Elkhorn Mountains Elk Project

Final Report | 2015–2018

June 10, 2019

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Funding

Funding was provided by the Elkhorn Working Group, United States Forest Service, Montana Department of Military Affairs, Rocky Mountain Elk Foundation, and Cinnabar Foundation. Additional funding was provided by revenues from the sale of Montana hunting and fishing licenses and matching Federal Aid in Wildlife Restoration grants to Montana Fish, Wildlife, and Parks.

Acknowledgments

We thank J. Capella, B. Hoffman, N. Mutchler, and T. Sutton for their work in vegetation sampling. We acknowledge the numerous private landowners for facilitating field sampling efforts, aircraft pilots B. Malo, M. Stott, and N. Cadwell for their work in capturing animals, T. Carlson and members of the Elkhorn Working Group for their collaborative support and input, and T. Paterson for technical support.

Executive Summary

The Elkhorn Mountains of west-central Montana are highly valued for their diverse land and wildlife resources and have been the focus of a concerted, interagency conservation effort to ensure consistent, landscape-scale management across agency jurisdictions. The management of the Elkhorn Mountains elk (*Cervus canadensis*) population and habitat are a core focus of these conservation efforts owing to their importance as a public resource for viewing and hunting opportunities, particularly for mature bull elk. Recent concerns regarding changes in elk distributions and their habitats, particularly due to extensive lodgepole pine (*Pinus contorta*) mortalities induced by an epidemic of mountain pine beetles (MPB; *Dendroctonus ponderosae*), have highlighted the need to better understand the availability of elk nutritional resources and habitat security. In collaboration with the Elkhorn Working Group, Helena-Lewis and Clark National Forest, Montana State University, and Montana Department of Military Affairs, Montana Fish, Wildlife & Parks (MFWP) initiated the Elkhorn Mountains Elk Project to evaluate the impact of the MPB infestation on elk habitat and distributions in the Elkhorn Mountains.

The focal study area included the Elkhorn Mountains and the adjacent valley bottoms along the Missouri River and Canyon Ferry Reservoir to the east and Prickly Pear Creek and the Boulder River to the west. The study area was predominantly contained within MFWP's hunting district (HD) 380, distinguished in Montana as having a unique spike regulation and being a premier hunting destination for mature bull elk. Lower elevations consisted of mixed open sage-grasslands and patches of timber on publicly- and privately-owned lands, in addition to residential and agricultural lands. Higher-elevation mountainous areas were dominated by publicly-owned conifer forests, with large tracks of lodgepole pine forests affected during 2005 – 2012 by MPB infestation. Approximately 1,655 km^2 (64%) of the study area was affected by the MPB infestation, with tree mortality approaching 90 percent over the affected area.

To gain insight into the nutritional condition and distributions of the Elkhorn elk population, we sampled and radio-collared 35 female and 25 male adult elk during winters 2015 and 2017. Female elk ingesta-free body fat levels averaged 6.6% (± 1.6% SD) and pregnancy rates averaged 0.92 (95% CI = 0.83 – 1.00). The annual survival rate for female elk was 0.83 (95% CI = 0.72 – 0.90) and for male elk was 0.61 (95% CI = 0.38 – 0.78). The primary sources of mortality for female (75%) and male (78%) elk were harvest-related (i.e., harvest or wounding loss), and we observed 2 cases of mountain lion predation on female elk (17%). We identified annual and seasonal ranges of female and male collared elk based on GPS collar locations. Female elk annual ranges generally occurred at lower elevations and with less canopy cover than male elk annual ranges, and core use areas (i.e., areas estimated to have higher relative densities of locations) were primarily centered on public lands in the east-southeast and private lands in the west portion of the Elkhorn Mountains. Male elk annual core use areas were primarily centered on public lands. During the archery season, female and male elk core use areas were composed on average of 67% and 55% public land, respectively. During the rifle season, female and male elk core use areas were composed on average of 70% and 64% public land, respectively. Generally, female elk were most widely distributed during the archery and rifle hunting seasons and most concentrated during summer and winter. Male elk were most widely distributed during the archery hunting season and most concentrated during spring and summer.

To characterize the availability of and the effects of MPB infestation on nutritional resources, we sampled elk diet and forage species across landcover types that included unaffected and affected lodgepole forests. Overall, the most abundant and species-diverse herbaceous forage occurred in riparian areas followed by grasslands and shrublands, with forage graminoids comprising the majority of the understory cover in all landcover classes. Forests had the lowest herbaceous forage abundance but higher levels of shrub forage abundance, forb and shrub forage cover, and shrub forage species richness than agricultural and riparian areas. Generally, levels of herbaceous forage abundance, graminoid forage cover, and herbaceous quality were greater in affected forests as compared to unaffected forests.

To evaluate how MPB affected areas have changed elk use of habitat and public lands, we summarized the seasonal use of landcover types, including unaffected and affected lodgepole pine forests, and public and private lands using location data collected prior to and after MPB infestation, respectively. During 1982 – 1992, MFWP conducted an elk telemetry study in the Elkhorn Mountains, and we compared our location data to locations of elk during that study. Proportional use of affected forests decreased from pre- to post-MPB infestation across all seasons for both sexes but was most pronounced during the summer and archery hunting season for females and the archery and rifle hunting seasons for males. Proportional use of private lands increased across all seasons, with an average increase from pre- to post-MPB infestation of 70% and 12% for females and males, respectively. We suspect that the MPB infestation in combination with other landscape changes, such as restrictions to public hunting access and change in land uses, have influenced changes in elk use patterns. Out of the 4 Boulder Valley population segments (i.e., Devils Fence, Elkhorn, Prickly Pear, and South Boulder), we observed an increase in year-long residency on private lands along I-15 of females in the Prickly Pear segment.

Additionally, female elk in the Elkhorn segment showed substantially reduced year-long use of State of Montana lands, favoring private lands along State Highway 69 instead. Movements to private lands were not as evident in the remaining population segments and the overall population seasonal ranges still indicated extensive use of public lands, even during the archery and rifle hunting seasons.

We evaluated elk selection for security areas during the fall archery and rifle hunting seasons based on GPS location data with a goal of providing recommendations for security standards for elk inhabiting forests impacted by MPB. We used a resource selection model to define characteristics of areas used by male and female elk during the hunting seasons, and we found that both female and male elk selected for areas farther from motorized routes and with greater canopy cover. Based on thresholds derived from our resource selection model, we recommend that definitions of elk security in the Elkhorn Mountains include objectives of canopy cover values ≥ 23–60% and distance from motorized routes ≥ 1,846–3,679 m, which represent the thresholds for areas that contain 75% and 50% of the elk use on the landscape, respectively. Although elk may use MPB-affected areas less than prior to MPB infestation, these forests maintained a high degree of canopy cover relative to Douglas fir and ponderosa pine forests and likely provide valuable security during the hunting seasons.

To understand if the MPB epidemic affected hunter effort and success in HD 380, we compared hunter effort, harvest, and success rate immediately prior to, during, and after the extensive tree mortalities. Levels of hunter effort have been on an increasing trajectory since the 1960's and were at record highs in 2015. Although hunter effort was higher and total harvest and hunter success rates were lower after the MPB infestation, these changes were likely more strongly influenced by changes in harvest regulations. For example, during peak tree mortality, the total number of available licenses/permits for antlerless and either-sex elk increased from 785 in 2008 to 1,010 in 2009 and 2010, corresponding to increases in the number of elk harvested and hunter success rate. Similar patterns were observed during the period after peak tree mortality. Additionally, all metrics of hunter opportunity fell within the range of levels typically observed, indicating that hunter harvest and success was not affected by the MPB infestation.

Although past harvest regulations have been largely successful at maintaining the elk population within objective levels (i.e., 1700 – 2300 elk), trends of increasing hunter effort and pressure, general decreased elk use of MPB-affected areas, and increased elk use of private lands, suggest that future harvest regulation changes may be necessary to maintain the elk population within designated objectives and to alter distributions to reduce conflicts related to forage competition with livestock and crop and property damage on private properties. As MPB-killed trees fall and become impediments to travel and movement through affected forests, forest treatments (i.e., prescribed fire or harvest of trees) may increase elk use of MPB-affected areas by reducing energetic costs of locomotion. However, these treatments would need to be designed to also preserve areas with adequate cover to meet the minimum requirements for elk security. Strategies for manipulating distributions of elk on private lands might include working with private land owners to restrict elk access to high value forage and increase levels of disturbance or hunter access on their properties to discourage elk from using these areas during the hunting seasons and other times of the year. These strategies may provide a more holistic approach for encouraging elk to remain broadly distributed across public and private lands during the fall hunting seasons, ensuring hunter access to elk on public lands and minimizing property damage by elk on private lands.

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Section 1 – Introduction

The Elkhorn Mountains, situated southeast of the city of Helena between the Boulder and Big Belt Mountains of west-central Montana, have been the focus of a unique and concerted effort to conserve and manage the range's diverse land and wildlife resources (U.S. Forest Service et al. 1993, Montana Fish Wildlife & Parks et al. 2000, Thomas et al. 2002). The entire mountain range is within the Elkhorn Cooperative Management Area (ECMA), a collaborative, interagency designation to help ensure consistent, landscape-scale management of natural resources across jurisdictions of the Beaverhead-Deerlodge and Helena-Lewis and Clark National Forests, Bureau of Land Management, Montana Fish, Wildlife and Parks (MFWP), and the Natural Resource Conservation Service. An important component of this effort has been the management of the Elkhorn elk (*Cervus canadensis*) population and its habitat. These elk are a highly valued resource by the public for viewing and hunting opportunities. Bull elk hunting in this region is particularly popular due to a unique spike regulation that generates a mature bull age structure. The elk population occupies a diverse landscape of public and private lands, and recent concerns regarding elk distributions and damage to crops and private property have highlighted the need to better understand the effects of vegetation treatments, grazing, mining, timber harvest, and recreational activities to elk habitat and movements.

Elk habitat in the Elkhorn Mountains has experienced substantial changes during the past 15 years. In 1996, a major epidemic of mountain pine beetles (MPB; *Dendroctonus ponderosae*) began affecting pine forests in regions of western North America (Meddens et al. 2012). MPBs affected nearly 18 million ha of pine forests, an outbreak that is unprecedented in spatial extent, severity, and duration (Chan-McLeod 2006, Meddens et al. 2012). Damage caused by MPBs results in widespread tree mortality, defoliation, and eventual blowdown of dead trees, and can strongly influence forest community composition and structure, timber production, wildfire dynamics, and wildlife habitat (Jenkins et al. 2008, Klenner and Arsenault 2009, Pfiefer et al. 2011, Simard et al. 2011, Saab et al. 2014). Wildlife responses to MPB outbreaks are dynamic and complex, and vary by taxa, sex, season, and the outbreak successional stage (Saab et al. 2014). In the Elkhorn Mountains, approximately 1,655 km^2 of ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*P. contora*) stands were impacted by this epidemic with tree mortalities that approached 90 percent over much of the affected area. Subsequently, the widespread defoliation of MPB-killed trees substantially altered forest structure and understory vegetation, potentially impacting elk seasonal ranges through a variety of processes. The opening of forest canopy cover can increase sunlight and reduce the moderation of temperatures in the soil and ambient environment (Stone 1995, Stone and Wolfe 1996, Saab et al. 2014). These changes may alter the distribution and availability of nutritional resources for elk through changes in understory plant species diversity, abundance, and phenology. Altered vertical and horizontal cover may subsequently affect elk thermal cover during the winter and summer seasons and security cover during the hunting seasons. Further, the falling of dead trees that typically occurs within 5 – 15 years after tree death (Lewis and Hartley 2005) may affect elk movements, access to nutritional resources, and security cover.

Despite the large scale of MPB infestations, the effects of MPB-affected forests on elk distributions, habitat selection, nutritional resources, and security during the hunting season remain largely unknown. Wildlife and forest managers in the Elkhorn Mountains need this information to mitigate the effects of MPB-infestation on elk habitat and maintain the elk population within population objectives. To fill this knowledge gap, MFWP worked with the ECMA partners, the Elkhorn Working Group (an independent citizen's group created to review and make recommendations to management agencies regarding elk and livestock management), Montana Department of Military Affairs, and Montana State University to develop the Elkhorn Mountains Elk Project. The goals of this project were to collect biological and movement information about the Elkhorn elk population and to assess the impacts of the MPB infestation on elk habitat, nutritional resources, resource selection, and security cover. Capitalizing on data collected from a previous elk habitat use study conducted in the Elkhorn Mountains from 1982 – 1992 (DeSimone and Vore 1992), this study provided an ideal opportunity to evaluate elk distributions and habitat selection before and after the MPB infestation that will be relevant across other areas of Montana and the western US experiencing MPB epidemics.

The Elkhorn Mountains Elk Project was designed to provide managers with information on elk ecology, habitat quality, and habitat use and to provide recommendations for managing elk habitat in areas impacted by MPB infestations. Information gained from this study may also be useful in guiding future MFWP harvest regulation recommendations. Specifically, project objectives were to:

1) Assess the health of the elk population by evaluating adult female body condition, pregnancy rate, and disease exposure rates,
2) Estimate adult female and male elk survival rates and cause-specific mortality rates,
3) Assess adult female and male elk seasonal distributions and movement patterns,
4) Assess the availability of and the effect of the MPB infestation on elk summer nutritional resources,

5) Evaluate elk seasonal use of MPB-impacted areas before and after the MPB infestation,
6) Evaluate the effect of the MPB infestation on male and female elk security during the fall hunting seasons,
7) Assess hunter effort and success before and after the MPB infestation, and
8) Assess the effects of vegetation restoration treatments on elk habitat use.

Section 2 – Study Area

Study area overview

The study area includes two regions of west-central Montana: the Elkhorn Mountains occupied by the Elkhorn elk population and the Little Belt Mountains (Figure 1). Our focal study region was the Elkhorn Mountains; however, we also sampled vegetation in the Little Belt Mountains to increase our sample size of non-beetle-affected forest cover types (see *Section 4 – Elk Nutritional Resources & the Effect of Mountain Pine Beetles*). The Elkhorn Mountains study region (2,600 km^2; 1,141 – 2,866 m elevation) is a relatively isolated mountain range with a climate characterized by short, cool summers (17.4°C mean July temperature) and long, cold winters (-4.8°C mean January temperature; PRISM Climate Group 2016). Mean annual precipitation ranges 263 – 959 mm. Land ownership is largely private lands (54%) surrounding public lands (46%) that make up the core of the mountain range. Public lands are managed by Helena-Lewis and Clark National Forest (44%), Bureau of Land Management (33%), Beaverhead-Deerlodge National Forest (15%) and the state of Montana (8%). Bureau of Land Management lands are jointly managed with the Montana Department of Military Affairs. Approximately 1,800 km^2 of public lands are designated as the Elkhorn Cooperative Management Area (ECMA) and managed in collaboration with the U.S. Forest Service (USFS), Bureau of Land Management, Natural Resources Conservation Service, and Montana Fish, Wildlife & Parks (MFWP). Within National Forest System lands, the ECMA is managed as the Elkhorn Wildlife Management Unit, a unique designation recognizing the diversity and value of wildlife in the Elkhorn Mountains.

The Little Belt Mountains study region (1,480 km^2; 1,142 – 2,498 m elevation) is located approximately 95 km northeast of the Elkhorn Mountains and includes the western half of the Little Belt Mountains. The Little Belt Mountains are similar in climate to, but slightly colder and wetter than, the Elkhorn Mountains. Summer (July) and winter (January) temperatures average 15.3°C and -5.9°C, respectively, and mean annual precipitation

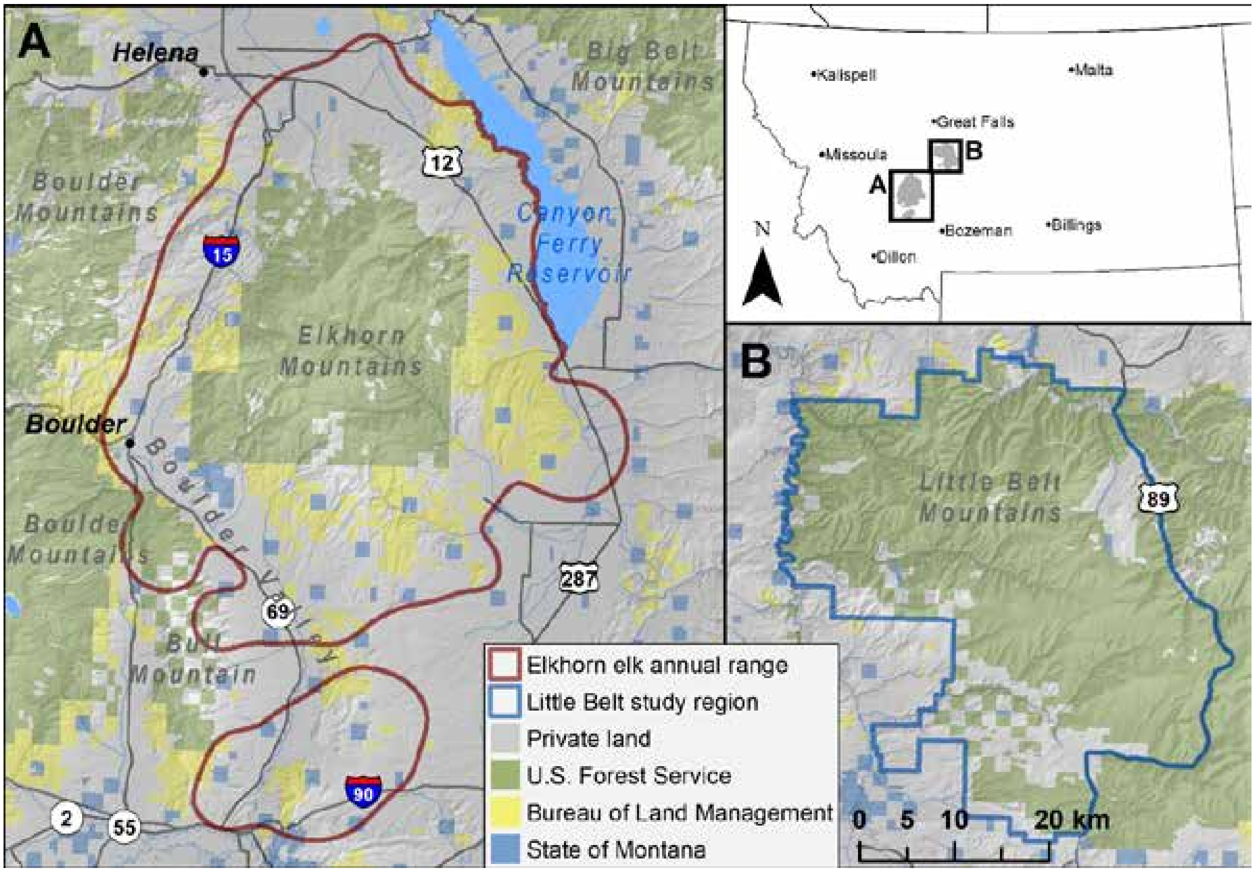

Figure 1 - The Elkhorn Mountains study region (A) delineated by the Elkhorn elk herd annual range (based on GPS collar data) and the Little Belt Mountains study region (B) in west-central Montana, USA, 2015 – 2018. Study regions are displayed at the same scale.

ranges 324 – 940 mm (PRISM Climate Group 2016). Land ownership within the study region is largely public (80%) with lands managed by Helena-Lewis and Clark National Forest. Private lands (20%) are primarily concentrated in the southwestern and east-central portions of the study region. Outside of the study region, private lands encompass the northern, western, and southern ends.

Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and moose (*Alces alces*) occupy both study regions and a small population of bighorn sheep (*Ovis canadensis*) is present in the Elkhorn Mountains. Carnivores include mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and American black bear (*Ursus americanus*). Grey wolves (*C. lupus*) occasionally traverse both study regions.

Lower elevations of the Elkhorn Mountains are dominated by a mixture of open sage-grassland (e.g., big sagebrush [*Artemisia tridentata*], bluebunch wheatgrass [*Pseudoroegnaria spicata*], Idaho fescue [*Festuca idahoensis*], rough fescue [*Festuca scabrella*], and bluegrasses [*Poa* spp.]) and patches of timber (primarily Rocky Mountain juniper [*Juniperus scopulorum*] or Douglas fir [*Pseudotsuga menziesii*]). Upper elevations are dominated by dry coniferous forests (e.g., lodgepole pine [*Pinus contorta*], Douglas fir, and ponderosa pine [*Pinus ponderosa*]) with small interspersed meadows (U.S. Forest

Service et al. 1993). Vegetation communities in the Little Belt Mountains are similar to the Elkhorn Mountains but are primarily dry coniferous forests with Douglas fir and scattered pockets of open sage-grassland at lower elevations and lodgepole pine and subalpine fir (*Abies lasiocarpa*) at higher elevations (Mincemoyer and Birdsall 2006). Understory species common to both regions include *Vaccinium* spp., common snowberry (*Symphoricarpos albus*), white spirea (*Spiraea betulifolia*), common bearberry (*Arctostaphylos uva-ursi*), common juniper (*Juniperus communis*), Wood's rose (*Rosa woodsii*), sedge (*Carex* spp.), pinegrass (*Calamagrostis rubescens*), western yarrow (*Achillea millefolium*), *Antennaria* spp., *Arnica* spp., *Astragalus* spp., *Fragaria* spp., harebell (*Campanula rotundifolia*), fireweed (*Chamerion angustifolium*), *Erigeron* spp., and *Valeriana* spp. Cultivated crops (pasture grasses and leguminous forbs) border the northern and southwestern (i.e., the Boulder Valley) portions of the Elkhorn Mountains and occur in the Belt Park area near Belt Creek and along a segment of Sheep Creek in the southwestern portion of the Little Belt Mountains.

Wildfire, timber harvest, and mountain pine beetle (MPB; *Dendroctonus ponderosae*; see below) damage have resulted in forests of varying successional stages across the study area. Historically (1700 – 1900), these forests generally experienced relatively frequent wildfire of low to medium severity (Arno 1980). Lower elevation lodgepole pine forests experienced relatively infrequent (35 – 100+ year fire intervals) wildfires of mixed severity and Douglas fir forests experienced relatively frequent (1 – 35 year fire intervals) wildfires of low to mixed severity (Barrett 2005). Since active fire suppression began in the early 1900s, however, wildfire has played a small role as a landscape disturbance. The Warm Springs fire in the Elkhorn Mountains in 1988 was the most significant wildfire, burning approximately 180 km^2. During the 2000s, wildfires burned only about 62 and 9 km^2 in the Elkhorn Mountain and the Little Belt Mountain study regions, respectively (U.S. Forest Service 2016a). Timber harvest peaked in the 1980s on what is now the Helena-Lewis and Clark National Forest, averaging 33.6 million board feet cut per year, but had declined 65% by the mid-2000s (U.S. Forest Service 2016b).

Mountain pine beetle infestation

Damage caused by MPB infestation is one of the most prevalent and severe disturbances in pine (*Pinus* spp.) forests of western North America (Raffa et al. 2008, Saab et al. 2014). Since 1997, MPB have affected an estimated 85,000 km^2 of pine forests in the western United States and British Columbia (Meddens et al. 2012), resulting in widespread tree mortality and defoliation of tree canopy that has strongly influenced forest community composition and structure, timber production, fuels and wildfire characteristics, and wildlife habitat (Jenkins et al. 2008, Klenner and Arsenault 2009, Pfiefer et al. 2011, Simard et al. 2011, Saab et al. 2014).

Areas affected by MPB infestations, as observed by tree canopy discoloration indicating mortality, are annually surveyed by aircraft by the USDA Forest Health Protection Aviation Program. Data from surveys are freely-available from the Aerial Detection Survey database (U.S. Forest Service 2017, 2018). Since the beginning of survey efforts in 2001 within our study area, MPBs have affected approximately 1,655 (64%) and 1,382 (93%) km^2 of the Elkhorn Mountains and Little Belt Mountains study regions, respectively (Figure 2 – Figure 3). The observed affected areas peaked in 2009 and 2010 in the Elkhorn Mountains and Little Belt Mountains study regions, respectively. The severity of affected areas was greater in the Elkhorn Mountains than the Little Belt Mountains study region.

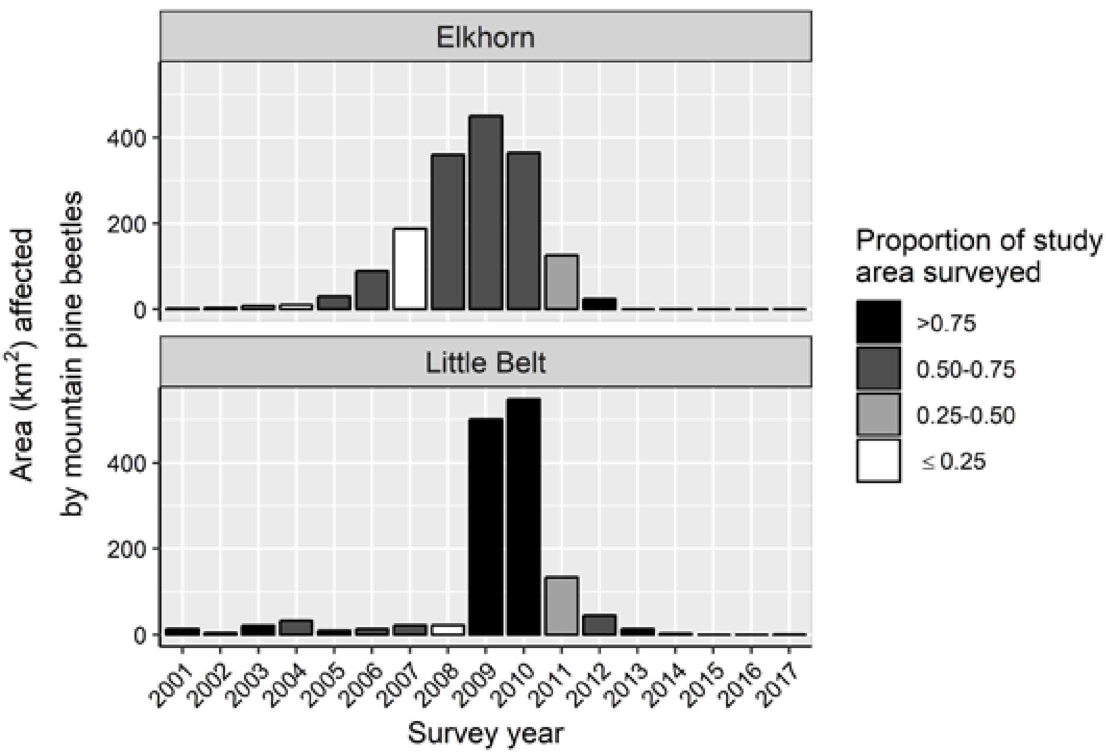

Figure 2 – Annual area (km^2) first affected by mountain pine beetle (Dendroctonus ponderosae) and survey effort (measured as proportion of study region surveyed by aerial flights) in the Elkhorn Mountains and Little Belt Mountains study regions in west-central Montana, USA, 2001 – 2017. Each years' data are based on newly observed color differences in tree canopy diagnosed as caused by mountain pine beetles.

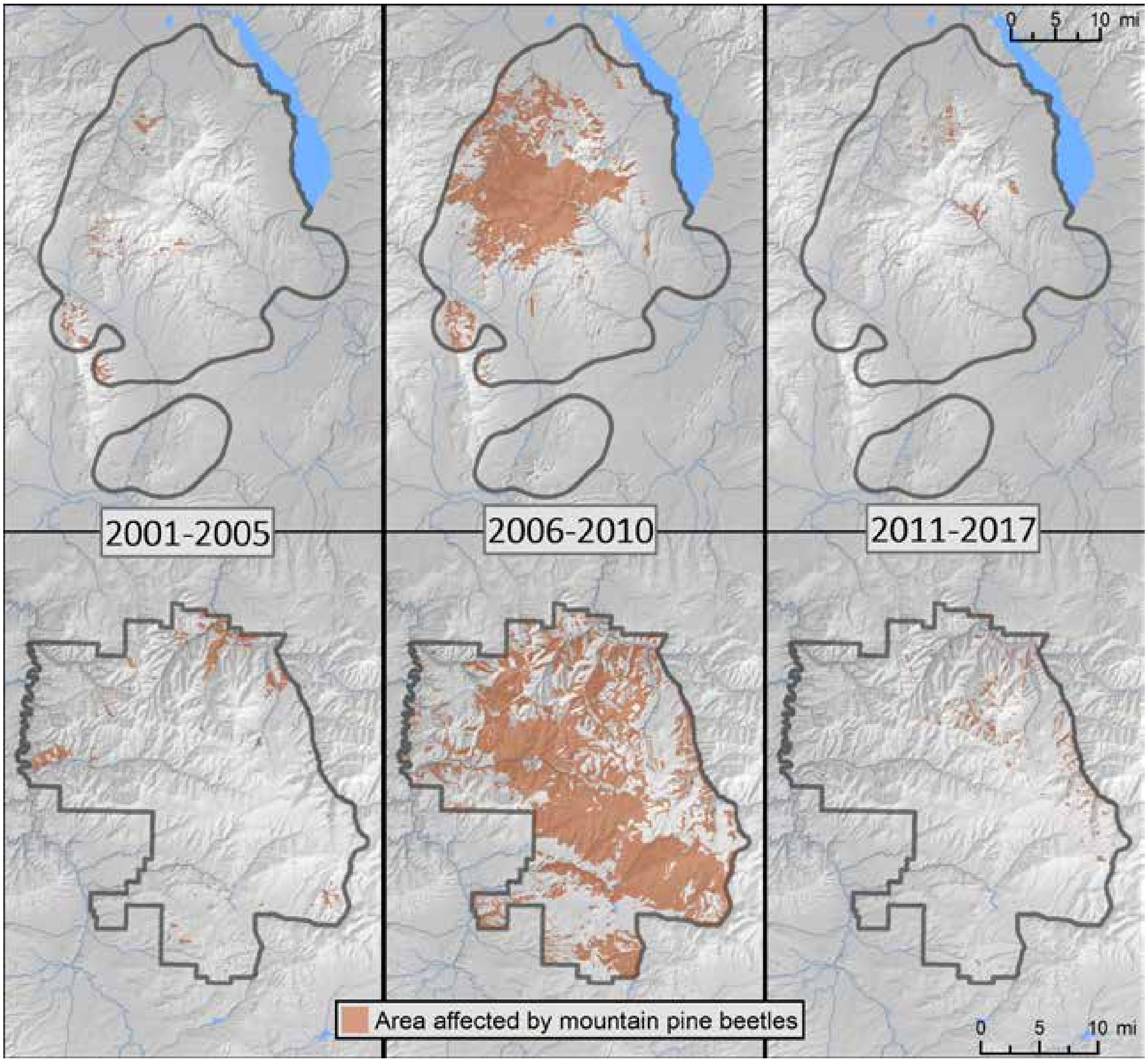

Figure 3 – Areas first affected by mountain pine beetle (Dendroctonus ponderosae) for three time periods in the Elkhorn Mountains (top panels) and Little Belt Mountains (bottom panels) study regions in west-central Montana, USA, 2001 – 2017. Affected areas are cumulative within time periods. Each years' data are based on newly observed color differences in tree canopy diagnosed as caused by mountain pine beetles. Note that study regions are displayed at different scales.

Elkhorn elk population

The Elkhorn elk population occurs within MFWP's hunting district (HD) 380 (Figure 4; also see *Section 3 – Elk Capture, Sampling, Survival, & Distributions*). During late-winter and early spring (late January – mid-March), MFWP conducts annual aerial elk surveys of HD380 from a fixed-wing airplane flying at low altitude. Surveys typically cover the entire range of the elk population within HD 380 and elk are counted within 10 semi-distinct Elk Herd Units (EHU) including North Crow, South Crow, Kimber, Sheep Creek, Prickly Pear, Elkhorn, Devils Fence, Spokane Hills, South Boulder, and Southeast (Figure 4). These EHU boundaries represent areas MFWP uses to group elk surveys and are expanded from boundaries identified from a previous 10-year VHF (very high frequency) collar study (DeSimone and Vore 1992). During surveys, elk are also classified into brow-tined bulls, yearling bulls, adult females (including yearlings), calves (8 – 10 months old), and unclassified. Due to imperfect detection, elk counts (i.e., the minimum number of known elk during the survey period) represent indices of elk population trends, and the number of calves per 100 adult females represents an index of calf recruitment. Limited surveys began after the release of 34 elk on Elkhorn Creek in the Elkhorn EHU in 1939 (DeSimone and Vore 1992). More rigorous surveys began in the winter of 1961 (Figure 5); however, surveys were focused primarily on the South Crow, North Crow, and Devils Fence EHU's until 1980 when surveys of each known winter range were made (excluding the newly surveyed Southeast EHU in 2018). Prior to 2015, the South Boulder EHU was not always flown and counts were included in the Devils Fence EHU.

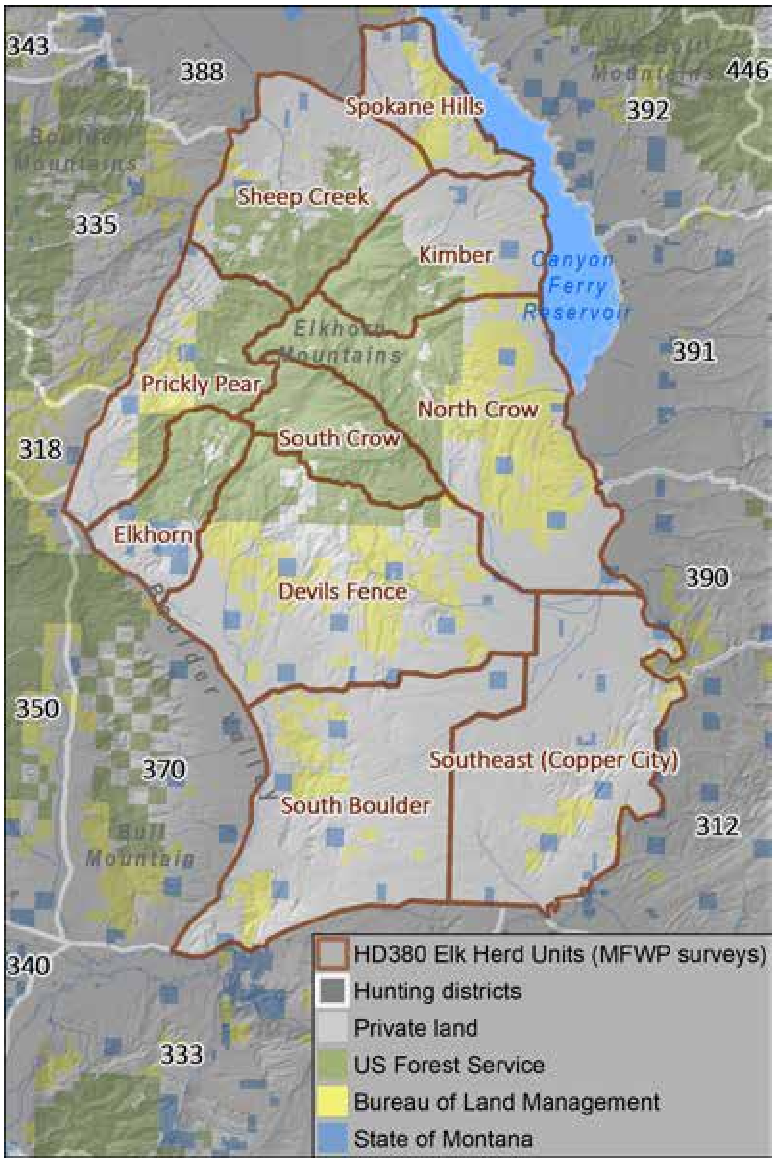

Figure 4 – Elk Herd Units in hunting district 380 surveyed on an annual basis (1994-2018) by Montana Fish, Wildlife, and Parks within the Elkhorn Mountains study region of west-central Montana, USA.

