Fall Elk Distribution in the Missouri River Breaks

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Summary

Increasing harvest of adult female elk is the primary management tool for curtailing elk population growth and reducing elk populations. However, this tool is not effective when elk are located on private properties that restrict hunter access to elk during the hunting season. The purpose of this project was to evaluate the effects of hunter access and other landscape factors on elk distribution during the archery and rifle hunting seasons in the Missouri River Breaks Elk Management Unit (EMU). We GPS collared and collected location information from 45 adult female elk for 2 years in 2 adjacent populations within this EMU: the Missouri River Breaks (MRB) population in hunting district (HD) 621 and the Larb Hills population in HD 622/631. We categorized hunter access into 3 categories: freely accessible to hunters, restricted hunter access, and no hunter access. To quantify the effects of hunter access and other factors on elk selection of home ranges and elk selection of locations within their home range, we conducted a resource selection modeling exercise. In our resource selection models, we first treated the individual elk-year as the sampling unit to estimate individual-level selection coefficients and second, we pooled data from all individuals to estimate population-level selection coefficients.

The MRB archery and rifle season elk population ranges were 97% accessible to hunters. A total of 2% of the ranges allowed no public hunter access and 1% restricted hunter access. Sixty-eight percent of all archery season elk locations occurred in areas accessible to hunters, 30% occurred in areas with no hunter access, and 2% occurred in areas with restricted hunter access. Ninety-one percent of all rifle season elk locations occurred in areas accessible to hunters, 9% occurred in areas with no hunter access, and <1% occurred in areas with restricted hunter access. The Larb Hills archery season elk population range was 79% accessible to hunters, 11% allowed no hunter access, and 10% restricted hunter access. Fifty percent of all archery season elk locations occurred in areas accessible to hunters, 40% occurred in areas with no hunter access, and 10% occurred in areas with restricted hunter access. The rifle season elk population range was 79% accessible to hunters, 10% allowed no hunter access, and 11% restricted hunter access. Sixty-six percent of all rifle season elk locations occurred in areas accessible to hunters, 29% occurred in areas with no hunter access, and 5% occurred in areas with restricted hunter access.

Resource selection model results showed that elk in both MRB and Larb Hills selected home ranges in areas with no hunter access, and hunter access was the strongest predictor of home range locations. In both populations, the selection for home ranges in areas with no hunter access was stronger in the archery season than the rifle season (MRB: $\hat{\beta}_{\mathrm{arch}}$ = 1.93, 95% CI = 0.22, 0.29, $\hat{\beta}_{\mathrm{rifle}}$ = 0.29, 95% CI = 0.04, 0.54 and Larb Hills: $\hat{\beta}_{\mathrm{arch}}$ = 0.55, 95% CI = 0.45, 0.64, $\hat{\beta}_{\mathrm{rifle}}$ = 0.16, 95% CI = 0.04, 0.29). Similarly, elk in both populations selected locations within their seasonal home range with no hunter access, and the strength of selection for locations with no hunter access was stronger in the archery season than the rifle season (MRB: $\hat{\beta}_{\mathrm{arch}}$ = 0.88, 95% CI = 0.85, 0.92, $\hat{\beta}_{\mathrm{rifle}}$ = 0.44, 95% CI = 0.37, 0.51 and Larb Hills: $\hat{\beta}_{\mathrm{arch}}$ = 1.34, 95% CI = 1.32, 1.37, $\hat{\beta}_{\mathrm{rifle}}$ = 1.00, 95% CI = 0.97, 1.03). However, although population-level selection for locations with no hunter access was strong, individual-level selection models found only 43% of MRB elk selected for locations with no hunter access during the archery season, 18% of elk selected for locations with no hunter access during the rifle season, and the majority of all MRB elk locations (i.e., 68% of archery locations and 91% of rifle locations) occurred in areas accessible to hunters. In Larb Hills, individual models confirmed results of the population-level analysis, and 76% and 60% of elk selected for locations with no hunter access during the archery

and rifle seasons. These results highlight that population-level selection coefficients may not always represent individual selection patterns, and that population-level and individual models together are useful in interpreting how animals are using the landscape.

Understanding the availability of elk, primarily antlerless elk, to hunters is vital to managing elk to population objectives while still providing hunting opportunity for elk on publicly accessible lands. We found that even relatively small geographic areas within an elk population range being managed for restricted hunter access or no hunter access may have a disproportionate affect on elk distribution and prevent effective harvest of female elk to maintain elk populations at objective levels. Our results showed that the majority of the female elk harvest occurred during the rifle season, and the majority of MRB elk spend the rifle hunting season in areas that are accessible to hunters. With a limited amount of areas with no hunter access or restricted hunter access within the hunting season ranges, MRB elk use dense cover, riparian areas and areas away from roads for security. In the Larb Hills, elk are less accessible to hunters during the rifle hunting season. This situation will limit the effectiveness of antlerless harvest as a tool for reducing population size towards objective levels. In this area, stakeholders may need to determine if they are willing to tolerate larger elk populations, more liberal hunting seasons resulting in higher hunter numbers or longer season length, or provide some level of hunter access to harvest female elk so the population can be reduced to objective levels. Working cooperatively with stakeholders to minimize hunter access restrictions is necessary for curtailing further elk population increases and maintaining a distribution of elk across public and private lands.

Background and Objectives

Elk populations in the Missouri River Breaks Elk Management Unit (EMU) have risen to high levels in many areas, and are currently above the population objective. Implementing liberal hunting seasons and quotas to manage elk numbers and provide hunter opportunity has resulted in hunter crowding and an uneven elk distribution relative to lands open to free public hunting. Further and in spite of over-objective elk populations, the elk hunter success and harvest rate in hunting district (HD) 621 has been rapidly declining, possibly because the distribution of elk during the fall has shifted to other hunting districts, including HD 622. In HD 622, higher hunter pressure and a greater proportion of private land that restricts public hunting access has resulted in problematic elk distributions. Both HDs have experienced a declining hunter success rate of the primary elk management tool (elk B/Cow licenses). This situation limits the ability of Montana Fish, Wildlife & Parks (MFWP) to manage elk within defined population objective levels through hunter harvest and results in decreasing hunting opportunities on public lands. The disproportionate distribution of elk located in areas that restrict or do not allow hunter access during the hunting season is not unique to the Missouri River Breaks. Similar situations have been reported in southwestern Montana and across the western United States (Proffitt et al. 2012). Limited hunter access to elk may also result in abnormally high elk density on localized scales, amplifying the risk of transmissible infectious diseases such as Chronic Wasting Disease (CWD) and brucellosis if they are introduced into the area.

In 2011, the Elk Archery Working Group recommended season changes in areas with limited archery permits, designed in part to affect this situation and distribute elk onto publicly accessible land proportional to available habitat and population size. Rifle season regulation changes are also currently being considered and implemented in other parts of Montana in order to achieve the same objective. Similarly, in 2011 MFWP, Region 1 of the U.S. Forest Service, and the Montana/ Dakotas BLM office collaboratively identified a shared management goal of maintaining elk distribution on public lands proportional to availability of public lands and elk herd size. This may also result in combinations of land management and hunting regulations that are designed to influence elk distribution. Quantification of the impacts of these land management and hunting regulation actions, in a manner that will allow them to be reliably applied with predictable outcomes in other areas, is critical.

