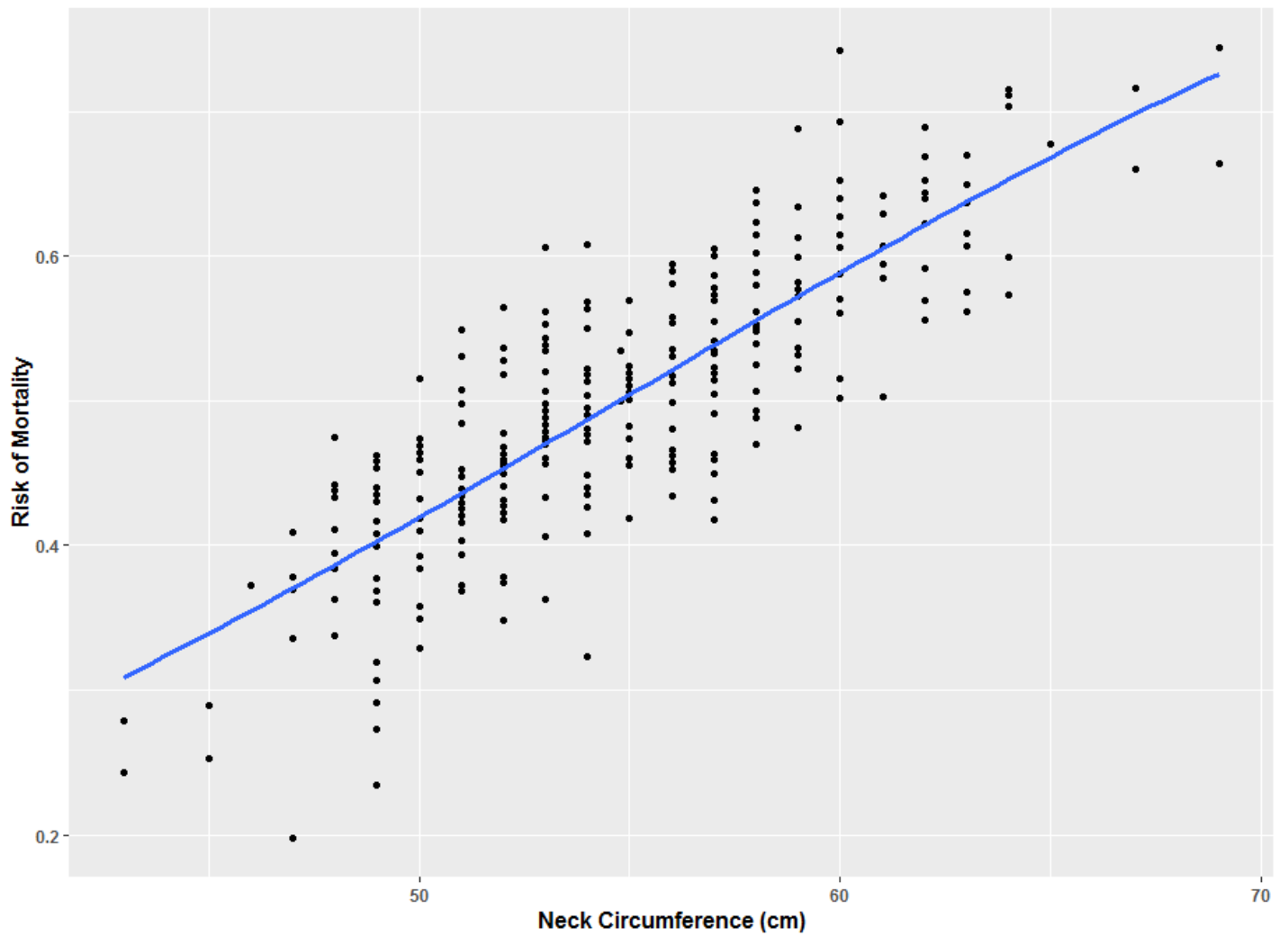


Figure 2-4. Predictive plot of risk of mortality as a function of neck circumference, based on top model. Model included neck circumference and body length.