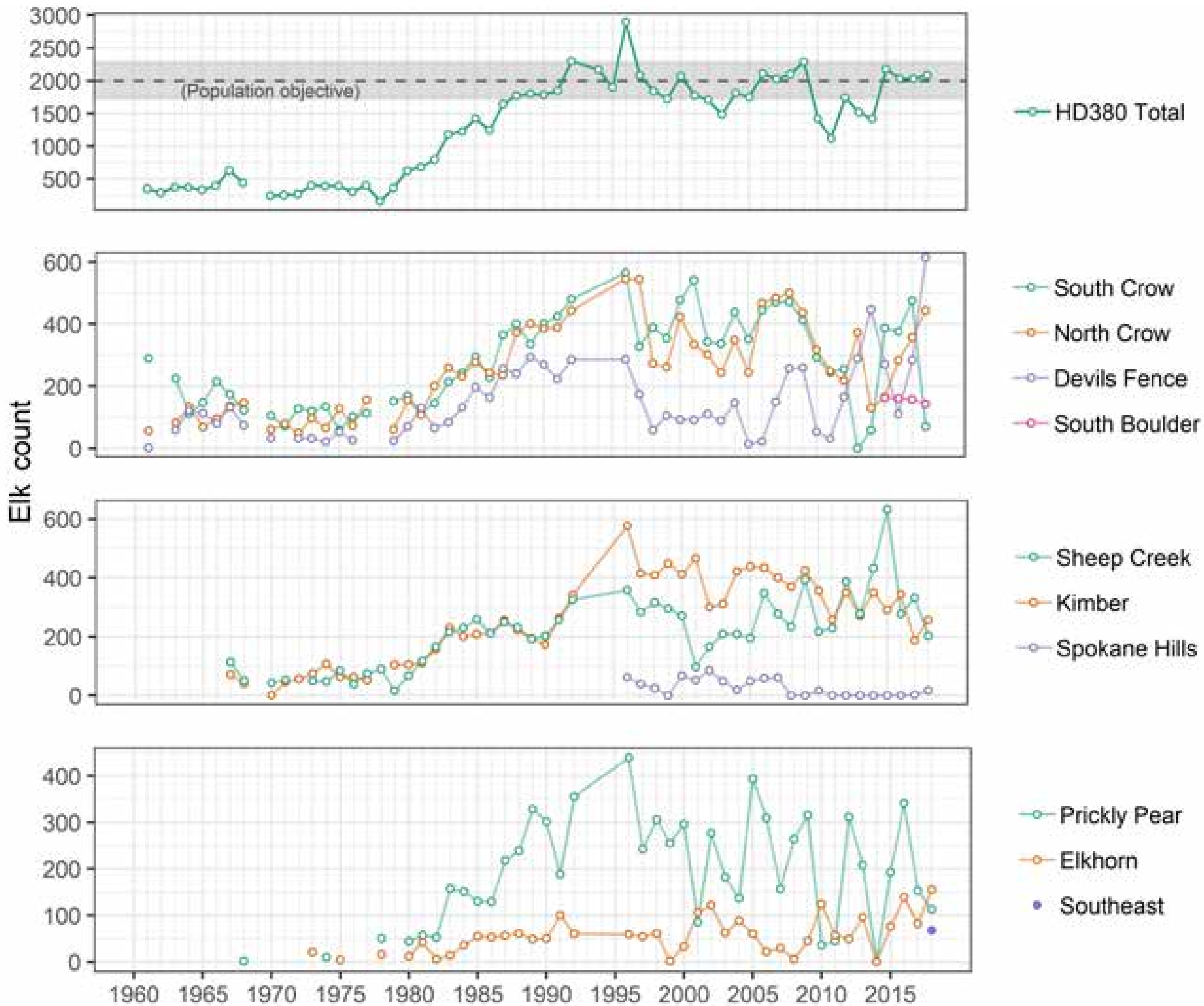

Figure 5 – Annual Elk Herd Unit counts in hunting district 380 from aerial winter surveys conducted by MFWP during 1961 – 2018 in west-central Montana, USA. Counts represent the minimum number of elk known during the survey period. Increased survey efforts covering the full extent of known elk winter ranges began in 1980 which may account for some of the increase in counts relative to pre-1980 counts. Counts made during 2003, 2010, 2011, 2013, and 2014 surveys are likely not reliable indicators of trend due to poor survey conditions.

During 1860 – 1890, game hunting to support mining communities essentially eradicated the original elk population in the Elkhorn Mountains. Between 1939 and 1960, the elk population gradually increased from the 34 elk released on Elkhorn Creek to about 250-300 elk. From 1961 – 1980, the survey data indicated a relatively stable elk population (Figure 5). The consistently surveyed South Crow and North Crow winter ranges indicated the population more than tripled from the average count of the 1960 – 70s (350 ± 99 [SD]) to the average count of the 1980s (1,236 ± 432). This increase was at least in part due to increased survey efforts across more of the elk winter range, however. From the 1990s, the population continued to increase to a maximum count of 2,893 elk in 1996. From 1997 to current, the population remained relatively stable, averaging 1,961 ± 185 (SD) elk. The most current (2018) count of 2,086 elk is above MFWP's population objective of 2,000 but within the objective range of 1,700 – 2,300 (see *Hunting regulations* in Section 7; Montana Fish, Wildlife & Parks 2004).

Recruitment rates across HD 380 varied from 1998 – 2018 (range 17.6 – 36.2) but have trended relatively stable, averaging 26.7 (± 5.6) calves per 100 adult females (Figure 6). Some of the variation in recruitment rates could be due to different observers performing counts across the years. Most recently (2015 – 2018), recruitment increased to an average of 33.2 (± 2.4) calves per 100 adult females. The number of bulls per 100 adult females varied from 1996 – 2018 (range 8.7 – 23.6) but also trended relatively stable, averaging 16.3 (± 5.5). More recent low counts of approximately 8.7 bulls per 100 adult females in 2015 – 2016 (likely a reflection of survey conditions rather than actual low bull numbers) increased to 22.3 in 2017 – 2018. Bull counts during 1994 – 2018 varied but remained relatively stable in trend, mirroring overall population counts (Figure 6). Across this period, the number of yearling (spike) bulls ranged 24 – 136 and averaged 66.4 (± 28.3). The number of brow-tined bulls ranged 51 – 246 and averaged 121.7 (± 53.7). Brow-tine bull counts sharply increased in 2017 and 2018 to 198 and 246, respectively, the largest recorded counts. Some of the observed increase in 2017 and 2018 was due to concerted efforts to fly surveys under conditions more conducive for finding brow-tined bull groups. Surveys completed during 2003, 2010, 2011, 2013, and 2014 were documented as unreliable due to poor survey conditions and were excluded from summaries. Please refer to Section 7 for detailed information on harvest regulations, effort, and success.

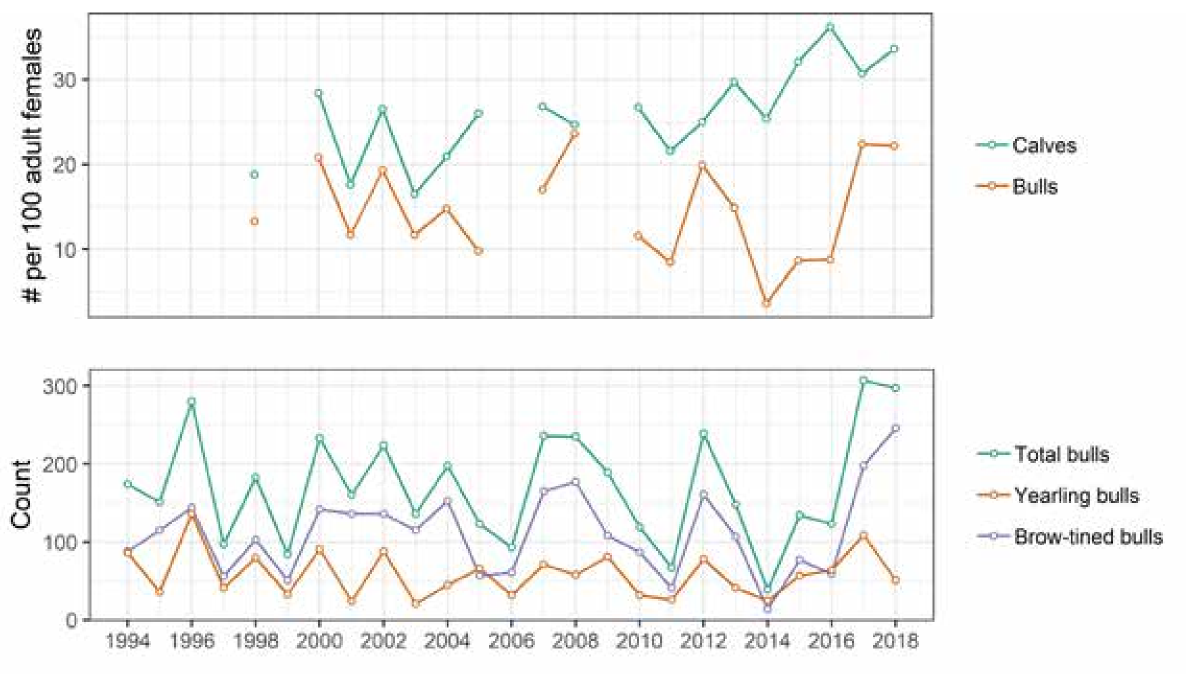

Figure 6 – Annual ratios of calves and bulls per 100 adult female elk and total counts for yearling (spike) and brow-tined bulls in hunting district 380 from aerial winter surveys conducted by MFWP during 1994 – 2018 in west-central Montana, USA. Surveys with large proportions of unclassified elk were removed from calf and bull ratios. Counts represent the minimum number of elk known during the survey period. Counts made during 2003, 2010, 2011, 2013, and 2014 surveys are likely not reliable indicators of trend due to poor survey conditions.

Section 3 – Elk Capture, Sampling, Survival, & Distributions

Introduction

The nutritional condition of elk, particularly adult females, can have important consequences to elk populations through altered survival and reproduction (Cook et al. 2004, 2013, 2016, Johnson et al. 2019). Maternal condition is strongly tied to the acquisition of summer nutritional resources and can have a large effect on overwinter survival, pregnancy rates, calf birth weight, and juvenile survival (Gaillard et al. 2000, Cook et al. 2004, 2013, Monteith et al. 2013, Johnson et al. 2019). Assessing levels of nutritional condition of elk may provide information about the health of the population as well as the quality of nutrition on the landscape available to elk. Additionally, the presence of diseases such as brucellosis or chronic wasting disease can indicate constraints on the population through suppression of survival and reproduction rates.

Adult female survival is a key vital rate in ungulate populations (Nelson and Peek 1982, Gaillard et al. 1998, 2000) and can have important effects on population growth rates (Eacker et al. 2016). Reduced adult female survival, whether due to harvest, predation, or other factors, can be the primary driver of declines in populations (e.g., Owen-Smith and Mason 2005, Hebblewhite and Merrill 2007). Harvest management strategies designed to increase or decrease elk populations often focus on manipulating adult female harvest rates to increase or decrease adult female survival. Adult male survival, on the other hand, has a limited influence on population growth rate, and harvest management strategies are generally designed to achieve specific hunter opportunity objectives (Biederbeck et al. 2001, Bender 2002).

The monitoring of collared elk for survival can help managers identify important drivers influencing elk populations. In addition, locations obtained from elk fitted with GPS collars can provide important information regarding elk seasonal distributions and movements.

Components of the Elkhorn Mountains landscape that may drive seasonal distributions include the public-private land mosaic with varying land uses, vegetation cover types, availability of nutritional resources, areas affected by mountain pine beetles, and hunter access opportunities. Seasonal patterns of habitat use by the Elkhorn elk are likely strongly influenced by this landscape mosaic offering variable habitat and forage quality and variable risks associated with human harvest. Response of elk to this heterogeneous landscape may have survival and reproductive consequences as elk seek to minimize mortality risks and maximize forage opportunities. Movements of elk may be affected by the loss of forest canopy cover and altered forest structure in areas affected by mountain pine beetles (see *Section 6 – Male & Female Elk Security during the Fall Hunting* Seasons). During the hunting seasons, elk may seek refuge from harvest risk by increasing use of private properties that limit or restrict hunter access. Increased use of private lands by big game species is a growing challenge in wildlife management because wildlife managers lose an important tool in achieving and maintaining population objectives if private land owners restrict public hunting opportunities (Haggerty and Travis 2006). A better understanding of seasonal elk distributions and movement behaviors is important as wildlife managers strive to balance concerns of private landowners and hunters regarding elk distributions and manage elk numbers within population objective levels. The delineation and description of elk seasonal ranges and movement patterns is useful to ensure that elk habitat and population management goals are directed to areas currently used by elk, as well as estimating the availability of elk on public lands during the hunting season.

We captured, sampled, and GPS-collared adult female and male elk in the Elkhorn elk population with the goals of: 1) assessing and summarizing body condition, pregnancy rate, and disease exposure levels to characterize the overall nutritional status of the population; 2) estimating sex-specific survival and identifying cause-specific mortality sources; and 3) describing sex-specific annual and seasonal ranges (spring, summer, fall, and winter/spring) and migratory behaviors.

Methods

Capture & health sampling

During winters 2015 and 2017, we captured adult (> 1.5 years old) elk by helicopter net-gunning and darting in accordance with an approved animal welfare protocol (IACUC #FWP09-2014 and FWP10-2017). We estimated elk age in years by tooth eruption and wear patterns. We measured chest girth and assessed body condition of female elk using a portable ultrasound machine to measure rump fat thickness and estimate levels of ingesta-free body fat (IFBF) following the revised methods of Cook et al. (2010). We did not sample body condition of male elk. We collected a blood sample and screened blood serum to assess exposure to a suite of common diseases previously known to occur in Montana, including brucellosis (*Brucellosis abortus*), infectious bovine rhinotracheitis, bovine viral diarrhea, and leptospirosis (*Leptospira*). We also determined pregnancy status from presence of pregnancy-specific protein-B in the blood serum (Noyes et al. 1997). We compared IFBF levels, disease exposure, and pregnancy rates to other Montana elk populations captured and sampled during winters 2014, 2015, and 2016.

Survival

We outfitted adult female and male elk with remote-upload GPS collars (Lotek Wireless Inc. model LifeCycle, New Market, Ontario, Canada) that triggered a mortality sensor if the collar was stationary for more than 12 hours. The collars also had standard VHF (very high frequency) radio capabilities that allowed tracking from the ground using hand-held receivers. Mortality events were remotely detected and were investigated as soon as possible. We estimated sex-specific survival rates annually and defined May 20 as the start date of the monitoring period based on the biological year when females are generally on calving range and nearing parturition. Elk entered into the study during a given winter season based on their capture date. Most individuals were monitored for 36 months; however, some individuals were monitored for a shorter period (12 months) because they were captured and collared during the third winter of the project or their collars failed to operate for the entire monitoring period.

We used the Kaplan-Meier (KM) estimator and log-rank tests in program R version 3.5.0 (R Core Team 2018) using the "survival" package to provide basic survival estimates and compare survival across monitoring periods (Pollock et al. 1989, R Core Team 2018). The log-rank test is similar to a chi-square test, where observed and expected numbers of events (i.e., mortalities) are formally compared between groups (i.e., P-values of the test estimates). We compared sex-specific and annual survival rates with log-rank tests. We treated year (2015 – 2016, 2016 – 2017, and 2017 – 2018) as a categorical variable in the survival analysis, with each year spanning the biological year from May 20 – May 19. We did not consider the effect of age due to the low variation in ages captured, with the majority of elk in the prime (2 – 9 years old) age category (Raithel et al. 2007), as well as potential inaccuracies of aging from teeth wear patterns.

We determined the cause and timing of mortality based on factors such as the presence of carnivore tracks and scat, wounds to the animal (location, depth, and size of bite and claw marks), signs of struggle, severity and timing of injuries (pre- or post-mortem based on subcutaneous hemorrhaging), patterns of consumption, presence and patterns of carcass caching, and signs of scavenging (Smith and Anderson 1996, Barber-Meyer et al. 2008). We also documented photographic evidence at each mortality site. We categorized mortality sources as mountain lion, wolf, unknown, natural (e.g., non-predation starvation or disease), and human-related (hunter harvest, vehicle or train collision, or fence entanglement). We only classified a mortality event to a specific cause if the confidence level was certain, which meant that evidence was sufficiently clear and unambiguous as to the source of mortality.

Distributions & movements

We programmed the remote-upload GPS collars outfitted on adult female and male elk (see above) to transmit 1 location every 23 hours through the Globalstar satellite network. Collars on adult females were designed to remain on the animal for life and on adult males were programmed to automatically release after 4 years.