The purposes of this project were to evaluate the effects of hunter access and other factors on archery and rifle hunting season elk distribution in 2 populations within the Missouri River Breaks EMU: the Missouri River Breaks (MRB) population in HD 621 and the Larb Hills population in HD 622/631. We also conducted a baseline elk health assessment to determine levels of exposure to diseases of interest. Results will help wildlife managers better understand factors affecting elk distribution in the Missouri River Breaks EMU and prescribe hunting season regulations to achieve goals described in Montana's elk management plan. Ultimately, managing elk within objective would prevent habitat degradation, minimize the potential for amplification of diseases like CWD, lessen impacts to other wildlife and help Montana Fish, Wildlife and Parks (MFWP) address property damage issues on private lands.

Study Area

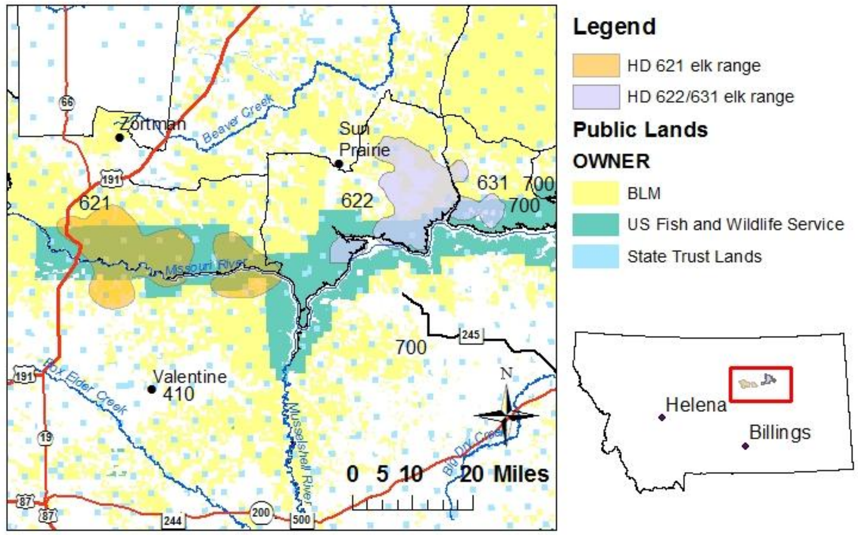

Figure 1. The study area included the Missouri River Breaks in hunting district (HD) 621 and Larb Hills-Iron Stake Ridge areas in HD 622/631 in south Philips County. Landownership included a mixture of privately owned lands (white), and public lands owned by the Bureau of Land Management (BLM, yellow), U. S. Fish and Wildlife Service (green), and State of Montana (blue).

The study area was located in south Philips and Valley counties and included portions of Montana HDs 621, 622 and 631. The core study area included the area along the Missouri River and east of Hwy 191 in HD 621 and the Larb Hills-Iron Stake Ridge area in HD 622/631 (Figure 1). The MRB elk population range includes the Missouri River and associated breaks habitat in the southern portion of HD 621, as well as similar habitat south of the Missouri River in HD 410. The core elk range is comprised of 87% public land and 13% private land. The public land is primarily owned by the U.S. Fish and Wildlife Service and managed for wildlife and habitat conservation. The Larb Hills elk population range in HD 622/631 includes the area north of Fort Peck Lake from Iron Stake Ridge northward through the Larb Hills and Timber Creek (Figure 1). The core elk range is comprised of 69% public land and 31% private lands. The public land is primarily owned by the Bureau of Land Management (BLM) and U.S. Fish and Wildlife Service. Private lands are primarily large tracts of ranchlands grazed by livestock. Landcover across the study area includes a mixture of sagebrush steppe, mixed grass prairie, Great Plains badlands, and Ponderosa Pine woodland and savanna.

Elk population trend is measured by biennial winter aerial surveys conducted by MFWP. The combined elk population count in HDs 621, 622, 631, and 632 increased from years 1995 to 2006 with a high of 4,226 elk observed in 2006. The combined elk population generally decreased from 2007-2014 to 2,596 elk observed in 2014 (Figure 2). An average of 2,834 elk was observed across the area during 1995-2014. Observed populations from these surveys are measured against the elk population objective of 1,700-2,000 that was established by the Breaks Elk Working Group in 1995. Elk populations have been above objective since 2001, ranging from at objective in 1997, to twice the objective in 2006, with a current level of 30% above objective.

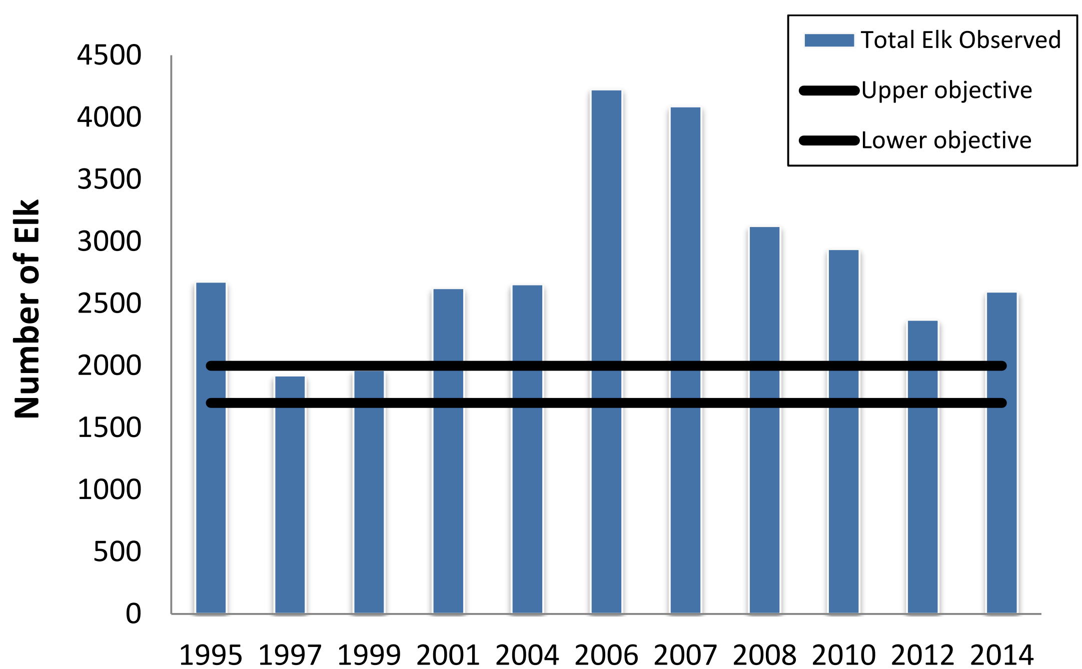

Figure 2. The total number of elk observed during aerial surveys in HDs 621, 622, 631, and 632 during 1995 – 2014 and the lower and upper elk population objective.

Elk hunting in the Missouri River Breaks EMU is by permit or special license drawing only. The primary elk management tool for moving the population up or down towards objective levels has been varying the number of antlerless elk B-licenses and/or antlerless elk permits valid during the 5-week general hunting season (Figure 3). Since 2001, elk populations have been above the objective and elk B-licenses have been increased in an attempt to move the population down to objective. An increase in the elk population in 2006 and 2007 resulted in a large increase in antlerless license levels. Immediately following 2007, the antlerless elk harvest was successful in lowering elk populations but not to objective levels. Since 2007, antlerless elk licenses have remained liberal in an attempt to bring the elk population down to objective levels, but antlerless elk harvest and hunter success has declined (Figure 3). The reason for recent declines in hunter success and harvest are unknown, but given the declines in hunter success resulting in insufficient harvest, the elk population is likely to remain over objective.