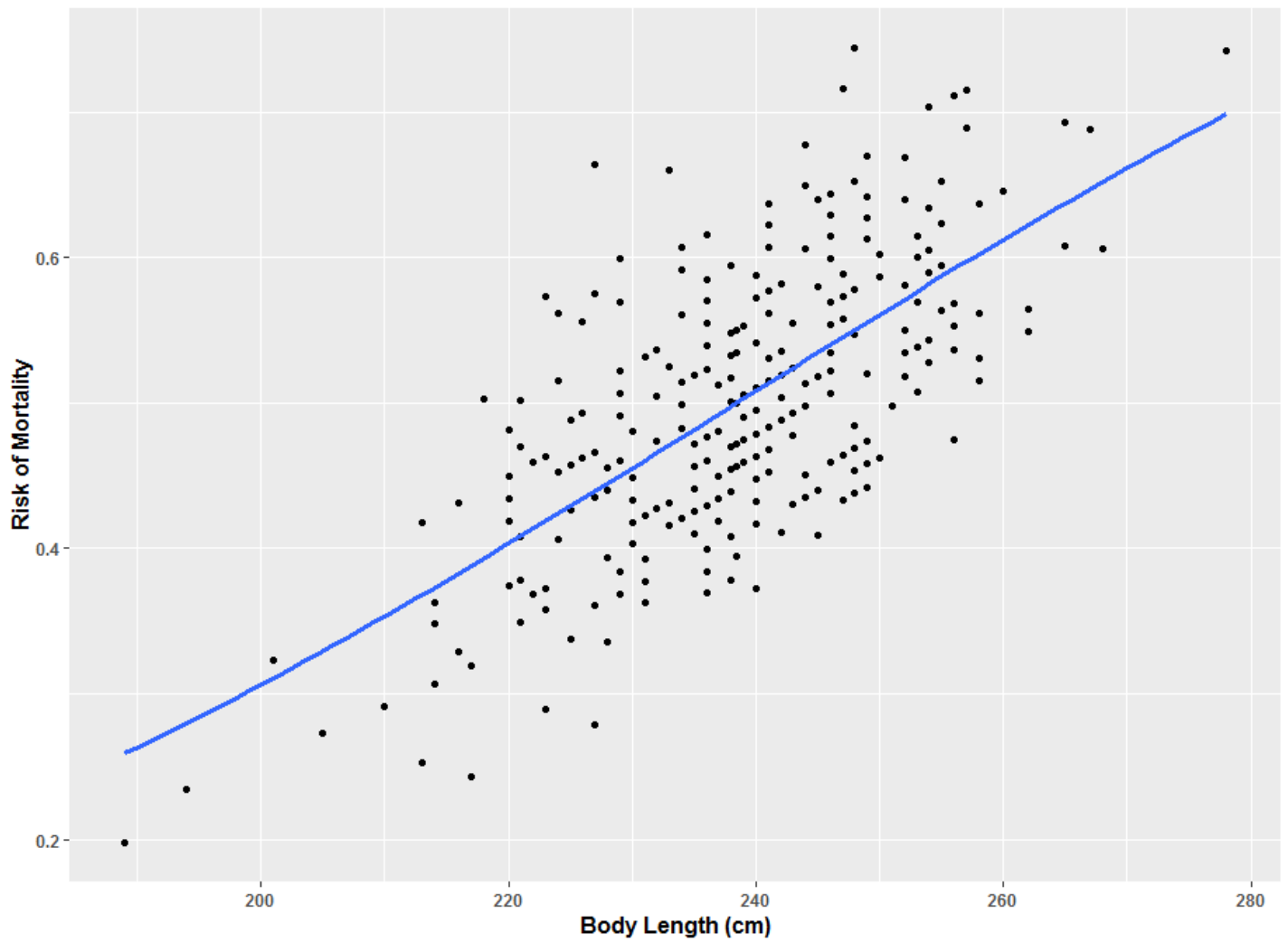


Figure 2-5. Predictive plot of risk of mortality as a function body length, based on top model. Model included neck circumference and body length.