We delineated annual and seasonal distributions for female and male elk based on GPS locations using the adehabitatHR package in program R version 3.5.0 (R Core Team 2018) by estimating a 95% kernel utilization distribution (KUD) for each year (2015, 2016, 2017) and season (spring, summer, archery hunting season, rifle hunting season, and winter). The 95% KUD represents the area in which the probability of relocating an animal is equal to 0.95. We additionally estimated a 50% KUD to identify core use areas (i.e., areas estimated to have higher relative densities of locations) of female and male elk for each year and season. We defined spring (i.e., calving) as May 20 – June 15, summer as July 1 to 1 week prior to the opening of archery season, and winter as 1 week after the close of rifle season to May 1. We defined the archery and rifle hunting seasons according to the annual Montana general elk archery and rifle season dates, where the 6-week archery season starts on the 1st Saturday in September and the 5-week rifle season starts 5 weeks prior to the Saturday after Thanksgiving. Gaps between delineated seasons were intended to exclude some movements between seasonal ranges. Annual distributions were defined as the spring season to the end of the winter season. We calculated and summarized annual and seasonal distributions for each sex separately.

We classified the migratory behavior of each elk as resident, intermediate, or migrant based on overlap of winter and summer KUDs, following the methods of Barker et al. (2018). In this analysis, we considered winter as February – March and summer as July – August. We more narrowly defined the winter and summer periods to reduce effects of elk migration and isolate seasonal ranges. For each elk, we calculated the volume of intersection between winter and summer home ranges (95% KUDs) and between core use areas (50% KUDs) within each elk's winter and summer home ranges. We classified individuals as migrants if winter and summer home ranges did not overlap (i.e., volume of intersection of 95% KUDs = 0), residents if core use areas overlapped (i.e., volume intersection of 50% KUDs > 0), and intermediates for all remaining individuals (i.e., volume of intersection of 50% KUDs = 0 and of 95% KUDs > 0).

Results

Capture & health sampling

We captured a total of 60 adult (> 1.5 years old) elk during winters 2015 and 2017 (Figure 7; Table 1). We captured 30 female and 15 male elk in February 2015 and an additional 5 female and 10 male elk in March 2017 to increase sample size. Age was estimated for all elk during 2015 but only 3 of the 15 elk captured during 2017. The estimated age of female and male elk averaged 6.4 (± 2.7 SD, range = 1.5 – 12) and 5.4 (± 2.2 SD, range = 3 – 10), respectively. Of the 30 female elk captured during 2015, we estimated IFBF in 28 females and pregnancy status in all females. During 2017, we sampled pregnancy but not IFBF in the 5 female elk captured due to the low sample size. The estimated IFBF of female elk averaged 6.6% (± 1.7% SD, range = 2.7 – 9.2%). Average IFBF levels for the Elkhorn population were lower than all western Montana populations sampled 2014 – 2016 (Figure 8). Based on non-overlapping 95% confidence intervals (CI; not shown), average IFBF levels for the Elkhorn population were significantly lower than the Black's Ford, Tobacco Roots, North Absaroka, Northern Yellowstone, and North Sapphire populations. Compared to the North Absaroka and Mill Creek populations captured during the same year (2015), IFBF levels for the Elkhorn population averaged 1.0% and 0.9% lower, respectively (7.6 ± 1.2% SD and 7.4 ± 2.0% SD, respectively).

During 2015, the average pregnancy rate of females > 2 years of age was 0.93 (95% CI = 0.84 – 1.00, n = 30), greater than the average pregnancy rate of 0.86 (95% CI = 0.82 – 0.90, n = 361) across

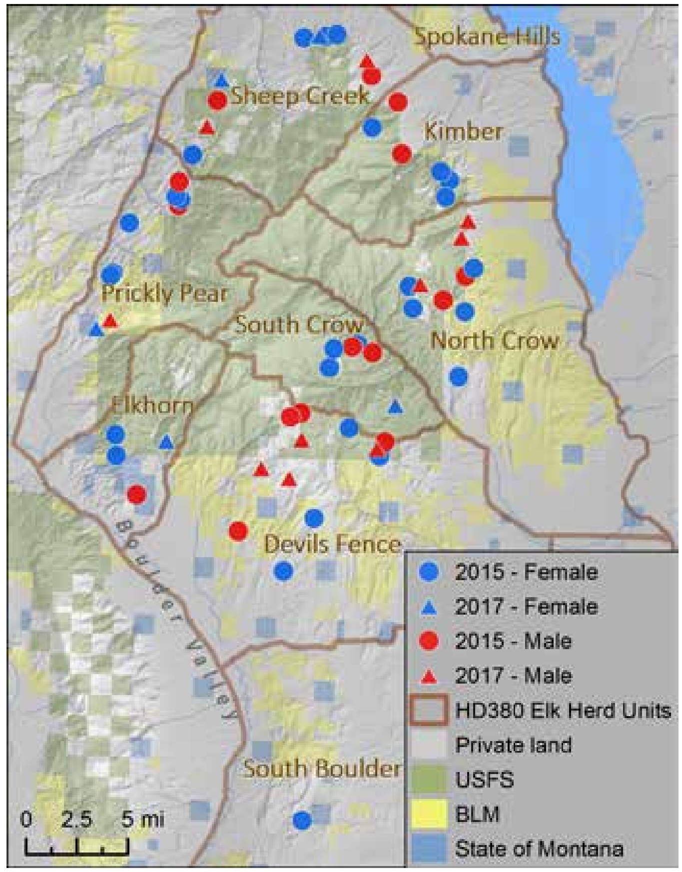

Figure 7 – Capture locations of female and male elk during winters 2015 and 2017 in the Elkhorn elk population in west-central Montana, USA.

Table 1 – Number of animals captured, sampled and collared per herd unit of adult female and male elk during winter 2015 and 2017 in the Elkhorn Mountains, west-central Montana, USA.

	2015		2017	
Elk Herd Unit	Female	Male	Female	Male
North Crow	6	2	0	3
South Crow	3	2	1	0
Kimber	4	2	0	0
Sheep Creek	4	2	2	2
Prickly Pear	5	2	1	1
Elkhorn	2	1	1	0
Devils Fence	5	4	0	4
South Boulder	1	0	0	0
Total	30	15	5	10

western Montana populations sampled 2014 – 2016 (Figure 9). All 5 females captured in 2017 were pregnant. In the Elkhorn population, IFBF levels for non-pregnant elk averaged 3.3% (95% CI = 2.1 – 4.4%, n = 2) and for pregnant elk averaged 6.8% (95% CI = 6.4 – 7.3%, n = 33; Figure 10). The estimated age of the 2 non-pregnant elk was 12, the oldest sampled females. Across western Montana populations sampled 2014 – 2016, IFBF levels for non-pregnant elk averaged 6.4% (95% CI = 5.8 – 7.0%, n = 43) and for pregnant elk averaged 8.0% (95% CI = 7.8 – 8.2, n = 253).

We sampled serology for exposure to diseases in 50 (female = 35, male = 15) adult elk. We found no serological evidence for exposure to brucellosis or leptospirosis or for the presence of bovine viral diarrhea in any of the elk sampled. We detected exposure to infectious bovine rhinotracheitis in 22 female and 11 male elk (44% and 22% of the total sampled elk, respectively).

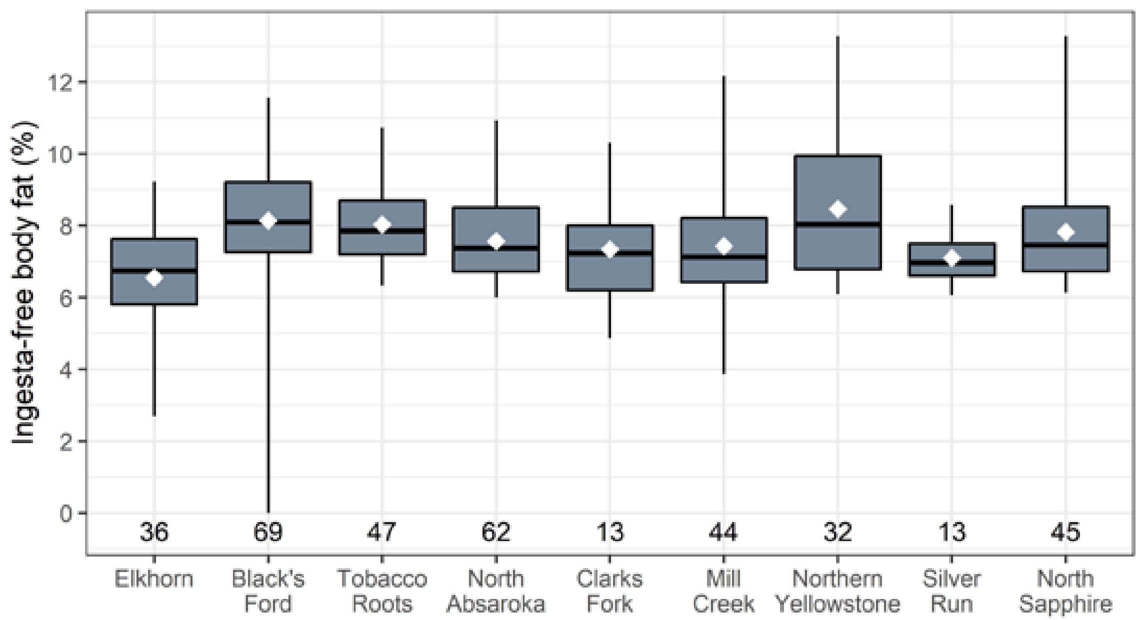

Figure 8 – Estimates of percent ingesta-free body fat for adult female elk in populations across western Montana sampled winters 2014 – 2016. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value. White diamonds represent the mean value.

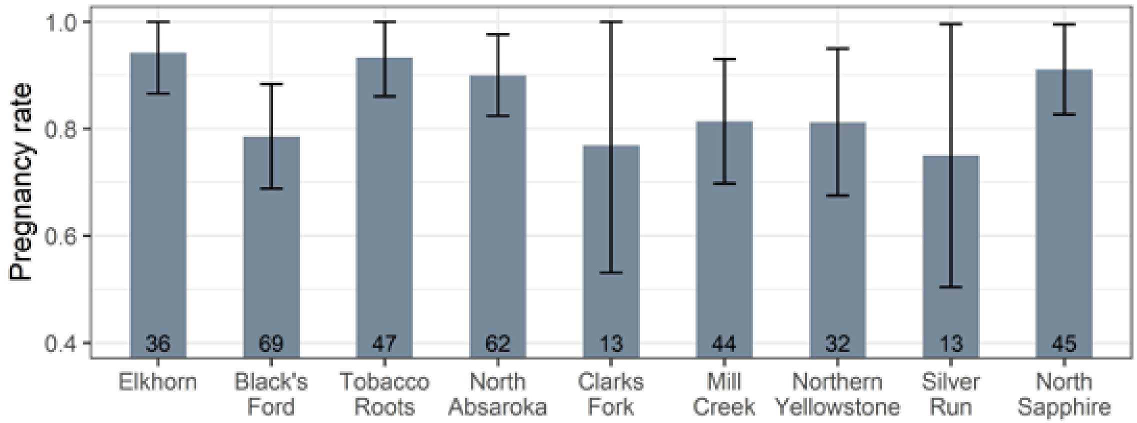

Figure 9 - Estimates of pregnancy rate for adult female elk in populations across western Montana sampled winters 2014 – 2016. Whisker lines represent 95% confidence intervals. Numbers at bottom are respective sample sizes.

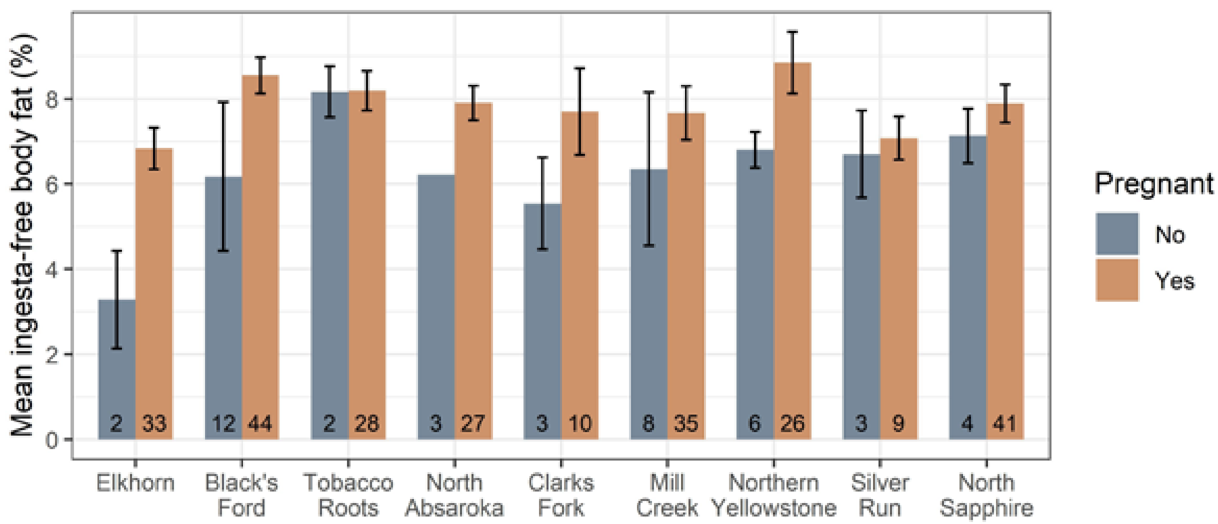

Figure 10 - Estimates of mean ingesta-free body fat for pregnant and non-pregnant adult female elk in populations across western Montana sampled winters 2014 - 2016. Whisker lines represent 95% confidence intervals. Numbers at bottom are respective sample sizes.

Survival

We deployed collars on 30 female and 15 male elk in February 2015 and 5 female and 10 male elk in March 2017. Across all monitoring periods (i.e., May 20 – May 19 each year for 2015 – 2016, 2016 – 2017, and 2017 – 2018), we observed a total of 12 female and 9 male mortalities (Figure 11). We removed the final year from 10 female and 13 male elk that were of unknown fate due to collar failure (however, see below). This resulted in a total of 35 female and 20 male elk included in our survival analysis, totaling 75 female and 32 male

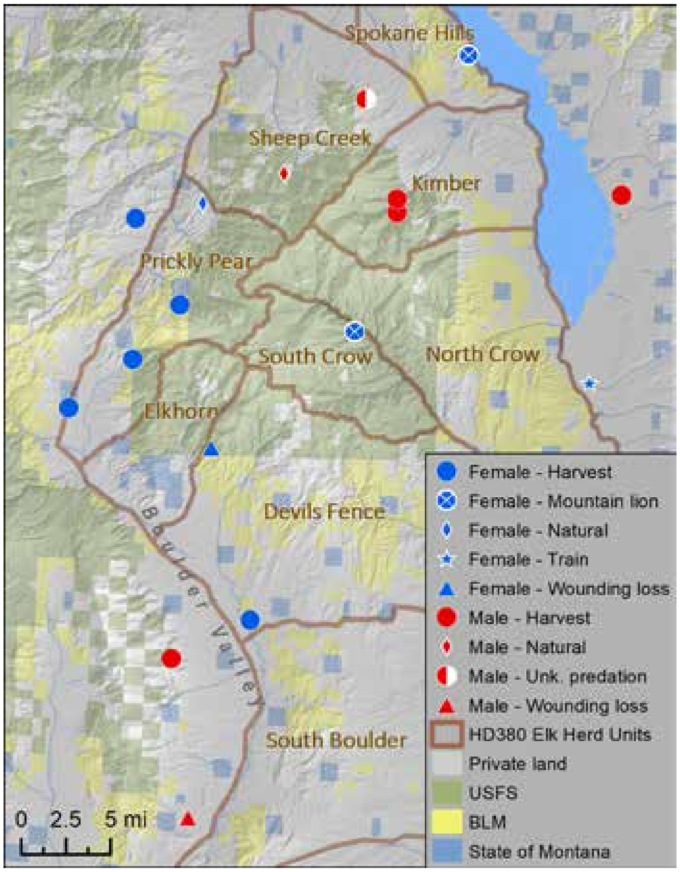

Figure 11 – Locations and cause of adult female (blue) and male (red) elk mortality in the Elkhorn elk population, west-central Montana, USA, during 2015 – 2017. Note that not all recorded mortalities are shown due to missing location information.

elk-years. During 2015 –2016, 30 female and 10 male elk entered the monitoring period and 5 female and 2 male mortalities occurred. During 2016 –2017, 28 female and 15 male elk entered the monitoring period and 3 female and 3 male mortalities occurred. During 2017 – 2018, 17 female and 7 male elk entered the monitoring period and 4 female and 4 male mortalities occurred.

Annual survival rates were significantly different between the sexes (Figure 12; log-rank test = 5.6 on 1 d.f., P = 0.02). The annual survival rate for female elk was 0.83 (95% CI = 0.72 – 0.90) and for male elk was 0.61 (95% CI = 0.38 – 0.78). Female elk survival rate was highest in 2016 – 2017 at 0.87 (95% CI = 0.65 – 0.96) and lowest in 2017 - 2018 at 0.77 (95% CI = 0.49 – 0.90; Figure 13); however, there was no evidence of a significant difference between years (log-rank test = 0.89 on 2 d.f., P = 0.60). Male elk survival rate was highest in 2015 – 2016 at 0.80 (95% CI = 0.41 – 0.95) and lowest in 2017 – 2018 at 0.43 (95% CI = 0.10 – 0.73); however, there was also no evidence of a significant difference between years (log-rank test = 3.28 on 2 d.f., P = 0.20).

A substantial proportion of the monitored elk had collars that failed (29% of females and 52% of males) during the study and were recorded as unknown fate. Collar malfunctions are expected in studies of elk, particularly for males when collars receive damage from antlers during the rut (typically late August to mid-October). Of the 13 males with collar failures, 8 (62%) occurred approximately during the rutting period. While it is likely that these unknown fate elk were simply collar malfunctions, illegal hunting is known to occur in the Elkhorn population, and some collar failures from this study may be due to poaching incidents.