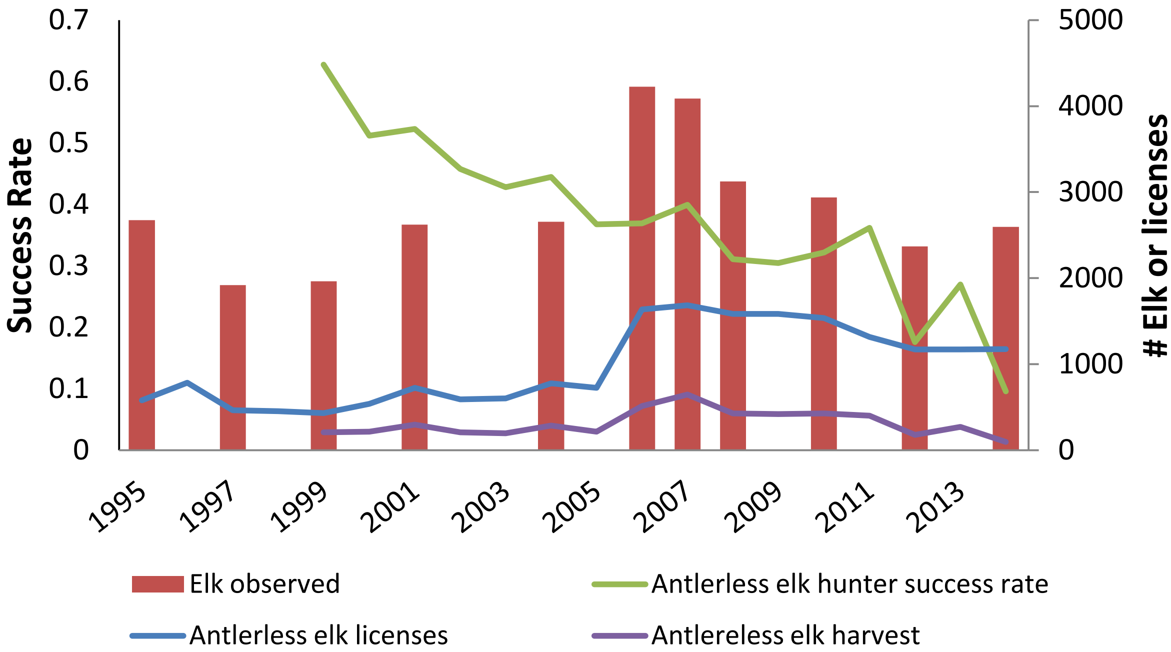

Figure 3. The number of elk observed during aerial surveys, antlerless elk hunting licenses, antlerless elk harvest, and hunter success in HDs 621, 622, 631, and 632 during 1995–2014. Methods

We captured 25 adult female elk in the MRB and 25 adult female elk in the Larb Hills population by helicopter netgunning. We collected a blood sample to determine pregnancy status and estimate levels of disease exposure. Blood serum samples were screened to detect antibodies indicating exposure to *Brucella abortus (Brucella)* and *Leptospira* (*Leptospira spp.)*, para-influenza 3, infectious bovine rhinotracheitis, bovine respiratory syncytial virus, and bovine viral diarrhea. We collected fecal samples to screen for parasite presence and abundance. We used ultrasonography to assess body condition and estimate the percentage ingesta-free body fat following methodology of Cook et al. (2010). We measured chest girth and used a predictive equation to convert chest girth to an estimate of body mass (Cook et al. 2010). We aged elk by tooth eruption and wear patterns (Hamlin et al. 2000) and permanently marked each animal with a pair of numbered, metal eartags.

We outfitted elk with store on board global positioning system (GPS) radiocollars (Lotek Wireless Inc. model 3300L, New Market, Ontario, Canada) that were built with a timed release mechanism set to release the collar after 2-years. Collars emitted a very high frequency (VHF) radio signal allowing them to be monitored from the ground or air. We programmed collars to record hourly locations 24 hours a day and to emit a distinct mortality signal if the collar was stationary for more than 6 hours. We monitored elk survival and locations monthly for two-years using aerial and ground telemetry. After collars released, we retrieved collars and downloaded the location data. Nineteen of the release mechanisms failed, and these elk were recaptured during March 2015 via helicopter netgunning so that we could retrieve the collars and download the location data. We used these locations to estimate elk survival rates, determine causes of mortality, and to define elk seasonal distribution and public and private land use patterns.

We used the Kaplan-Meier method (KM; Pollock et al. 1989) to estimate and compare survival rates across populations (MRB and Larb Hills) and years. The KM method provides a time sensitive survival estimate based on the number of individuals that experience a mortality event at a given time vs. the number of individuals being monitored at that specific point in time, and follows the formula: $\hat{S}(t) = \prod(1 - d_j/n_j)$, where d_j is the number of individuals who experience a mortality event at time t, and n_j is the number of individuals who are at risk of mortality at time t. We removed (i.e., right censored) individuals from the monitoring pool that experienced radio collar failure. For all comparisons between herds, we treated year as a categorical variable.

We evaluated the effects of 5 covariates on elk resource selection: distance to dense cover, distance to roads, terrain roughness, hunter access and land cover type. We defined dense cover based on the canopy cover landcover product from LANDFIRE (www.landfire.gov) and considered areas with ≥ 40% canopy cover as dense cover. We log transformed distance to cover to represent a threshold response of elk to dense cover, where below a threshold distance to cover, the effects of cover diminished. We used the Montana Department of Transportation roads layer to define roads on private and state lands, and a local Bureau of Land Management (BLM) and United States Fish and Wildlife Service (USFWS) roads layer to define roads on BLM and USFWS lands, respectively. We log transformed distance to roads to represent a threshold response of elk to roads. We defined terrain roughness based on a 30 m digital elevation model (DEM). We estimated terrain roughness as the total amount of elevation difference between a given pixel of the DEM and all of its neighbors (Riley et al. 1999). We classified hunter access into 3 categories: accessible to public hunting, no public hunting, and some level of restricted public hunting. Accessible areas included public lands that allowed hunting and all privately owned lands enrolled in a State of Montana's Block Management program. Areas of no public hunting included a public land wildlife viewing area where hunting is not allowed and privately owned lands that restricted access to the public through lease agreements with paying clients. Areas with some level of restricted public hunting included private lands that charged a trespass fee or allowed for hunting without a fee to only family and friends. We defined landcover type based on the Montana Spatial Data Inventory landcover model. We broadly classified land cover into 4 categories: grasslands and shrublands, badlands, forest, and riparian. All non-habitat (i.e., developed areas, rivers and lakes, etc.) were clipped from land cover data and excluded from the analysis.

Resource selection model development

To evaluate factors affecting elk distribution during the fall hunting seasons, we evaluated the second-order selection of hunting season home ranges within the population range (S_2), and the third-order selection of hunting season locations within individual home range (S_3) using a used-available sampling design (Manly et al. 2002, Johnson et al. 2006). We separated the hunting season into the archery period and rifle period. We evaluated second order selection by comparing individual archery and rifle season home ranges within the available herd level hunting season range. We estimated individual and herd level ranges using 95% fixed-kernel isopleths calculated using the reference bandwidth. We sampled the individual home range by generating 100 random points within each home range. This sample represented the used home range locations. We did not consider the actual elk locations within the home range as the used sample because contrasting the actual elk locations with population level availability would represent selection somewhere between the second and third order, rather than strictly the second order. We randomly generated 5 available locations per used location within the herd level hunting season range to represent the available choice set. We identified a set of 6 biologically plausible hypotheses about how elk may position their archery and rifle season home ranges, and expressed these hypotheses as 5 covariates. We then evaluated a total of 32 competing models including all combinations of the 5 covariates and the null model.