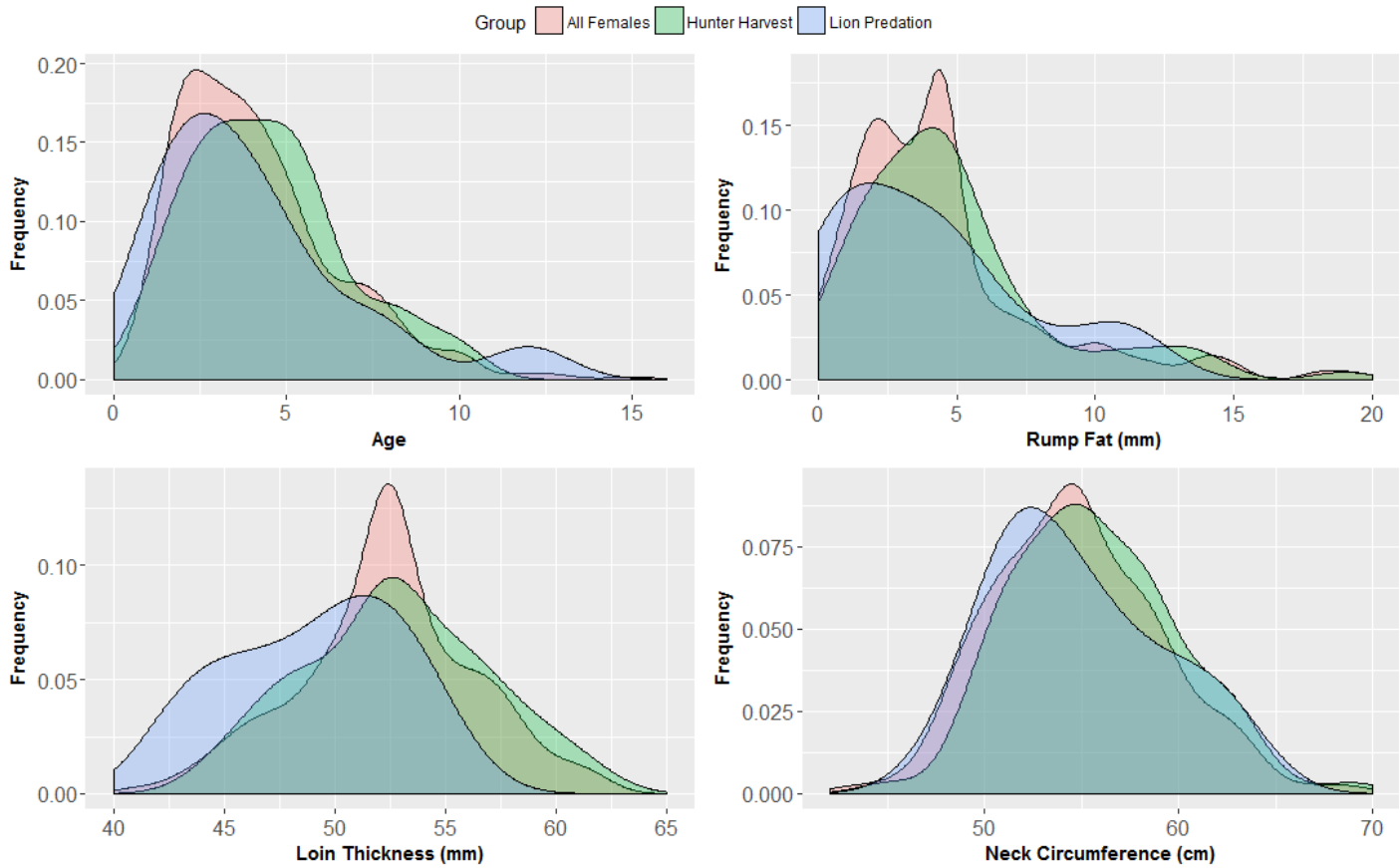


Figure 2-6. Distribution of age, rump fat, loin thickness, and neck circumference for all collared females (red), those harvested by hunters (green), and those predated by mountain lions (blue). We detected statistical differences in loin thickness and neck circumference between groups.