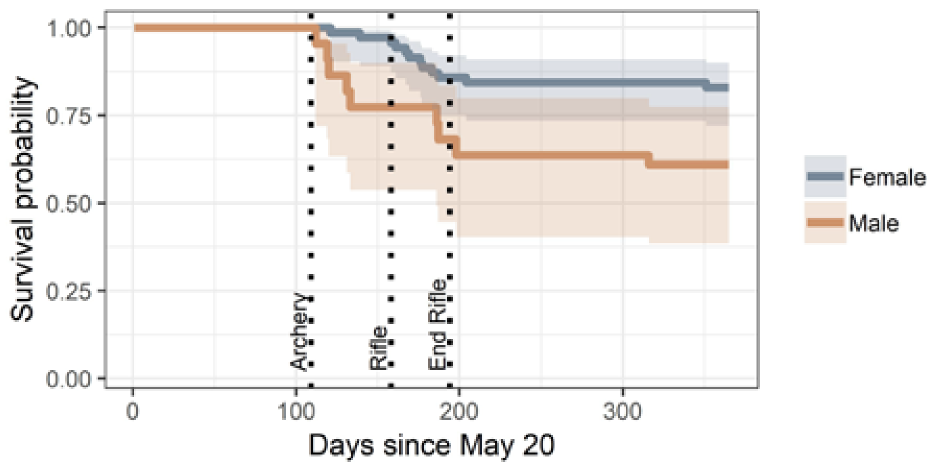

Figure 12 – Annual survival curves and 95% confidence intervals pooled across all years of the study for female and male elk in the Elkhorn population in west-central Montana, USA. Estimates are based on monitoring periods May 20 – May 19 for 2015 – 2016, 2016 – 2017, and 2017 – 2018. Dotted vertical lines represent relevant days of the archery and rifle general hunting seasons (based on 2015 dates).

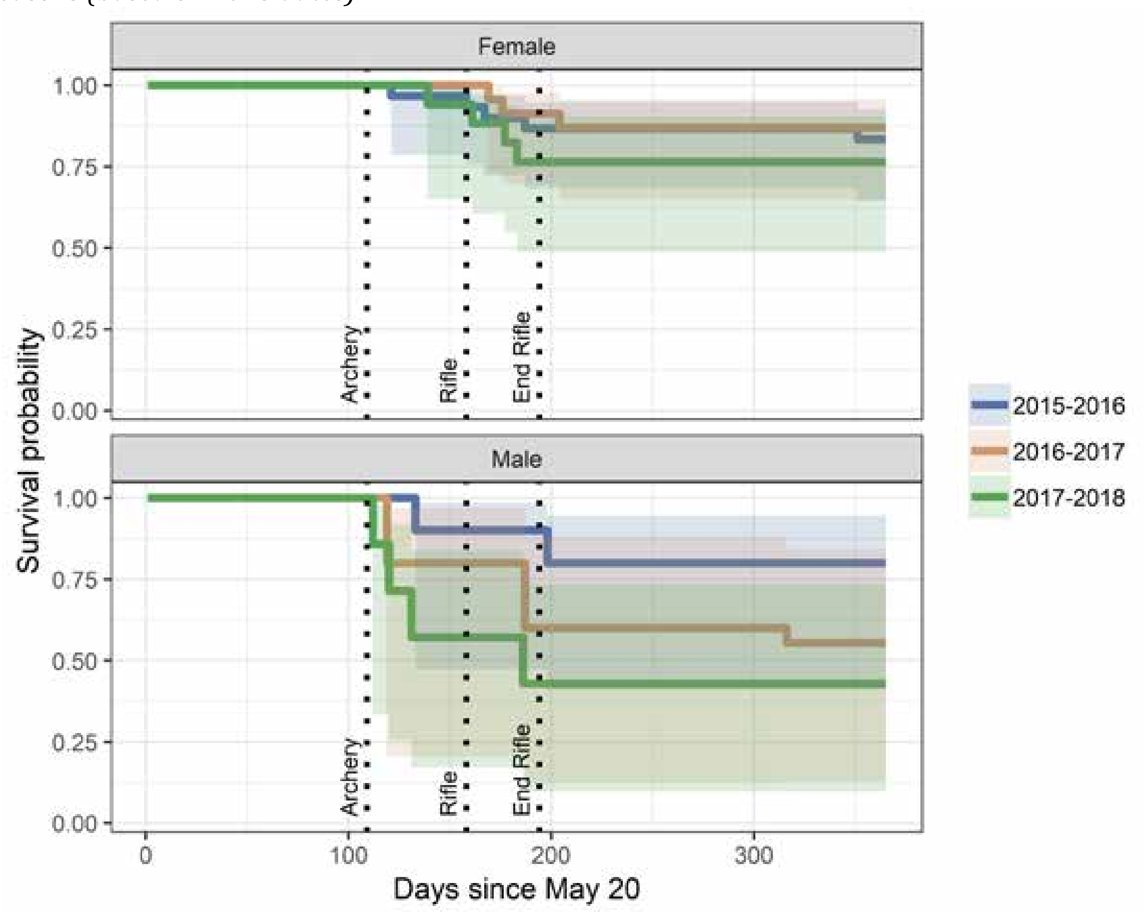

Figure 13 – Survival curves and 95% confidence intervals by year for female (top) and male (bottom) elk in the Elkhorn population of west-central Montana, USA. Survival estimates are based on the monitoring periods May 20 – May 19 for 2015 – 2016, 2016 – 2017, and 2017 – 2018. Dotted vertical lines represent relevant days of archery and rifle general hunting seasons.

Table 2 – Number and percent (per sex) of mortalities by season and cause of death observed from GPS-collared adult female and male elk in the Elkhorn population in west-central Montana, USA, 2014 – 2018.

		No. (%) mortalities	
Season	Cause	Female	Male
Archery	Harvest	2 (16.7)	3 (33.3)
	Wounding Loss	--	1 (11.1)
	Illegal Harvest	--	1 (11.1)
Rifle	Harvest	5 (41.7)	2 (22.2)
	Wounding Loss	1 (8.3)	--
	Mountain Lion	2 (16.7)	--
Winter	Natural	1 (8.3)	1 (11.1)
	Train collision	1 (8.3)	--
	Unknown predation	--	1 (11.1)
Total		12	9

We investigated 12 female and 9 male mortalities (Figure 11; Table 2). The female mortalities included 9 (75%) human-related, 2 (17%) mountain lion predations, and 1 (8%) natural. The human-related mortalities included 2 archery season harvests, 5 rifle season harvests, 1 rifle season wounding loss, and 1 train collision. Of the harvest-related mortalities, 4 occurred on public lands, 3 on private lands, and 1 on unknown land ownership. The male mortalities included 7 (78%) human-related, 1 (11%) unknown predation, and 1 (11%) natural. The human-related mortalities included 3 archery season harvests, 1 archery season wounding loss, 1 archery season illegal harvest, and 2 rifle season harvests. Of the harvest-related mortalities, 1 occurred on public land, 5 on private lands, and 1 on unknown land ownership.

Figure 14 – Left: a partially-buried collared adult female elk typical of mountain lion prey-caching behavior. Right: a collared adult male elk in poor nutritional condition possibly due to a previous leg injury. Elkhorn Mountains, west-central Montana, USA, 2015.

Distributions & movements

Between 2015 and 2017, 59 individuals (24,329 locations for 35 females and 8,554 locations for 24 males) were instrumented with GPS collars which collected a total of 41,067 GPS locations after censoring locations with a DOP > 10 (D'Eon and Delparte 2005). Fix success rate of GPS collars was 96% prior to censoring. An additional male was captured in 2015 but died from predation prior to the collection of locations by the GPS collar. Per individual elk, we collected an average of 557 locations (range 33 – 1,071) over

Table 3 – Summary of GPS locations for each season from collared female and male elk in the Elkhorn elk population in west-central Montana, USA, 2015 – 2017.

			Elevation (m)		Slope (°)		Can. cover (%)	
Sex	Season	No. Locations	Mean	SD	Mean	SD	Mean	SD
F	Spring	1,718	1728.5	299.6	10.5	5.8	19.4	22.9
	Summer	3,610	1796.5	323.6	10.9	6.2	22.4	23.6
	Archery	2,718	1722.9	309.0	11.5	7.0	20.4	23.2
	Rifle	2,255	1753.2	313.4	12.5	7.1	21.7	24.7
	Winter	11,037	1639.5	247.9	10.9	6.2	8.6	17.4
M	Spring	1,033	1908.1	228.6	12.8	6.2	29.8	23.9
	Summer	2,062	2008.9	284.4	11.5	6.0	32.4	21.5
	Archery	1,241	1766.0	286.8	12.7	7.2	21.5	24.1
	Rifle	831	1849.5	314.1	14.2	7.0	27.8	23.9
	Winter	5,529	1776.3	231.8	13.9	6.8	21.5	23.4

an average of 662 days (range 156 – 1,161). Elevation of female elk locations averaged 1,696 m (range 1,160 – 2,639 m) and of male elk averaged 1,838 m (range 1,171 – 2,725 m). Slope of female elk locations averaged 11.1° (range 0.0 – 39.4°) and of male elk averaged 13.2° (range 0.2 – 40.4°). Canopy cover of female elk locations averaged 14.7% (range 0.0 – 95.0%) and of male elk averaged 24.8% (range 0.0 – 75.0%). Elevation, slope, and canopy cover of female and male elk varied by season (Table 3).

We used 23,034 GPS locations to delineate annual and seasonal distributions after constraining locations to our defined seasons. Annual distributions varied by sex, with female ranges 21 – 33% larger and averaging lower in elevation and canopy cover than male ranges (Table 4; Figure 15 – Figure 16). Female core use areas within the annual ranges generally occurred at lower elevations than males and were primarily located on National Forest System (NFS) and Bureau of Land Management (BLM) lands in the South Crow, North Crow, Kimber, and Devil's Fence Elk Herd Unit (EHU) and on private lands in the Prickly Pear and Sheep Creek EHU (refer to Figure 4 for EHU boundaries). Male core use areas within the annual range were primarily located on NFS and BLM lands in the North Crow, South Crow, Devil's Fence, Prickly Pear, and Sheep Creek EHU.

Table 4 – Area (km^2), number of collared elk included in annual range estimation, and elevation and canopy cover summaries by sex and year of annual ranges in the Elkhorn elk population in west-central Montana, USA, 2015 – 2017. Year was defined as the biological year spanning May 20 to May 1 of the following year.

				Elevation (m)		Can. cover (%)	
Sex	Year	Area (km^2)	No. elk	Mean	SD	Mean	SD
F	2015	1701.7	30	1667.6	326.9	18.3	23.5
	2016	1634.6	30	1689.9	338.3	19.9	23.9
	2017	1569.0	23	1711.7	332.3	21.6	24.4
M	2015	1142.9	15	1729.0	359.1	22.2	24.2
	2016	1045.0	17	1842.8	298.3	26.1	24.7
	2017	1233.2	11	1801.6	309.7	23.1	24.8

Seasonal ranges varied by sex and year, with females generally using areas at lower elevation and with less canopy cover than males (Table 5;

Figure 17 – Figure 21). For females, spring ranges tended to be relatively large, representing wide dispersion of individuals across private and public lands during this time (Figure 17). Spring core use areas of females occurred in 5 general regions, including northern Prickly Pear, southern Sheep Creek, central Kimber, central North Crow (primarily on NFS lands), South Crow, and northern Devil's Fence (primarily on NFS and BLM lands) EHU. The average land ownership composition of spring core use areas of females was 55% NFS, 9% BLM, 1% state of Montana, and 35% private lands (Figure 22). For males, distributions during the spring season tended to be relatively small in area. Core use areas of males during the spring season occurred primarily on NFS and BLM lands of Prickly Pear, Sheep Creek, Kimber, northern Devil's Fence, and western portions of North Crow EHU. Core use areas of males in the Prickly Pear, Sheep Creek, and Devil's Fence also includes scattered blocks of private land. The average land ownership composition of spring core use areas of males was 60% NFS, 7% BLM, 1% state of Montana, and 32% private lands.

Summer ranges for both female and male elk contracted in area compared to the spring season and averaged highest elevation and canopy cover compared to other seasonal ranges (Figure 18). Female and male core use areas during summer generally occurred in similar regions as the spring core use areas but with an increase of use on NFS lands for females and males, respectively (Figure 22). For females, the average land ownership composition of summer core use areas was 65% NFS, 8% BLM, 1% state of Montana, and 27% private lands. For males, the average land ownership composition of summer core use areas was 71% NFS, 4% BLM, < 1% state of Montana, and 25% private lands.

Table 5 – Area (km²), number of elk included in seasonal range estimation, and elevation (m) and canopy cover (%) summaries by sex and year for seasonal ranges in the Elkhorn elk population in west-central Montana, USA, 2015 – 2017. See text for definitions of seasons.

		Female				Male			
Year	Season	Area (km²)	No. elk	Mean elev. (m)	Mean c.c. (%)	Area (km²)	No. elk	Mean elev. (m)	Mean c.c. (%)
2014	Winter*	1429.0	30	1634.9	16.5	945.2	15	1763.1	23.7
2015	Spring	1749.9	30	1690.1	19.1	655.6	14	1878.7	29.4
	Summer	1566.0	30	1714.8	20.7	409.8	14	2009.1	36.9
	Archery	1695.6	30	1690.1	19.7	1357.5	14	1736.7	23.4
	Rifle	1781.1	29	1691.7	20.6	1025.3	12	1734.2	23.1
	Winter	1454.6	26	1613.2	15.7	1269.6	9	1639.5	17.9
2016	Spring	1544.3	24	1724.1	21.0	755.2	8	1838.9	28.1
	Summer	1372.4	25	1747.3	22.9	597.0	8	1902.3	30.7
	Archery	1912.9	23	1667.3	18.7	1751.4	7	1685.1	21.3
	Rifle	1840.3	23	1681.5	18.9	512.3	3	1933.1	31.2
	Winter	1387.1	23	1627.8	17.1	842.4	11	1850.6	26.2
2017	Spring	1521.2	23	1760.9	23.4	776.2	11	1923.8	31.5
	Summer	1279.9	23	1809.3	26.6	617.5	11	1942.3	31.2
	Archery	1825.7	23	1712.3	21.0	1557.9	9	1714.3	19.1
	Rifle	1786.1	22	1713.4	21.6	1011.1	5	1776.8	23.0
	Winter	1411.9	21	1585.1	16.4	544.1	4	1800.7	20.7

* Based on shorter temporal period of GPS locations due to captures occurring in the latter half of this season (i.e., February 2015).

For females, the archery and rifle season ranges tended to be largest in area of all seasonal ranges, representing wide dispersion of individuals across the landscape (Figure 19 – Figure 20), and averaged lower in elevation and canopy cover. Core use areas of females only marginally shifted to include more private lands and lands restricting public hunter access during the archery and rifle seasons compared to the summer season (Figure 22 – Figure 23). For archery core use areas of females, the average land ownership composition was 55% NFS, 11% BLM, 1% state of Montana, and 33% private lands. The average percent accessible to public hunting was 69%, a decrease from 75% during the summer. For rifle core use areas of females, the average land ownership composition was 59% NFS, 10% BLM, 1% state of Montana, and 30% private lands. The average percent accessible to public hunting was 74%.

For males, the archery season range was the largest in area compared to other seasonal ranges and, in comparison to the summer range, was distributed across more lands owned by BLM, state of Montana, and private owners and with restricted public hunter access. During the archery season in 2016, one male swam across Canyon Ferry Reservoir and occupied BLM, state of Montana, and private lands until returning to the west side of the reservoir at the beginning of the rifle season. Archery season core use areas of males covered broader areas of Sheep Creek, Kimber, and Prickly Pear EHU. Additionally, males shifted distributions southward to private lands in the Boulder Valley (south-west Devil's Fence and South Boulder EHU). The average land ownership composition of archery core use areas of males was 47% NFS, 6% BLM, 2% state of Montana, and 45% private lands. The average percent accessible to public hunting was 62%, a decrease from 82% during the summer.

The rifle season range of males contracted and averaged higher elevation and canopy cover compared to the archery season; however, data for 2016 and 2017 were from only 3 and 5 individuals, respectively. Distributions of males during the rifle season were generally in similar geographic regions as during the archery season; however, within core use areas, the amount of NFS lands increased to 67%, of private lands decreased to 24%, and of lands accessible to public hunting increased to 79% (Figure 22 – Figure 23). In addition, males occupying the Boulder Valley redistributed northward to the north-west and south-east portions of Devil's Fence EHU.

During the winter season, female and male ranges shifted to broader areas of private lands that surround the Elkhorn Mountains at lower elevations, with males averaging higher elevation and canopy cover than females (Figure 21). Winter core use areas of females included northern Sheep Creek, north-western Prickly Pear, southern Kimball, central North Crow, south-eastern South Crow, and northern Devil's Fence EHU. The average land ownership composition of winter core use areas of females was 43% NFS, 12% BLM, 1% state of Montana, and 44% private lands. Winter core use area of males included northern Prickly Pear, western and eastern Sheep Creek, central Kimber, north-central North Crow, and northern Devil's Fence EHU. The winter core use areas during the 2014 biological year (not shown in Figure 21) were similar to subsequent years but also included the region between the core use areas located in North Crow and South Crow EHU. The average land ownership composition of winter core use areas of males was 46% NFS, 16% BLM, 2% state of Montana, and 36% private lands.

To classify migratory behaviors, we estimated individual winter and summer home ranges and core use areas for 31 females and 20 males in 1 to 3 years resulting in a total of 97 elk-years. For females, volume of intersection of winter and summer for home ranges averaged 21% (range 0 – 75%) and for core use areas averaged 5% (range 0 – 34%). For males, volume of intersection of winter and summer for home ranges averaged 12% (range 0 – 44%) and for core use areas averaged 1% (range 0 – 1%).