We evaluated third-order selection by comparing individual hunting season locations within the available individual hunting season home range. We estimated individual home range using 95% fixed-kernel isopleths calculated using the reference bandwidth. We randomly generated 5 available locations per used location within the individual home range to represent the available choice set. In the third order analysis, we evaluated the same set of 32 competing models as described previously.

We used generalized linear models with a binomial distribution to compare attributes of used and available locations. After identifying a set of biologically plausible covariates for second order and third order selection, we evaluated all potential model combinations. We screened covariates for colinearity and eliminated models containing covariates with $r>0.7$ (Dormann et al. 2013). We standardized all continuous covariates to allow for comparisons of effect size. We fit models in Program R and selected the best model for each individual based on AIC score. First, we treated the individual animal-year as the sampling unit. This approach allowed us to evaluate individual animals' patterns of selection and assess individual and annual variation in selection. However, because some animals never used areas that restricted hunter access and other animals always used areas that restricted hunter access, we were unable to estimate the access selection coefficient properly (i.e., there was complete separation in the used locations dataset). Therefore, we were unable to use the coefficients and standard errors from models with animal-year as the sampling unit to estimate population-level selection coefficients.

Instead, to estimate population-level resource selection coefficients, we conducted a second model selection process using a combined dataset that included data from all individuals and years. We standardized the number of locations for all individuals in the dataset. In this analysis, the variance of the selection coefficients was underestimated because it accounted for only the location-level variance but not the variance among individual animals. The second analysis with population as the sampling unit allowed us to estimate the overall populations' patterns of selection and predict the relative probability of use within the study area.

Results

Elk pregnancy, body condition, and disease exposure

We captured and sampled a total of 53 female elk. Three elk died during capture and we outfitted the remaining 50 elk with radiocollars. Mean elk age was 5.1 ranging from 2 to 13 years old. The adult pregnancy rate was 0.88 in MRB and 0.72 in Larb Hills (Table 1).

Overall winter body condition was similar between MRB and Larb Hills, however after accounting for lactation status, lactating females in Larb Hills had lower levels of body fat than non-lactating females in MRB and Larb Hills (Figure 1). The small sample size (n = 2) of lactating females in

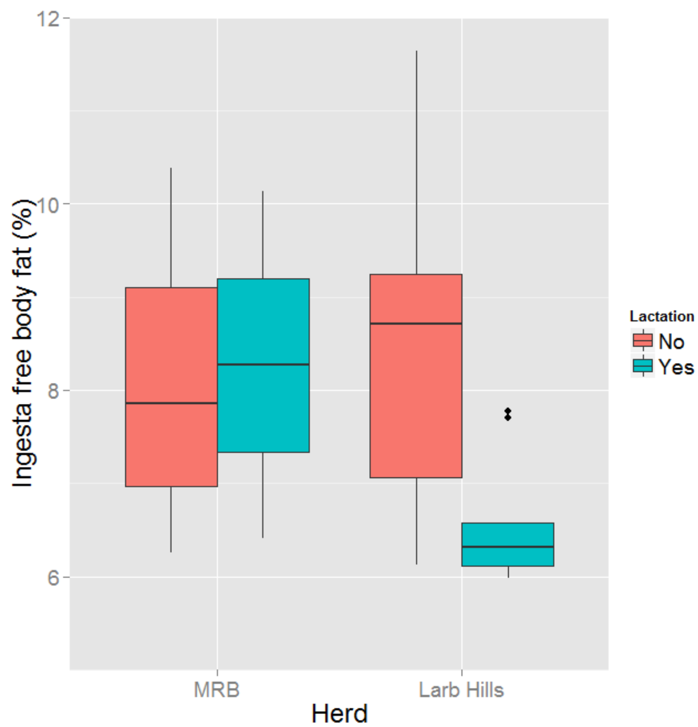

Figure 1. Boxplot of percent ingesta-free body fat of lactating and non-lactating adult female elk in MRB and Larb Hills during February 2013. Horizontal lines through boxes represent median values and the length of box represents the middle 50% of observations.

MRB limited inference as to population-level body condition of lactating females in MRB. Corresponding to their relatively low levels of body fat, lactating females in Larb Hills had lower than average pregnancy rate of 0.67 (n = 9, Table 1). The mean elk body mass did not differ between herds. Mean body mass in MRB was 251.4 kg (SD = 19.0) and mean body mass in Larb Hills was 255.1 kg (SD = 14.4).

We found some elk were exposed to *Leptospira*, para-influenza 3, and infectious bovine rhinotracheitis (Table 2). Strains of leptospirosis detected included can (n = 1), pom (n = 1), and ict (n = 3). We did not detect any exposure to *Brucella*, bovine respiratory syncytial virus, or bovine viral diarrhea. Levels of exposure were similar between herds and within the normal range for free-ranging elk in Montana.

Elk survival

We deployed a total of 50 collars on elk. One collar released early and 2 collars malfunctioned. Of the remaining 47 collared elk, 40 survived the first year of monitoring and 32 survived the full two-year monitoring period. The annual survival rate for MRB elk was 0.84 (95% CI = 0.69 – 0.92) and for Larb Hills was 0.83 (95% CI = 0.68 – 0.91). Annual survival rate and the timing of mortality events was

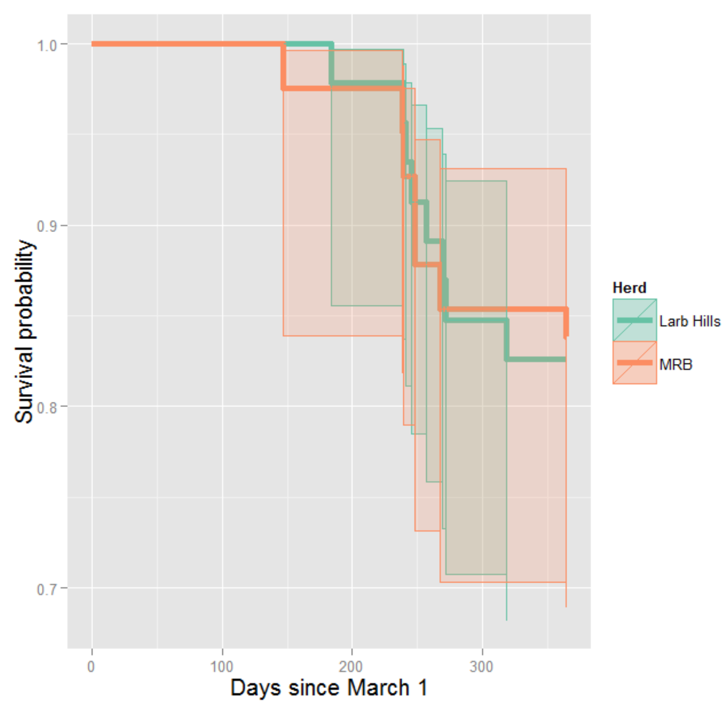

Figure 2. Kaplan-Meier survival curves with 95% confidence bands for adult female elk in MRB (green) and Larb Hills (orange) during 2013 - 2015.

similar for both herds (Figure 2).

Hunter harvest was the primary cause of mortality. Of the 15 documented mortality events, causes of mortality included 1 archery harvest, 8 rifle harvest, 1 illegal harvest, 2 wounding loss, 1 lion predation, and 2 unknown causes (Table 3). Of the 9 elk legally harvested, 8 were harvested in areas accessible to hunters and 1 was harvested on private land that did not allow public hunter access. Hunters were known to avoid harvesting collared elk, so mortality caused by hunting may be slightly higher for the two herd units.

Elk movements and seasonal ranges

Of the 50 collars deployed, we retrieved location data from 46 collars. Two collars malfunctioned and were lost, 1 collar did not collect location data (i.e., the VHF beacon worked but the GPS sensor malfunctioned), and 1 collar dropped off early. We did not document any movement between elk populations, however, there was some minor overlap of MRB and Larb Hills elk population ranges in the UL Bend area.