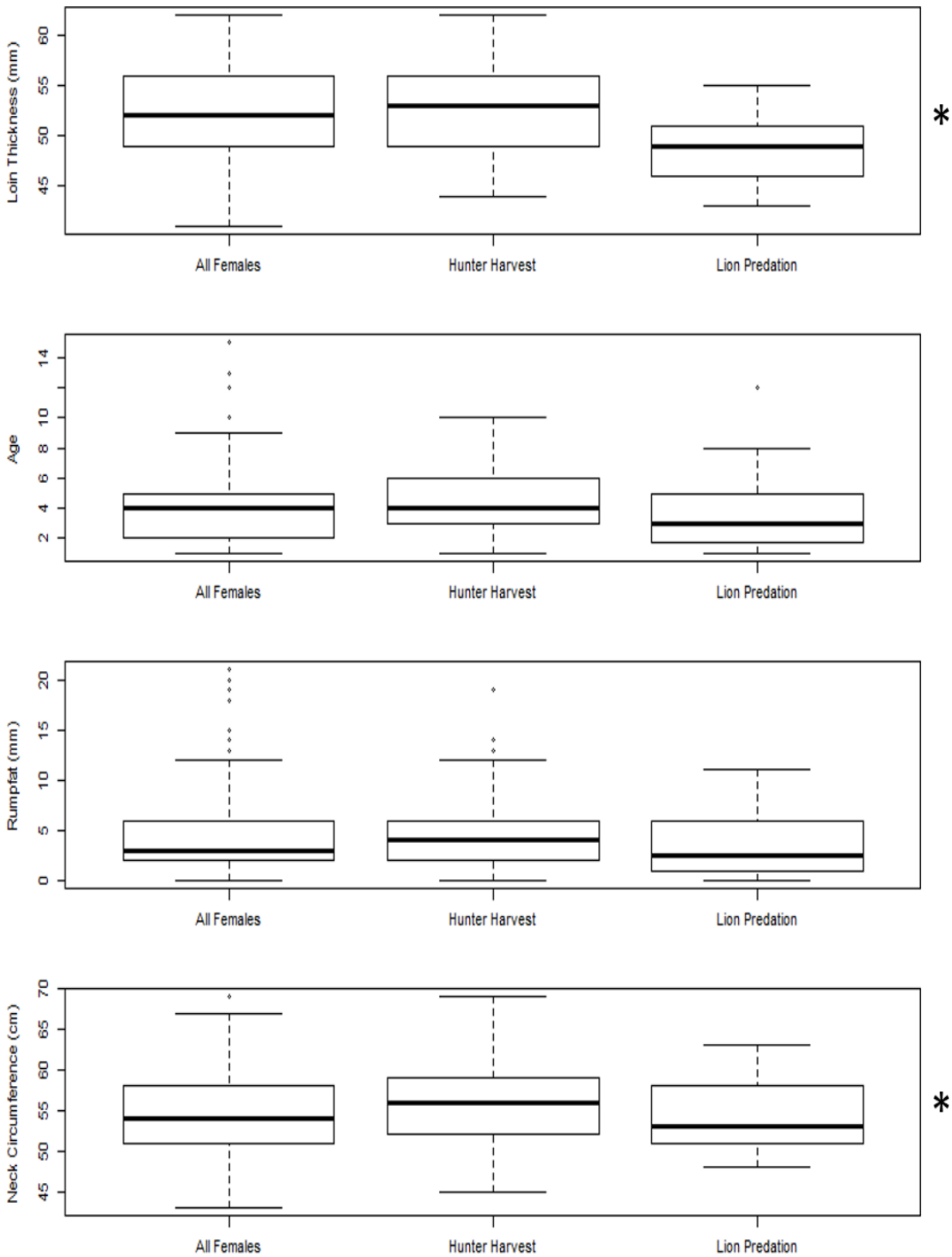


Figure 2-7. Loin thickness, age, rump fat, and neck circumference of harvested and predated females compared to the entire collared herd. An asterisk to the right of the panel indicates significant differences.

TABLES

Table 2-1. Annual survival of elk over a three-year span, calculated including hunter harvest and with harvest censored.

	With Harvest	SE	Without Harvest	SE
2015	75.3	0.042	97.8	0.016
2016	78.9	0.033	95.9	0.015
2017	80.7	0.031	92.8	0.019

Table 2-2. AICc model selection results for 26 candidate Cox Proportional Hazard models. Models with over 5% of the cumulative weight (and the null model for comparison) are shown below. Top model included neck circumference and body length and held 43.1% of the total weight.

	d.f.	AICc	Δ AICc	Weight
Neck + Body Length	2	944.2	0.00	0.431
Chest Girth + Neck + Body Length + Hoof	4	946.1	1.91	0.165
Neck + Age + Body Length	3	946.2	2.02	0.157
Loin + Neck + BCS + Body Length	4	946.9	2.69	0.112
Body Length + Hoof + Neck + Age	4	947.4	3.18	0.088
Null	0	952.4	8.21	0.007

Table 2-3. Hazard ratios and associated p – values from top model from AICc selection. Neck circumference, body length, age and rump fat were negatively associated with survival.

	exp(β)	Lower .95	Upper .95	p - value
Neck Circumference	1.065	1.016	1.115	0.008
Body Length	1.019	0.999	1.038	0.056

Table 2-4. Mean values of age and body measurements for all collared elk, harvested elk, and elk predated by mountain lions, with associated p – values.

	All Females	Lion Predation	Hunter Harvest	P – value
Age	4.16	4.06	4.47	0.413
Hoof circum. (cm)	61.22	59.95	61.23	0.127
Neck circum. (cm)	54.78	54.80	55.87	0.084*
Loin Thickness (mm)	52.33	48.64	52.85	0.003*
Chest Girth (cm)	160.41	159.73	161.28	0.758
Body Length (cm)	238.51	240.80	240.29	0.227
Body Condition Score	2.81	2.75	2.86	0.641
Rump Fat (mm)	4.52	3.97	4.87	0.609
Ingesta Free Body Fat	6.65	6.45	6.77	0.648
Body Mass (kg)	252.06	250.18	254.46	0.758