Across all elk, we classified 49% (n = 25) as residents, 27% (n = 14) as intermediates, and 24% (n = 12) as migrants. Of the females, we classified 65% (n = 20) as residents, 10% (n = 3) as intermediates, and 26% (n = 8) as migrants (Figure 24). Of the males, we classified 25% (n = 5) as residents, 55% (n = 11) as intermediates, and 20% (n = 4) as migrants. Across all elk, residents composed 41%, 37%, and 50% in 2015 (n = 41), 2016 (n = 27), and 2017 (n = 26), respectively. Intermediates composed 39%, 37%, and 31% in 2015, 2016, and 2017, respectively. Migrants composed 20%, 27%, and 19% in 2015, 2016, and 2017, respectively. We observed one instance of switching between migratory and resident behaviors that included a male classified as a resident in 2015 that switched to a migrant in 2016 and an intermediate in 2017. We observed both residents and migrants switching to or from intermediate behaviors between years (n = 9 and n = 1, respectively).

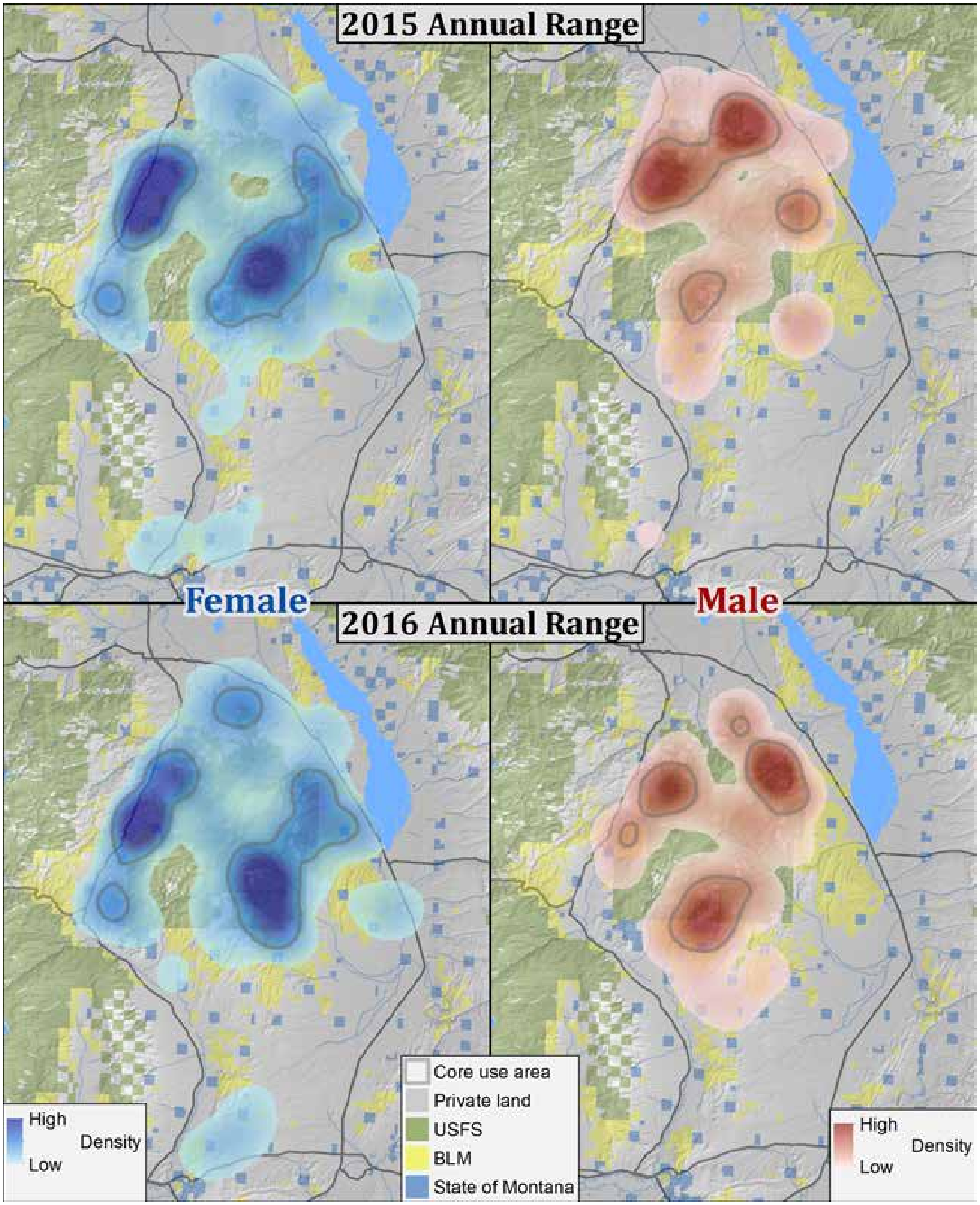

Figure 15 – Annual ranges of female (left panels) and male (right panels) elk for 2015 (upper panels) and 2016 (lower panels) in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate higher density of elk GPS locations (i.e., higher probability of locating an animal) and gray lines indicate core use areas. Annual ranges span May 20 to May 1 of the following year.

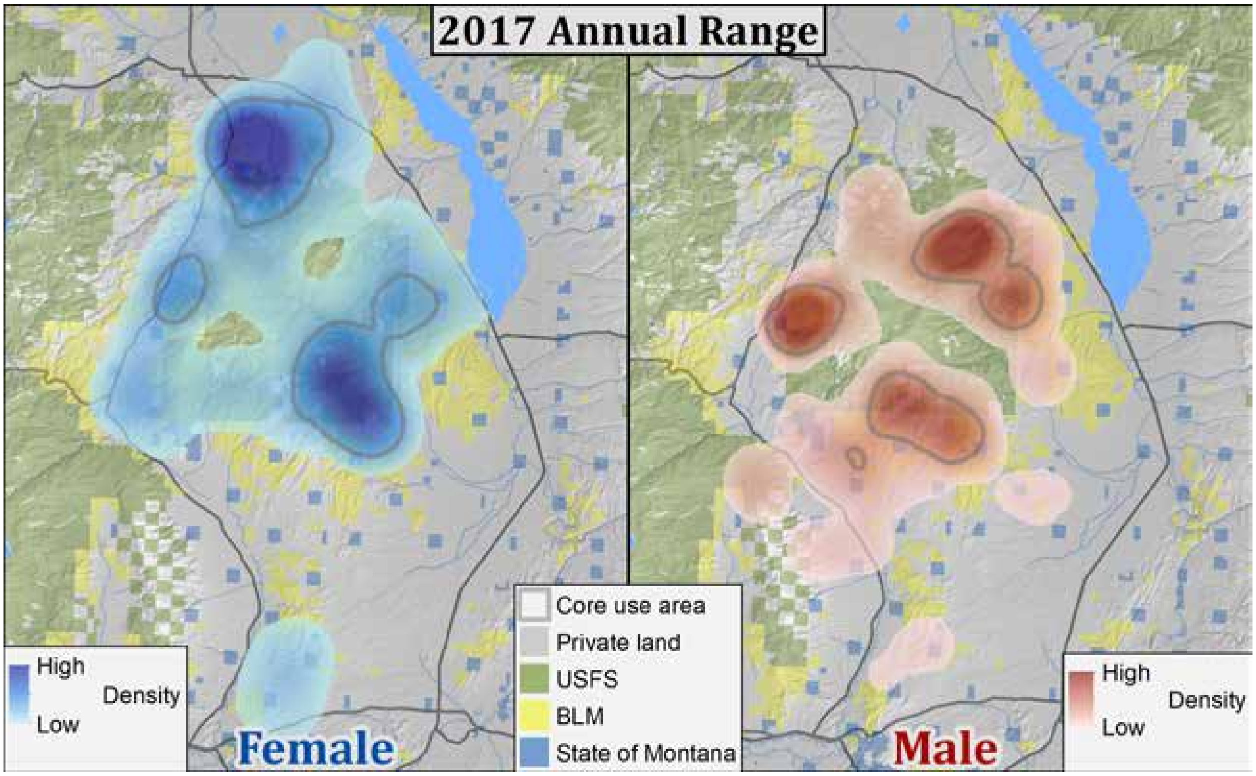

Figure 16 – Annual ranges of female (left panel) and male (right panel) elk for 2017 in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate higher density of elk GPS locations (i.e., higher probability of locating an animal) and gray lines indicate core use areas. Annual ranges span May 20 to May 1 of the following year.

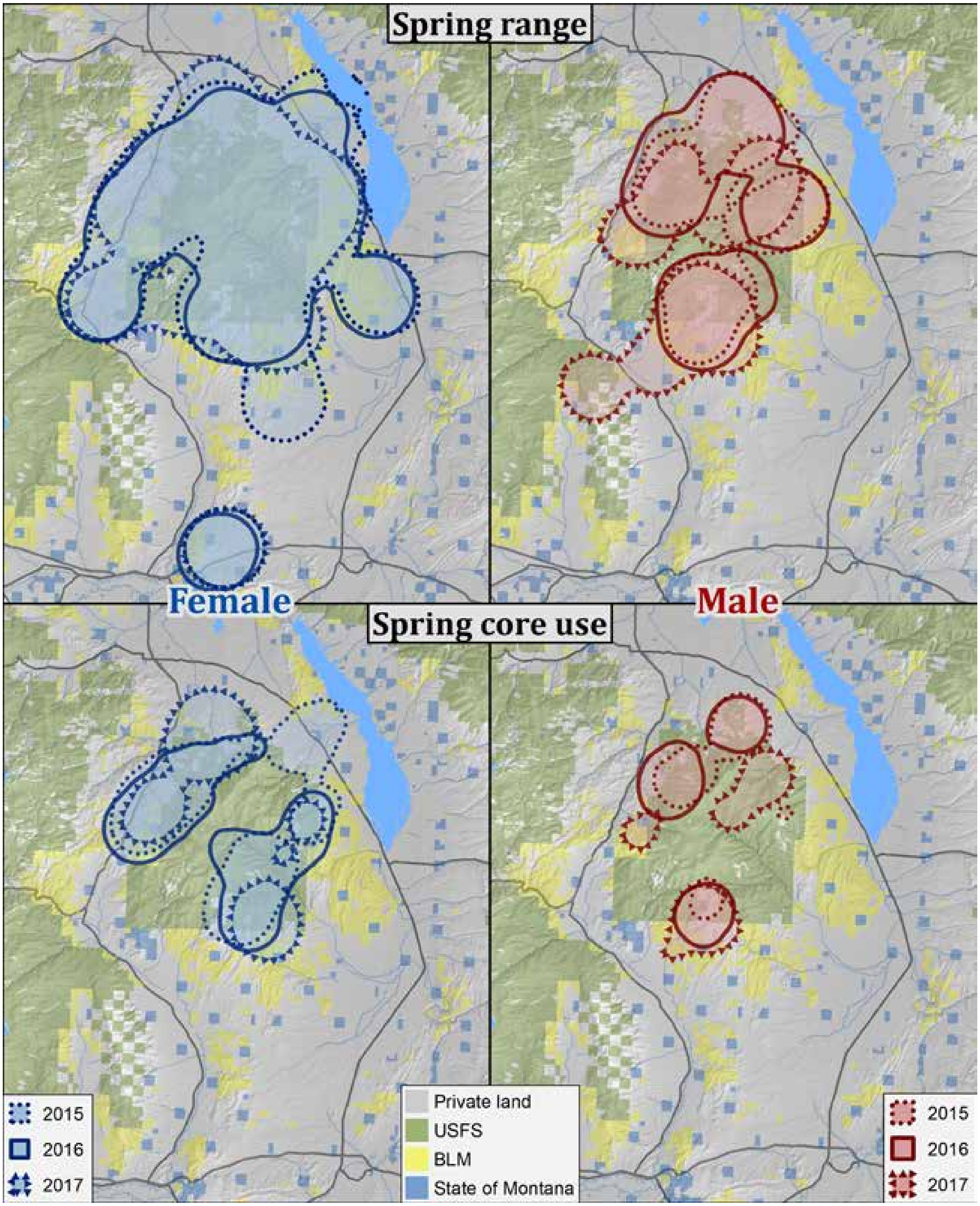

Figure 17 – Spring (May 20 – June 15) seasonal range (upper panels) and core use areas (lower panels) of female (left panels) and male (right panels) elk in the Elkhorn elk population of west-central Montana, USA, 2015 – 2017.

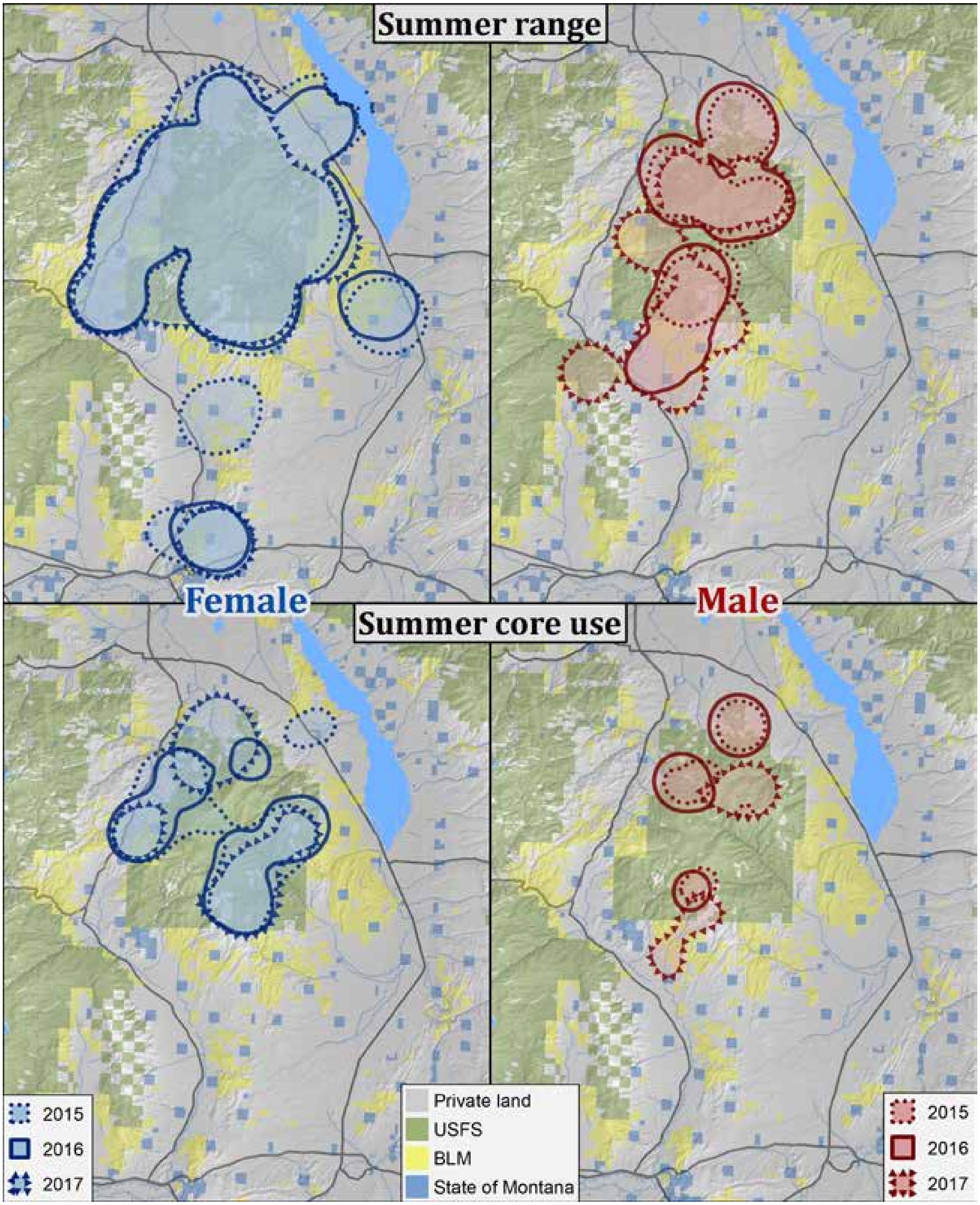

Figure 18 – Summer (July 1 – one week prior to archery season opening date) seasonal range (upper panels) and core use areas (lower panels) of female (left panels) and male (right panels) elk in the Elkhorn elk population of west-central Montana, USA, 2015 – 2017.