A total of 22 individual elk and 37 elk- years were included in the MRB archery season analysis and a total of 20 individual elk and 33 elk- years were included in the MRB rifle season analysis. The 2013–2014 MRB population archery season range was 87% publically owned and approximately 97% was accessible to hunters. A total of 2% of the archery season range allowed no public hunter access and 1% restricted hunter access. A 5.1 km^2 wildlife viewing area in the southern part of the range was closed to all hunting, as well as several small, private parcels scattered across of the range. Landcover included 21% forests, 6% riparian, 16% badland, and the remainder grassland and shrubland. Motorized roads were common and evenly distributed throughout the range and the average distance to a motorized road was 11.0 km. Dense cover was distributed across the range primarily along riparian corridors and average distance to cover was 5.6 km. The 2013–2014 MRB population rifle season range had 90% overlap with the archery season range. The rifle season range was 87% publically owned and approximately 97% was accessible to hunters. A total of 2% of the rifle range allowed no public hunter access and 1% restricted hunter access.

A total of 23 individual elk and 43 elk- years were included in the Larb Hills archery season analysis and a total of 21 individual elk and 38 elk- years were included in the Larb Hills rifle season analysis. The 2013–2014 Larb Hills population archery season range was 69% publically owned and approximately 79% was accessible to hunters. A total of 11% of the archery range allowed no public hunter access and 10% restricted hunter access. Several large, adjacent parcels at the core of the range allowed no hunter access or restricted hunter access. Landcover included 10% forests, 2% riparian, 36% badland, and the remainder grassland and shrublands. Motorized roads were common and evenly distributed throughout the range and the average distance to a motorized road was 11.4 km. Dense cover was distributed across the range primarily along riparian corridors and average distance to cover was 6.5 km. The 2013–2014 Larb Hills rifle season range had 86% overlap with the archery season range. The 2013–2014 rifle season range was 74% publically owned and approximately 79% was accessible to hunters. A total of 10% of the rifle range allowed no public hunter access and 11% restricted hunter access.

Second order selection of elk home ranges

In the MRB, the best archery season resource selection model varied among individuals. Elk most commonly selected for home ranges in rough terrain (n = 19), near dense cover (n = 17), and with no hunter access (n = 14, Table 4). Of the 15 individual elk sampled in 2 years, 9 never selected for areas without hunter access, 4 selected for areas with no hunter access in both years, and 2 selected for areas with no hunter access in 1 year but not the second year. The best population level archery season model included all covariates. The standardized population level coefficients showed elk most strongly select for home ranges in areas with no hunter access ($\hat{\beta}$ = 1.93, 95% CI = 1.75, 2.10, Table 5). Elk also selected home ranges in riparian ($\hat{\beta}$ = 0.47, 95% CI = 0.29, 0.64) or badland ($\hat{\beta}$ = 0.31, 95% CI = 0.21, 0.42) areas over grassland and shrubland areas, and home ranges in rough terrain ($\hat{\beta}$ = 0.23, 95% CI = 0.18, 0.29), near dense cover ($\hat{\beta}$ = -0.17, 95% CI = -0.22, -0.13), and closer to roads ($\hat{\beta}$ = -0.17, 95% CI = -0.20, -0.14).

In the MRB, the best rifle season resource selection model varied among individuals. Elk most commonly selected for home ranges near dense cover (n = 19) and in rough terrain (n = 17, Table 4). Of the 13 individual elk sampled in 2 years, 10 elk never selected for areas with no hunter access, and 3 elk selected for areas with no hunter access in 1 year but not the second year. The best population level rifle season model included all covariates. The standardized population level coefficients showed elk most strongly select home ranges in areas accessible to hunters instead of areas that restrict hunter access ($\hat{\beta}$ = -0.95, 95% CI = -1.59, -0.31), in riparian ($\hat{\beta}$ = 0.69, 95% CI = 0.49, 0.88) and badland ($\hat{\beta}$ = 0.45, 95% CI = 0.34, 0.56) areas over grassland/ shrubland areas, and in areas that allow no hunter access instead of areas accessible to hunters ($\hat{\beta}$ = 0.29, 95% CI = 0.04, 0.54, Table 5). Elk also selected home ranges in rough terrain ($\hat{\beta}$ = 0.23, 95% CI = 0.18, 0.28), in areas near dense cover ($\hat{\beta}$ = -0.19, 95% CI = -0.24, -0.15), and near roads ($\hat{\beta}$ = -0.08, 95% CI = -0.12, -0.05).

In the Larb Hills, the best archery season resource selection model varied among individuals. Elk most commonly selected for home ranges in areas that allowed no hunter access (n = 21), that restricted hunter access (n = 13), and in rough terrain (n = 10, Table 4). Of the 20 individual elk sampled in 2 years, 7 elk never selected for areas with no hunter access, 5 selected areas with no hunter access in both years, and 8 elk selected for areas with no hunter access in 1 year but not the second year. Two elk selected for areas that restricted hunter access in both years, 12 elk never selected for areas that restricted hunter access, and 6 elk selected for areas that restricted hunter access in 1 year but not the second year. The best population level archery season model included all covariates except for terrain roughness. The standardized population level coefficients showed elk most strongly select for areas that allowed no hunter access ($\hat{\beta}$ = 0.55, 95% CI = 0.45, 0.64, Table 5). Elk also selected home ranges in grassland and shrublands over riparian areas ($\hat{\beta}$ = -0.30, 95% CI = -0.59, -0.02) and away from dense cover ($\hat{\beta}$ = 0.06, 95% CI = 0.02, 0.10).

In the Larb Hills, the best rifle season resource selection model varied among individuals. Elk most commonly selected for home ranges in areas that allowed no hunter access (n = 12), in rough terrain (n = 12), and in areas near dense cover (n = 11, Table 4). Of the 17 individual elk sampled in 2 years, 8 elk never selected for areas with no hunter access, 2 selected areas with no hunter access in both years, and 7 selected for areas with no hunter access in 1 year but not the second year. The best population level rifle season model included all covariates. The standardized population level coefficients showed elk most strongly select for areas with no hunter access ($\hat{\beta}$ = 0.16, 95% CI = 0.04, 0.28, Table 5). Elk also selected for grassland/ shrublands over badland areas ($\hat{\beta}$ = -0.12, 95% CI = -0.21, -0.04), areas nearer to roads ($\hat{\beta}$ = -0.08, 95% CI = -0.11, -0.04), and areas near dense cover ($\hat{\beta}$ = -0.07, 95% CI = -0.11, -0.04).

Third order selection of elk locations

In the MRB, 68% of all archery season locations occurred in areas accessible to hunters, 30% occurred in areas with no hunter access, and 2% occurred in areas with restricted hunter access. The best archery season resource selection model varied among individuals. Within their annual archery season home range, elk most commonly selected for locations near dense cover (n = 24), away from roads (n = 23), and in riparian areas (n = 20, Table 6). Of the 15 individual elk sampled in 2 years, 8 elk never selected for areas with no hunter access, 4 selected for areas with no hunter access in both years, and 3 changed their selection for areas with no hunter access areas between years. The best population level archery season model included all covariates. The standardized population level coefficients show elk selected most strongly for locations that restrict hunter access ($\hat{\beta}$ = 1.73, 95% CI = 1.63, 1.83), and with no hunter access ($\hat{\beta}$ = 0.88, 95% CI = 0.85, 0.92, Table 7). Elk also selected for locations in riparian ($\hat{\beta}$ = 0.69, 95% CI = 0.64, 0.74) and forested ($\hat{\beta}$ = 0.33, 95% CI = 0.29, 0.36) areas and against badland areas ($\hat{\beta}$ = -0.06, 95% CI = -0.10, -0.02) relative to grasslands and shrublands. Elk selected for locations away from roads ($\hat{\beta}$ = 0.19, 95% CI = 0.17, 0.20) and near dense cover ($\hat{\beta}$ = -0.14, 95% CI = -0.15, -0.12).

In the MRB, 91% of all rifle season locations occurred in areas accessible to hunters, 9% occurred in areas with no hunter access, and <1% occurred in areas with restricted hunter access. The best rifle season resource selection model varied among individuals. Elk most commonly selected for locations away from roads (n = 24), near dense cover (n = 19), and in badlands instead of grasslands or shrublands (n = 18). Of the 13 individual elk sampled in 2 years, 9 elk never selected for areas with no hunter access and 4 elk selected for areas with no hunter access in 1 year but not the second year. The best population level rifle season model included all covariates except for terrain roughness. The standardized population level coefficients show elk selected locations in accessible areas over restricted hunter access ($\hat{\beta}$ = -1.43, 95% CI =-1.88, -0.98) and selected locations in no hunter access over accessible locations ($\hat{\beta}$ = 0.44, 95% CI =0.37, 0.51, Table 7). Elk also selected for riparian ($\hat{\beta}$ = 0.43, 95% CI = 0.37, 0.48) and badland

($\hat{\beta}$ = 0.26, 95% CI = 0.22, 0.29) locations and against forests ($\hat{\beta}$ = -0.37, 95% CI = -0.41, -0.33) relative to grassland and shrublands. Elk selected for locations near dense cover ($\hat{\beta}$ = -0.21, 95% CI = -0.23, -0.20) and away from roads ($\hat{\beta}$ = 0.16, 95% CI = 0.14, 0.18). During the rifle season, elk selection for locations in no hunter access was only half as strong as selection for these areas during the archery season (Table 7). Selection patterns for restricted access also differed during the archery and rifle seasons, with elk selecting locations in areas with restricted hunter access during the archery season and avoiding these areas during the rifle season. During the archery and rifle season selection coefficients for other covariates were similar.

In the Larb Hills, 50% of all archery season locations occurred in areas accessible to hunters, 40% occurred in areas with no hunter access, and10% occurred in areas with restricted hunter access. The best archery season resource selection model varied among individuals. Elk most commonly selected for locations in areas that allowed no hunter access (n = 33), that restricted hunter access (n = 31), away from roads (n = 30), and near dense cover (n = 26, Table 6). Of the 20 individual elk sampled in 2 years, 3 elk never selected for locations with no hunter access, 14 selected locations that allowed no hunter access in both years, and 3 elk selected for areas with no hunter access in 1 year but not the second year. Four elk never selected for locations that restricted hunter access, 12 elk selected for locations that restricted hunter access both years, and 4 elk selected for locations that restricted hunter access in 1 year but not the second year. The best population level archery season model included all covariates. The standardized population level coefficients showed elk select most strongly for locations with no hunter access ($\hat{\beta}$ = 1.34, 95% CI = 1.32, 1.37, Table 7) and that restricted hunter access ($\hat{\beta}$ = 0.59, 95% CI = 0.56, 0.63). Elk also selected locations in forested ($\hat{\beta}$ = 0.44, 95% CI = 0.40, 0.48) and riparian ($\hat{\beta}$ = 0.17, 95% CI = 0.08, 0.26) areas over grassland and shrublands, and locations away from roads ($\hat{\beta}$ = 0.32, 95% CI = 0.31, 0.34), near dense cover ($\hat{\beta}$ = -0.15, 95% CI = -0.16, -0.14), and in less rough terrain ($\hat{\beta}$ = -0.15, 95% CI = -0.16, -0.13).

In the Larb Hills, 66% of all rifle season locations occurred in areas accessible to hunters, 29% occurred in areas with no hunter access, and 5% occurred in areas with restricted hunter access. The best rifle season resource selection model varied among individuals. Elk most commonly selected for locations with no hunter access (n = 23), away from roads (n = 23), and in rough terrain (n = 16, Table 6). Of the 17 individual elk sampled in 2 years, 5 elk never selected for locations with no hunter access, 9 selected for locations with no hunter access in both years, and 3 elk selected for locations with no access in 1 year but not the second year. The best population level rifle season model included all covariates. The standardized population level coefficients showed elk select most strongly for locations with no hunter access ($\hat{\beta}$ = 1.00, 95% CI = 0.97, 1.03, Table 7). Elk also selected for locations in accessible areas over areas that restricted access ($\hat{\beta}$ = -0.38, 95% CI = -0.44, -0.33), away from roads ($\hat{\beta}$ = 0.22, 95% CI = 0.21, 0.24), closer to dense cover ($\hat{\beta}$ = -0.04, 95% CI = -0.06, -0.03) and in less rough terrain ($\hat{\beta}$ = -0.04, 95% CI = -0.06, -0.03). Elk selected for grasslands and shrublands over badlands ($\hat{\beta}$ = -0.12, 95% CI = -0.15, -0.09) and forests ($\hat{\beta}$ = -0.19, 95% CI = -0.24, -0.15). The strength of selection for locations with no hunter access was stronger during the archery season as compared to the rifle season (Table 7). Elk selection for restricted hunter access differed between the archery and rifle seasons. During the archery season, elk selected locations in restricted hunter access, but during the rifle season elk avoided these areas relative to accessible areas.

Discussion

Based on these data and analyses, it is unlikely that hunter access issues are an important factor in preventing sufficient adult female elk harvest to maintain or reduce the MRB population in HD 621. We found that the majority of adult female elk mortality occurred as hunter harvest during the rifle hunting period, consistent with the fact that on average, 77% of the annual hunter harvest in the MRB during the last decade has occurred during the rifle season (MFWP, unpublished data). During the rifle season we found that MRB elk are primarily using areas that are accessible to hunters (i.e., 91% of all rifle season elk locations occurred in areas accessible to hunters). During the rifle season, MRB elk did select for home ranges in areas with no hunter access and locations within their home ranges in areas with no hunter access. However, the magnitude of this effect at the population level was relatively small (Table 2 and 4, $\hat{\beta}_{\text{second-order}}$ = 0.29, 95% CI = 0.04, 0.54; $\hat{\beta}_{\text{third-order}}$ = 0.44, 95% CI = 0.37, 0.51), and areas with no hunter access comprised only a small portion of the rifle season elk range. Further, individual animal RSF analyses indicated only a small proportion of the population displayed selection for home ranges (15% of sampled elk-years) or locations within home ranges (18% of sampled elk-years) with no access during the rifle season. Although we found that elk selected for locations in accessible areas instead of areas with restricted hunter access, this pattern is likely a sampling artifact because such a small portion (<1%) of the elk herd range restricted hunter access. Elk use of this area was limited during the rifle season, but small increases in the number of elk locations in this area can have disproportionate effects on selection coefficients because the total area that restricted hunter access was very small compared to the elk herd range. A reduction in available forage in these relatively small restricted areas due to high elk use during archery season may also be displacing elk from restricted areas during rifle season.

During the archery season, MRB elk selected more strongly for areas with restricted hunter access or no hunter access than during the rifle season. However, 68% of all archery season elk locations still occurred in areas accessible to hunters. Moderate levels of elk accessibility combined with relatively low female elk harvest during the archery season likely result in a limited effect of hunter access patterns during archery season on achieving adequate elk harvest to meet population objectives. The stronger behavioral response to the archery season is likely related to the relatively high amount of archery hunting pressure in this study area, despite limited archery harvest of female elk.