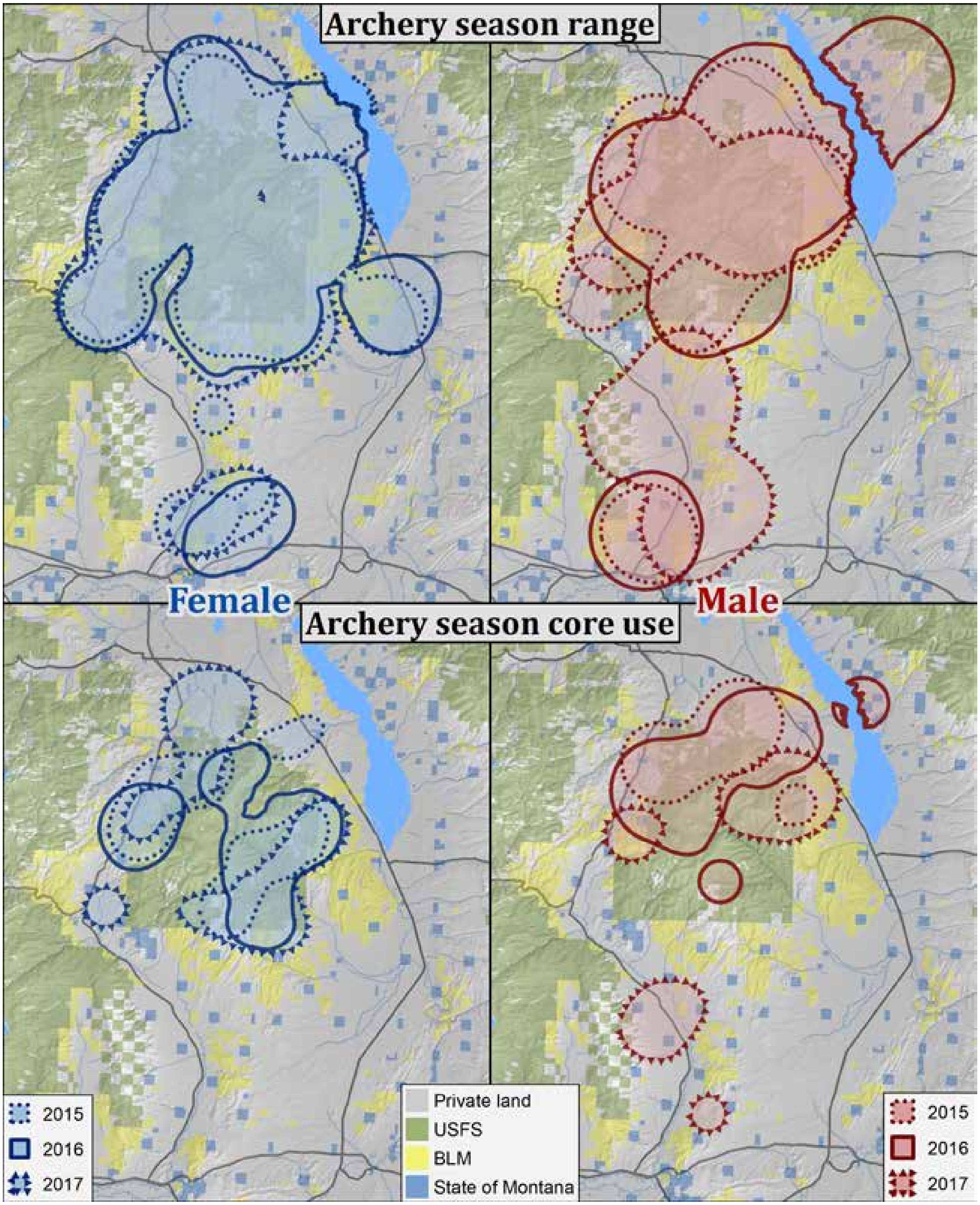

Figure 19 – Archery hunting season range (upper panels) and core use areas (lower panels) of female (left panels) and male (right panels) elk in the Elkhorn elk population of west-central Montana, USA, 2015 – 2017.

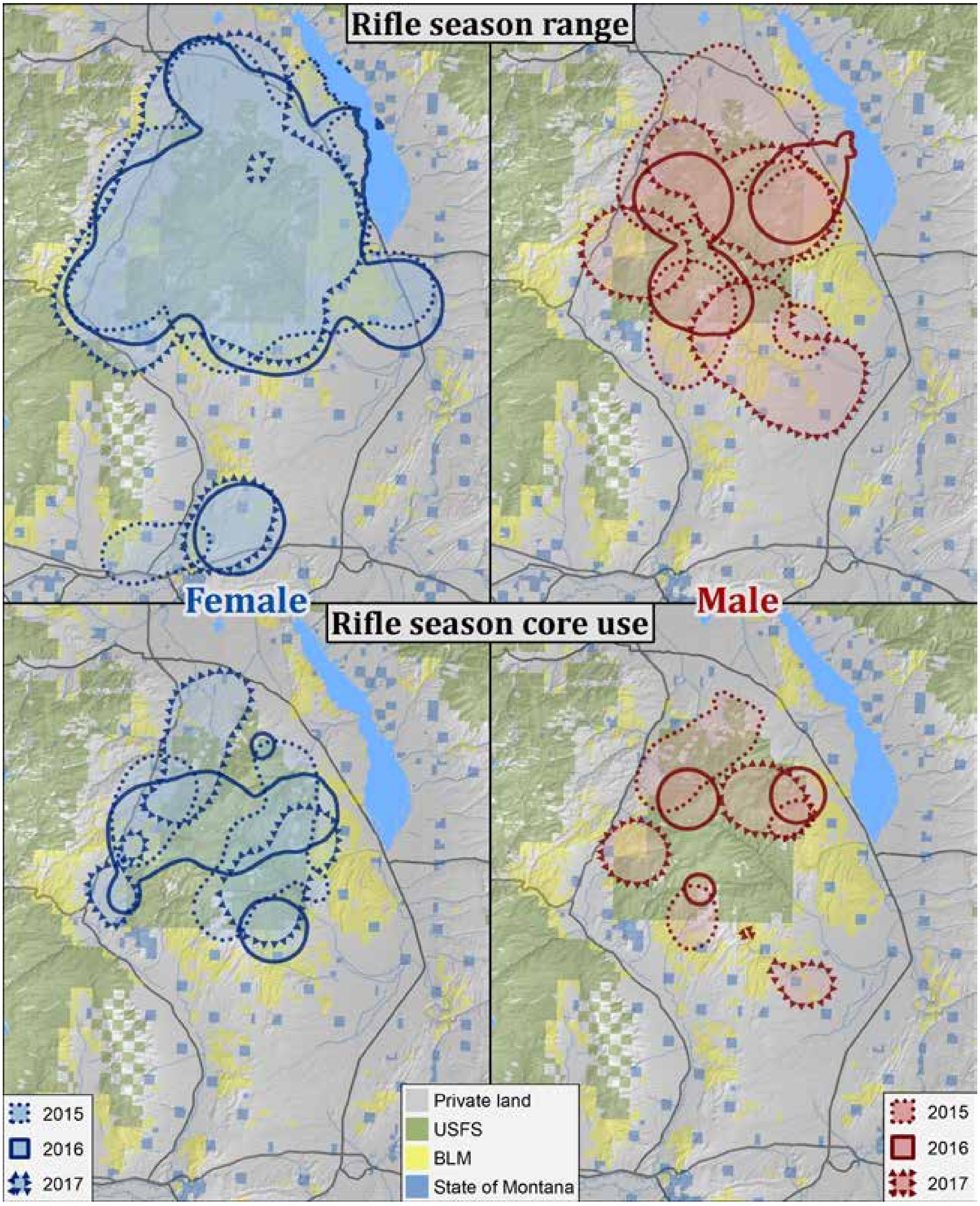

Figure 20 – Rifle hunting season range (upper panels) and core use areas (lower panels) of female (left panels) and male (right panels) elk in the Elkhorn elk population of west-central Montana, USA, 2015 – 2017.

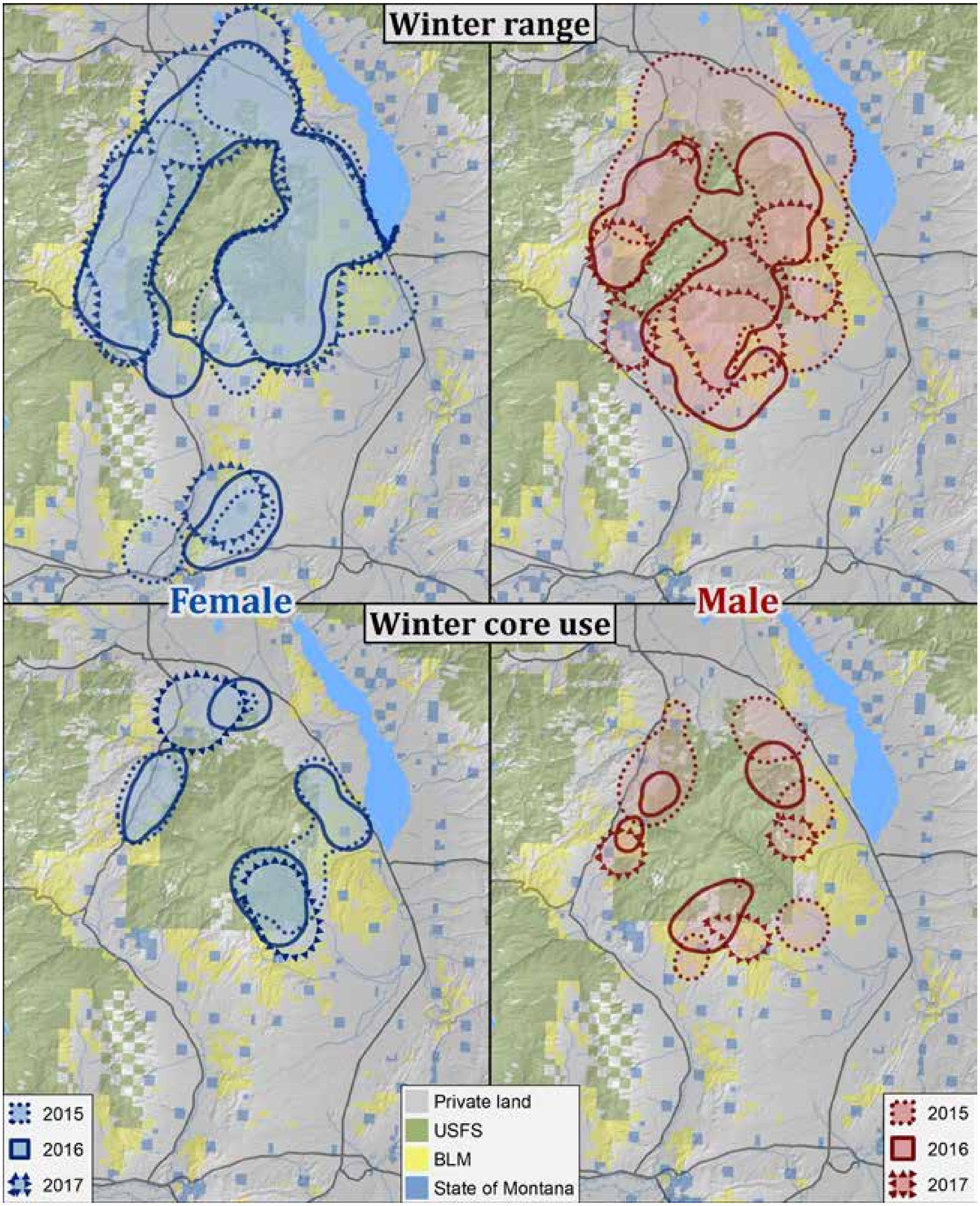

Figure 21 – Winter (one week after rifle season closing date – May 1) seasonal range (upper panels) and core use areas (lower panels) of female (left panels) and male (right panels) elk in the Elkhorn elk population of west-central Montana, USA, 2015 – 2017. Winter ranges for the 2014 biological year are not shown to simplify maps but were generally similar to the years shown.

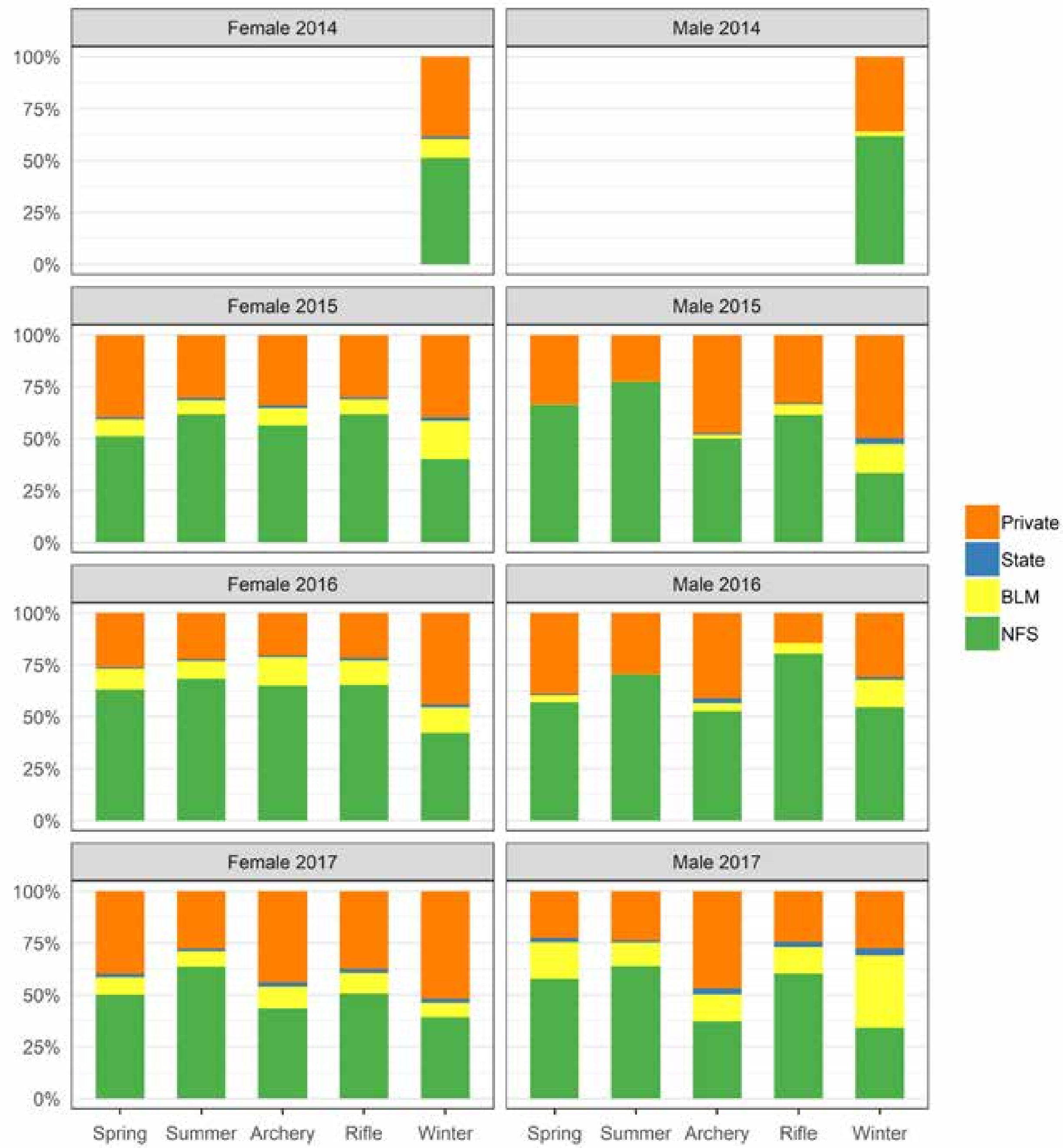

Figure 22 – Percent of private, state, Bureau of Land Management (BLM), and U.S. National Forest System (NFS) land ownership within adult female (left) and male (right) seasonal core use areas for GPS-collared elk in the Elkhorn population in west-central Montana, USA, for biological years (May 20 – May 1) spanning 2014 – 2017. Percentages of other city, county, and federal ownerships were too small for display.

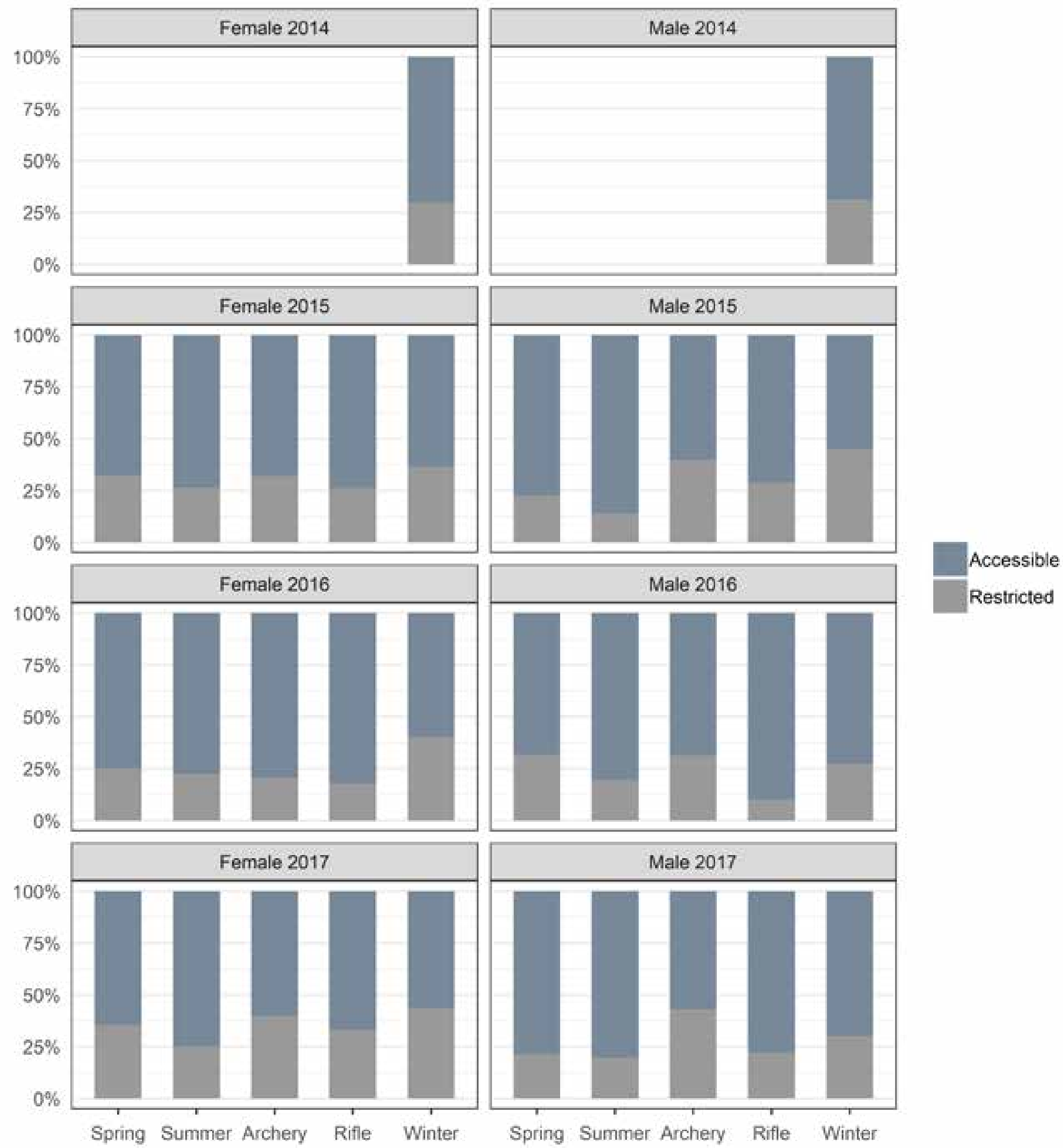

Figure 23 – Percent of lands accessible and restricted to public hunter access within adult female (left) and male (right) seasonal core use areas for GPS-collared elk in the Elkhorn population in west-central Montana, USA, for biological years (May 20 – May 1) spanning 2014 – 2017. Accessible lands include public lands and private lands enrolled in Montana Fish, Wildlife and Park's Block Management Program that permit freely-accessible hunting to the public.