In the Larb Hills, elk habitat selection patterns may indeed influence hunter success patterns and the effectiveness of harvest regulations at meeting population objectives. As in the MRB, Larb Hills elk selected more strongly for areas with restricted hunter access or no hunter access during the archery season than during the rifle season. Additionally, the majority of adult female mortality that we documented in the Larb Hills was associated with rifle harvest, and the majority of hunter harvest (79%) annually during the last decade has occurred during the rifle season. Larb Hills elk selected for home ranges during the rifle season in areas with no hunter access or restricted hunter access. Within their home ranges, elk selected most strongly for locations in areas with no hunter access or restricted hunter access. Elk selection for areas that restrict or allow no hunter access during the rifle season may limit the effectiveness of female harvest as a tool for reducing population size towards objective levels. This pattern may partially explain recent declines in hunter success, and may limit the effectiveness of further increasing hunter opportunity in attempt to achieve a sufficient harvest to reduce elk populations to objective levels, unless hunter access issues are simultaneously addressed. Further increasing hunter opportunity has the potential to result in increasing elk selection for areas that restrict hunter access as hunter activity on publically accessible lands increases, and could further exacerbate the problem. Such an approach could also potentially result in lower hunter satisfaction due to hunter crowding issues or perceived hunter crowding issues on lands that are open to public hunting, which has been an issue in the past in this area (Lewis and Herbert 2001). In this area, stakeholders may need to determine if they are willing to tolerate larger elk populations, tolerate higher number of hunters or longer season length, or provide some level of hunting access on currently restricted private land to more hunters to harvest antlerless elk so the population can be reduced to objective levels.

Elk in the MRB and Larb Hills selected locations in riparian and badland areas, near dense cover, in rough terrain, and away from roads. In the MRB where elk did not uniformly select for areas with no or restricted hunter access, this selection pattern was consistent at the population and individual elk levels and may partially explain recent declines in hunter success as hunter opportunity has increased. In Larb Hills, where elk consistently selected for areas with no or restricted hunter access, this pattern was not as clear at the population level even though individual elk commonly displayed the pattern.

In both areas, the effects of roads on rifle season elk habitat selection were not as strong as documented elsewhere, where the effect of elk avoiding roads typically dominates other effects on elk habitat selection during hunting season (see McCorqodale 2013 for review). Roads had little effect on selection of home ranges in our study areas, but roads had a consistent effect on elk selection of locations within their home ranges. With roads common throughout the Missouri Breaks EMU, elk have relatively few options available for selecting home ranges away from roads or out of the view shed from roads, and therefore second order responses to roads are less than may be observed in other areas with relatively fewer roads. The majority of knowledge regarding elk avoidance of roads that has been used to guide elk management has been based on studies conducted in montane and forested environments (Sawyer et al. 2007). In these environments, the effect of roads on elk distribution has been widely-studied, and roads have strong effects on both second and third order elk habitat selection (Lyon 1983, Rowland et al. 2000, Johnson et al. 2004, Montgomery et al. 2013). Our results challenge traditional elk habitat use paradigms, and highlight the need to better understand elk habitat selection and use in prairie-breaks habitats across the Intermountain West.

The differences we observed between population level and individual elk habitat selection patterns were revealing. Population level selection patterns generally describe areas that elk tend to occur, relative to other areas where elk are less likely to occur. In this study many of the elk habitat selection patterns we observed at the population level were either not consistently reflective of individual elk selection patterns or much stronger than observed in individual elk. In some cases, clear selection patterns by a few individual elk, which were either not consistent with or contrary to selection patters of other elk in the population, resulted in a statistically significant population-level selection pattern. At the individual level, habitat selection patterns were variable, and this variation was masked at the population level. Most (but not all) elk in our study for more than one year had consistent selection patterns relative to hunter access, either selecting or not selecting for areas with no or restricted hunter access in both years they were studied. If elk maintain consistent selection patterns from year to year, then population-level habitat selection patterns may need to be used cautiously in harvest management. While population-level selection patterns may reflect the likelihood of a general hunter to encounter elk with a particular habitat preference, elk with those selection patterns may experience increased mortality rates and therefore decline in the population relative to elk that are not as frequently encountered by hunters. This may cause the number and proportion of elk that select for areas with no or restricted hunter access, or that use landscape features that make them more difficult for hunters to encounter, to increase. Given the individual variation in habitat selection that we observed and possible implications for population structuring, hunting seasons designed to decrease these populations should be applied carefully to ensure elk remain distributed across publicly accessible land at desirable levels.

The adult female survival rates we estimated in this study are consistent with declining elk populations. For example, the survival rates we estimated in both the MRB and Larb Hills herds are equivalent to survival rates experienced by adult female elk in the northern range of Yellowstone National Park during their most rapid phase of decline in recent decades (Evans et al. 2006). Harvest was the primary cause of adult female mortality that we observed, indicating that hunting seasons may be having the desired effect of reducing elk populations in this area toward population objectives. In particular, the Larb Hills population may be susceptible to decline with current levels of harvest. Larb Hills elk also had lower body fat levels and an estimated pregnancy rate of 0.72. Typical pregnancy rates in southwest Montana average 0.90 (MFWP 2015) and in northwest Montana range from 0.65 – 0.95 (Kastler 1998). The lower levels of body fat for lactating elk in Larb Hills combined with lower pregnancy rates suggest that nutrition may be limiting elk body condition and reproductive performance (Cook et al. 2013). This could be due to nutritional trade-offs associated with avoiding hunters, or could be due to nutrition generally limiting population growth at the current elk density and with current environmental conditions. This could be also be intensified when elk densities are high during fall on restricted access areas resulting in reduced forage availability.

Our baseline health assessment found no evidence that elk in the MRB or Larb Hills were exposed to *Brucella abortus*, bovine viral diarrhea, or bovine respiratory syncytial virus. We did confirm low levels of elk exposure to Leptospira and moderate levels of exposure to Para-influenza 3 and infectious bovine rhinotracheitis. The area is grazed by domestic cattle and domestic bison, as well as free-ranging elk, which allows for potential interspecies pathogen transmission. Elsewhere in Montana, elk infected with *B. abortus* have been implicated in transmission of *B. abortus* to domestic livestock resulting in economic losses for ranchers and increased regulatory requirements within the brucellosis endemic area. Elk surveillance for *B. abortus* in eastern Montana has been limited and our sampling increases confidence that the disease is not present in the Missouri Breaks area. Elk health sampling was conducted during 1981 – 1983 on the Charles M. Russell National Wildlife Refuge. In 1981, 7 of 21 hunter-harvested elk tested positive for exposure to Leptospira. During 1982–1983, additional elk were live-trapped and tested for exposure to *B. abortus* and Leptospira. Zero of 39 elk tested positive for exposure to *B. abortus* and 2 of 37 elk tested positive for exposure to Leptospira (test results for the remaining 2 elk were undetermined). Our results confirm Leptospira is endemic in this area, likely in a variety of mammals including elk. The disease has no known consequences for elk health and reproductive performance; however some species of Leptosprira may have a negative impact on livestock reproduction. The presence of para-influenza 3 in elk likely has little impact on the elk population. This virus is common and highly transmissible in ungulates, but generally does not produce symptoms. Infectious bovine rhinotracheitis is a respiratory virus that is not common in elk, but also not known to have important consequences for elk. In cattle, the disease may cause shipping fever, but cattle may be vaccinated against the disease.

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Table 1. The sample size, pregnancy rate, mean and standard deviation (SD) of percentage of ingesta free body fat (IFBF), and mean and standard deviation (SD) of body mass of lactating and nonlactating elk in MRB and Larb Hills.

Population	Lactation Staus	Sample Size	Pregnancy Rate	IFBF (%)	SD (IFBF)	Body mass (kg)	SD (Body mass)
MRB	No	22	0.86	8.00	1.27	250.0	18.6
	Yes	2	1.00	8.27	2.63	265.1	24.2
	Total	24	0.88	8.02	1.34	251.4	19.0
Larb Hills	No	17	0.75	8.40	1.69	253.3	16.4
	Yes	9	0.67	6.55	0.69	258.3	9.9
	Total	26	0.72	7.76	1.67	255.1	14.4

Table 2. Level of disease exposure determined by serologic screening of elk blood serum during February 2013.

		Brucella	*Leptospira*	Para-influenza 3[1]	Infectious Bovine Rhinotracheitis	Bovine Respiratory Syncytial Virus	Bovine Viral Diarrhea I	Bovine Viral Diarrhea II
MRB	Sample Size	27	27	24	27	27	27	27
	Number Exposed	0	3	8	12	0	0	0
	Percent Exposed	0.0%	11.1%	33.3%	44.4%	0.0%	0.0%	0.0%
Larb Hills	Sample Size	26	26	22	26	26	26	26
	Number Exposed	0	2	4	8	0	0	0
	Percent Exposed	0.0%	7.7%	18.2%	30.8%	0.0%	0.0%	0.0%

[1]Sample size is lower because some tests were inconclusive.

Table 3. The number and source of adult female elk mortalities during March 1, 2013 – March 1, 2015 in the Missouri River Breaks (MRB) and Larb Hills study areas. Year 2013 represents March 1, 2013 – February 28, 2014 and Year 2014 represents March 1, 2014 – February 28, 2015.

Population	Year	Sample Size	Mortality Events	Harvest Archery	Harvest Rifle	Harvest Illegal	Wounding Loss	Lion Predation	Unknown
MRB	2013	22	3	0	2	0	0	1	0
	2014	19	4	0	2	0	1	0	1
	Total	22	7	0	4	0	1	1	1
Larb Hills	2013	25	4	0	2	0	1	0	1
	2014	21	4	1	2	1	0	0	0
	Total	25	8	1	4	1	1	0	1

Table 4. The covariates and hypotheses evaluated in second order resource selection models for elk in two areas of the Missouri Rover Breaks during archery and rifle season and the number of occasions that the hypothesis was supported by a covariate with a confidence interval that did not include zero in individual animals' top ranked models.

		MRB		**Larb Hills**	
Covariate	Hypothesis	Archery	Rifle	Archery	Rifle
Land Cover	Animals select for badlands over grassland and shrublands	9	12	5	4
Land Cover	Animals select for riparian areas over grassland and shrublands	9	7	2	0
Land Cover	Animals select for forested areas over grassland and shrublands	6	8	3	4
No Access	Animals select areas that do not allow public hunter access	14	5	21	12
Restricted Access	Animals select areas that restrict hunter access	3	1	13	5
Terrain Roughness	Animals select for more rugged terrain that may limit hunter access	19	17	10	12
Distance to Cover	Animals select areas closer to dense forest cover	17	19	6	11
Distance to Road	Animals select areas away from roads.	4	3	7	5
Total elk-years		37	33	43	38

Table 5. The standardized population level coefficients and 95% confidence intervals (in parentheses) representing the effects of covariates on second order elk resource selection during the archery and rifle hunting seasons in two study areas in the Missouri River Breaks area of Montana during 2012–2014.

	MRB		**Larb Hills**	
Covariate	Archery	Rifle	Archery	Rifle
Badland	0.31 (0.21, 0.42)	0.45 (0.34, 0.56)	-0.06 (-0.12, 0.02)	-0.12 (-0.21, -0.04)
Riparian	0.47 (0.29, 0.64)	0.69 (0.49, 0.88)	-0.30 (-0.59, -0.02)	-0.09 (-0.40, 0.21)
Forest	0.08 (-0.02, 0.19)	0.10 (-0.01, 0.21)	-0.09 (-0.22, 0.05)	-0.01(-0.14, 0.13)
No Access	1.93 (1.75, 2.10)	0.29 (0.04, 0.54)	0.55 (0.45, 0.64)	0.16 (0.04, 0.29)
Restricted Access	-0.67 (-1.35, 0.01)	-0.95 (-1.60, 0.31)	0.06 (-0.05, 0.18)	0.02 (-0.10, 0.13)
Terrain Roughness	0.23 (0.18, 0.29)	0.23 (0.18, 0.28)	-	0.06 (0.01, 0.10)
Distance to Cover	-0.17 (-0.22, -0.13)	-0.19 (-0.24, -0.15)	0.06 (0.02, 0.10)	-0.07 (-0.11, -0.03)
Distance to Road	-0.17 (-0.20, -0.14)	-0.08 (-0.12, -0.05)	-0.03 (-0.07, 0.01)	-0.08 (-0.11, -0.04)

Table 6. The covariates and hypotheses evaluated in third order resource selection models for elk exposed to archery and rifle hunting risk in the Missouri River Breaks area and the number of occasions that the covariate was included with a confidence interval that did not include zero in individual animals top ranked models.

		MRB		**Larb Hills**	
Covariate	Hypothesis	Archery	Rifle	Archery	Rifle
Land Cover	Animals select for badlands over grassland and shrublands	15	18	3	6
Land Cover	Animals select for riparian areas over grassland and shrublands	20	14	11	6
Land Cover	Animals select for forested areas over grassland and shrublands	6	1	18	10
No Access	Animals select areas that do not allow public hunter acess	16	6	33	23
Restricted Access	Animals select areas that restrict hunter access	3	0	31	6
Terrain Roughness	Animals select for more rugged terrain that may limit hunter access	11	14	4	16
Distance to Cover	Animals select areas closer to dense forest cover	24	19	26	10
Distance to Road	Animals select areas away from roads.	23	24	30	23
Total elk-years		37	33	43	38

Table 7. The standardized population level coefficients and standard error (in parentheses) representing the effects of covariates on third order elk resource selection during the archery and rifle hunting seasons in the Missouri River Breaks area of Montana during 2012–2014.

	MRB		**Larb Hills**	
Covariate	Archery	Rifle	Archery	Rifle
Badland	-0.06 (-0.10, -0.02)	0.26 (0.22, 0.29)	-0.13 (-0.16, -0.10)	-0.12 (-0.15, -0.08)
Riparian	0.69 (0.64, 0.74)	0.43 (0.37, 0.48)	0.17 (0.08, 0.26)	-0.03 (-0.14, 0.08)
Forest	0.33 (0.29, 0.36)	-0.37 (-0.41, -0.34)	0.44 (0.40, 0.48)	-0.19 (-0.24, -0.15)
No Access	0.88 (0.85, 0.92)	0.44 (0.37, 0.51)	1.34 (1.32, 1.37)	1.00 (0.97, 1.03)
Restricted Access	1.73 (1.63, 1.83)	-1.43 (-1.88, -0.98)	0.59 (0.55, 0.63)	-0.38 (-0.44, -0.33)
Terrain Roughness	-0.01 (-0.03, 0.01)	-	-0.15 (-0.16, -0.13)	-0.04 (-0.06, -0.03)
Distance to Cover	-0.14 (-0.15, -0.12)	-0.21 (-0.23, -0.20)	-0.15 (-0.16, -0.14)	-0.04 (0.06, -0.03)
Distance to Road	0.19 (0.17, 0.20)	0.16 (0.14, 0.17)	0.32 (0.31, 0.34)	0.22 (0.21, 0.23)