Discussion

Capture & health sampling

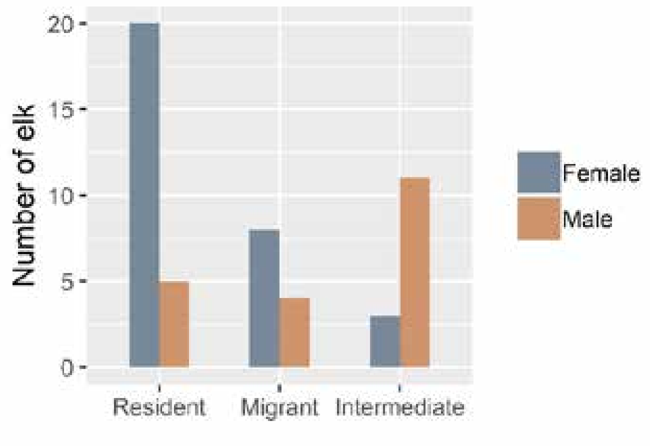

Figure 24 – Number of collared female and male elk classified into resident, migrant, and intermediate migratory behaviors in the Elkhorn population of west-central Montana, USA, 2015 – 2017.

We captured 60 adult female (n = 35) and male (n = 25) elk during winters 2015 and 2017. We assessed the nutritional status and overall health of the Elkhorn elk population based on IFBF estimates, pregnancy rates, and disease exposure in female elk. We found lower IFBF levels compared to other elk populations in western Montana, indicating there may be some nutritional constraints on the Elkhorn population. Pregnancy rate (0.89), however, was slightly above the average rate of other western Montana elk populations, suggesting that any nutritional constraints that may exist were not severe enough to limit breeding probability (Monteith et al. 2013, Cook et al. 2013, Proffitt et al. 2016a). Pregnancy rates were higher than the estimate of 0.68 reported from a previous study in the Elkhorn Mountains (1982 – 1991; DeSimone and Vore 1992). We found above-normal exposure to infectious bovine rhinotracheitis (74% of sampled female elk), but no exposure to brucellosis or other diseases common to elk populations in western Montana.

Survival

We deployed collars on 30 adult female and 15 adult male elk in February 2015 and 5 adult female and 10 adult male elk in March 2017 and monitored their survival through May 31, 2018. We observed a total of 12 female and 9 male mortalities. We found that female survival ($\bar{x}$ = 0.83, 95% CI = 0.72 – 0.90) was constant across years and estimated to be slightly below the range reported for other harvested and non-harvested populations across North America (0.84 – 0.94; Brodie et al. 2013) and in Montana, such as the North Sapphire population ($\bar{x}$ = 0.91; Proffitt et al. 2017).

Male survival ($\bar{x}$ = 0.61, 95% CI = 0.20 – 0.65) was estimated to be significantly lower than female survival, variable across years (but with overlapping 95% confidence intervals), and slightly above the range of typical annual survival rates found by several studies in male-harvested populations in Montana, Idaho, Wyoming, Utah, and Oregon (0.45 – 0.60; Kimball and Wolfe 1974, Unsworth et al. 1993, DeSimone et al. 1996, Smith and Anderson 1998, Biederbeck et al. 2001, Hamlin and Ross 2002, Proffitt et al. 2017). Annual survival estimates of males were above estimates reported from a previous monitoring study of the Elkhorn population during 1984-1991 ($\bar{x}$ = 0.47, range 0.05 – 0.76; also see *Section 7 – Effect of Mountain Pine Beetle on Hunter Effort, Harvest, &* Success ; DeSimone et al. 1996). In Montana, the annual survival estimate for males were higher than the North Sapphire ($\bar{x}$

= 0.46; Proffitt et al. 2017) and Gravelly-Snowcrest ($\bar{x}$ = 0.25, range 0.08 – 0.46; Hamlin and Ross 2002) populations.

Human-related harvest is the primary source of mortality in hunted elk populations (Raedeke et al. 2002, Brodie et al. 2013). This was the case for the Elkhorn population with hunter harvests (harvest and wounding loss) accounting for 75% and 78% of female and male elk mortalities, respectively. Hunter harvests accounted for 71 – 95% of female and 87 – 91% of male mortalities in Montana (DeSimone et al. 1996, Hamlin and Ross 2002, Proffitt et al. 2017) and 86 – 90% of male mortalities outside Montana (Kimball and Wolfe 1974, Unsworth et al. 1993, Smith and Anderson 1998, Biederbeck et al. 2001, Raedeke et al. 2002). Approximately 50% and 22% of harvests of female and male elk in the current study occurred on public lands, respectively.

We observed 3 instances of predation of 2 females killed by mountain lions (17% of female mortalities) and 1 male killed by an unknown predator species (11% of male mortalities). These predator-caused mortalities were higher than those reported for the Elkhorns previously (~3%; DeSimone et al. 1996) and for the Gravelly-Snowcrest and North Sapphire populations (0%; Hamlin and Ross 2002, Proffitt et al. 2017) but lower than those reported for the East Fork and West Fork of the Bitterroot populations (29 – 50%; Proffitt et al. 2016b). We observed 2 instances of natural mortalities of 1 female (8% of female mortalities) and 1 male (11% of male mortalities) that occurred during the winter season. The male mortality appeared to be associated to poor nutritional condition due to a broken leg.

Distributions & movements

We used GPS locations of collared adult female and male elk to delineate annual (2015 – 2017) and seasonal distributions (spring, summer, archery hunting season, rifle hunting season, and winter) and classify migratory behaviors (resident, intermediate, migrant). Distributions and movement patterns of collared animals varied by season and sex. Female annual ranges averaged lower in elevation and canopy cover than males with core use areas primarily occurring on NFS and BLM lands in the South Crow, North Crow, Kimber, and Devil's Fence EHU and on private lands in the Prickly Pear and Sheep Creek EHU. Male annual core use areas primarily occurred on NFS and BLM lands in the North Crow, South Crow, Devil's Fence, Prickly Pear, and Sheep Creek EHU. Seasonally, the population showed typical movement characteristics with distributions shifting from lower elevation areas on a mix of public and private lands during the winter to higher elevation areas on or adjacent to public lands during the spring and summer seasons. Portions of North Crow, South Crow, Devil's Fence, Prickly Pear, and Sheep Creek received use by females across all seasons, however, indicating that a portion of the female population remained resident on winter-range year round.

Generally, core use areas of females and males during the spring and summer seasons did not overlap substantially. Following the spring and summer seasons, distributional shifts of both sexes corresponded with the transition to the archery and rifle seasons. Females and males generally became more broadly distributed across the Elkhorn Mountains, including on lower elevation private lands, and increased overlap of core use areas. Both females and males primarily occurred on areas accessible to public hunting during the hunting seasons, but males more substantially increased their use of areas restricted to public hunting during the archery season. Hunting pressure occurred on both sexes during this study (see *Hunting regulations: past & present* in *Section 7 – Effect of Mountain Pine Beetle on Hunter Effort, Harvest, & Success*). During the archery season, hunters could harvest spike bull and antlerless elk (general license), either-sex (limited permit), and antlerless elk (limited B license). During the rifle season, hunters could harvest spike bull (general license), antlerless elk (youth hunt general license or limited B license), and either-sex (limited permit). Following the hunting seasons, both sexes shifted distributions to lower elevations with core use areas primarily on private lands, properties restricting public hunting access, and the periphery of NFS lands.

Partial migration, in which individuals from the same population have varying migratory strategies, is common in elk populations (Luccarini et al. 2006, Hebblewhite et al. 2008, Cagnacci et al. 2011, Middleton et al. 2013, Barker 2018, Barker et al. 2019). In southwestern Montana, elk populations vary from partially migratory, such as in the Tobacco Roots, Clarks Fork, and West Fork of the Bitterroot populations, to entirely migratory, such as in the Yellowstone, Madison, and Silver Run populations (Barker 2018). Of the collared elk in the Elkhorn population, we classified 49% as residents, 27% as intermediates, and 24% as migrants, with a larger proportion of females classified as residents (65%) and migrants (26%) than males (25% and 20%, respectively). Males were primarily intermediates (55%). For female elk, these proportions are most similar to the Tobacco Roots and West Fork of the Bitterroot elk populations in southwestern Montana that are comprised largely of elk exhibiting resident behavior (Barker 2018).

Section 4 – Elk Nutritional Resources & the Effect of Mountain Pine Beetles

Introduction

Seasonal distributions, survival, and reproduction of ungulates are strongly influenced by the distribution and availability of nutritional resources (Bischof et al. 2012, Cook et al. 2013, Long et al. 2014, Merkle et al. 2016, Middleton et al. 2018). In northern latitudes with strong seasonality, acquiring adequate forage during the summer and autumn (henceforth, late summer) allows ungulates to replenish winter-depleted body fat reserves and accrue sufficient fat to survive the winter. In elk, nutritional intake during the late summer is particularly important for females to support the energetic cost of lactating and to become pregnant (Cook et al. 2004, 2016). Additionally, elk calves exposed to better late summer nutrition exhibit faster growth rates and higher winter survival (Cook et al. 1996). Late summer nutritional resources is therefore directly tied to population performance; where late summer nutritional resources are limited, population performance can be negatively affected (Cook et al. 2013, Proffitt et al. 2016a).

Forest disturbance, such as wildfire, timber harvest, and disease, can alter vegetation and has the potential to affect the availability and distribution of late summer nutritional resources for elk (Keane et al. 2002, Long et al. 2008, Hebblewhite et al. 2009, Allred et al. 2011, Cook et al. 2016). Mountain pine beetle (MPB) infestations have caused widespread disturbance to pine (*Pinus* spp.) forests in western North America by killing trees and subsequently modifying ecological processes and impacting wildlife populations and habitat (Stone 1995, Kayes and Tinker 2012, Saab et al. 2014). Little is known, however, regarding the effects of MPB infestations on elk forage which may have important consequences to the distribution, nutritional condition, and demographics of elk.

The Elkhorn Mountains were severely affected by MPB infestations starting in the early 2000's (see *Mountain pine beetle infestation* in *Section 2 – Study Area*). Wildlife and forest managers responsible for managing the Elkhorn elk population and habitat have limited information on the availability of elk forage across the landscape and how MPB infestations may have altered elk forage in lodgepole pine (*Pinus contorta*) forests. This information is valuable for inferring the potential nutritional and demographic consequences of infestations on the elk population. Our goals were to 1) characterize the availability of late summer nutritional resources within an area impacted by MPBs (i.e., the Elkhorn Mountains) and 2) characterize the effects of MPB on late summer nutritional resources by comparing unaffected forests across other study areas in southwestern Montana inhabited by elk.

Methods

We estimated overstory canopy cover and 4 measures of late summer forage from ground-based vegetation sampling completed during July – August of 2016 and 2017 from within the Elkhorn elk annual range (see methods described below): forage abundance (g of forage species biomass per m^2), forage cover (average percent cover of forage species), forage species richness (total number of forage species), and herbaceous quality (kcal/g of herbaceous species). We compared the forage metrics in 7 landcover classes aggregated from classifications identified in the study area (see *Appendix A – Development & Accuracy of Landcover Classifications*), including agriculture (i.e., cultivated and other agriculture), grassland, shrubland, riparian (i.e., valley and upland wetland riparian), forest (i.e., low and high elevation conifer), and 2 MPB classes of lodgepole forest: unaffected and affected. We did not consider early seral lodgepole sites due to low sample sizes.

We identified late summer forage species as those comprising 95% of the diet based on Level B fecal plant fragment analyses (Wildlife Habitat and Nutrition Laboratory, Pullman, WA, USA) of pellet samples. We randomly selected 2 – 4 pellet sampling sites every 14 days from July to September in 2015 and 2016. We used GPS collar locations recorded within 72 hours to identify sampling sites and distributed sampling effort across the Elk Herd Units (see *Elkhorn elk population* in *Section 2 – Study Area*). We collected fresh (< 48 hours old) composite samples of 20 pellets collected from 10 pellet groups (i.e., 10 individual elk) within a 500 m^2 area.

We sampled vegetation at random sites within landcover classes during the time of peak vegetative growth (July – August) and considered each of these samples to represent late summer. We excluded sites in agricultural areas that were sampled after crop harvest. Each sampling site consisted of five 1 m^2 quadrats with each quadrat placed 10 m increments along a 40 m transect oriented to the contour of the slope. We measured overstory canopy cover, composition of understory species, and percent cover of understory species and lifeforms (i.e., forb, graminoid, and shrub). We estimated overstory canopy cover using a spherical densitometer and averaged across quadrats. We estimated understory cover of each species and lifeform independently, allowing total cover per quadrat to exceed 100%. We established a nested 0.25 m^2 clip plot within the 0, 20, and 40 m quadrats and collected all graminoid and forb biomass >1 cm above ground to represent the available foraging height of elk. On shrubs, we clipped all current season new growth (i.e., leaves and non-woody stems). We dried samples at 50°C in a drying oven for 48 hours and measured dry weight to the nearest gram. We apportioned the dry weight to plant lifeform based on the percent cover of each lifeform.

To estimate forage abundance at each sampling site, we first apportioned clipped, dry biomass (g per 0.25 m^2) of each lifeform to each species based on rescaled percent cover (species cover proportional to cover within the appropriate lifeform). Second, we filtered the species to include only forage species and summed biomass across lifeform. Finally, we averaged biomass per lifeform across clip plots, and scaled up to square meters (0.25 m^2 x 4 = 1 m^2). We calculated herbaceous biomass as the sum of graminoid and forb biomass.

To estimate forage cover at each sampling site, we summed percent cover of forage species for each lifeform within each quadrat and averaged percent cover of lifeform across quadrats. We estimated forage cover for each lifeform separately (i.e., did not combine graminoid and forb cover into herbaceous cover) because percent cover of each lifeform was estimated independently, allowing total cover in each quadrat to exceed 100%. Because estimates of percent cover of each species were also estimated independently, forage cover may be overestimated where cover of species overlapped. To estimate forage species richness at each sampling site, we counted the total number of unique forage species recorded across all quadrats.

We estimated herbaceous quality at up to 5 randomly selected sample sites in each of the MPB infestation classes. To estimate herbaceous quality, we combined the forb and graminoid biomass samples from all the clip plots at each sampling site. We estimated dry matter digestibility (Robbins et al. 1987b, 1987a, Hanley et al. 1992) for each herbaceous composite sample using sequential detergent fiber analysis (Van Soest 1982; Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, WA, USA). We converted dry matter digestibility to digestible energy (DE) measured as kcal/g of herbaceous vegetation using an equation developed by Cook et al. (2016).

Several limitations existed prior to and following vegetation sampling in the Elkhorn study area. First, unaffected lodgepole forests were very rare in the study area. As a result, we sampled vegetation in unaffected lodgepole areas from the nearby Little Belt Mountains in 2017 (see *Section 2 – Study Area*). To further increase sample sizes for affected sites, we also sampled vegetation in affected areas located in the Little Belt study area. Because the Little Belt study area may not represent forage conditions in the Elkhorn study area due to climatic or geologic differences, we additionally estimated and compared the forage metrics for unaffected lodgepole sites from within the late summer ranges of 3 other elk populations in the Bitterroot Valley of west-central Montana collected as part of recent studies. These populations included the West Fork and East Fork of the Bitterroot (henceforth, South Bitterroot) sampled during 2012 – 2013 (Proffitt et al. 2016b) and the North Sapphire sampled during 2014 – 2015 (Proffitt et al. 2017).

Second, the majority (67.8%) of vegetation sampling, particularly at unaffected lodgepole sites (100%), occurred in August when vegetation is primarily senesced. In addition, insufficient information was available to estimate the digestibility of individual forage species in different phenological stages. As a result, we could not reliably estimate a forage quality metric that would represent the entire late summer period. Instead, we estimated herbaceous quality at sampling sites based on digestibility analyses of biomass collections of all herbaceous vegetation (i.e., forage species were not differentiated; see methods below). Although the herbaceous quality estimates were primarily representative of August conditions and not specific to forage species, the 3 remaining forage metrics (i.e., abundance, cover, and species richness) reflect attributes of forage vegetation that likely remain constant across the late summer period regardless of the timing of sampling.

Lastly, the intensified sampling in the Little Belt study area in 2017 had several consequences, including that: 1) the majority (89%) of agriculture, grassland, riparian, and forest landcover classes were sampled in 2016, 2) the majority (80%) of the 2 MPB infestation classes were sampled in 2017, and 3) the majority (61%) of unaffected classes were sampled in the Little Belt study area. To assess the reliability of combining data within landcover classes collected across years (2016 and 2017) and study areas (Elkhorn and Little Belt) and assist in the interpretation of elk forage across all study areas (including the North Sapphire and South Bitterroot), we obtained terrain (i.e., elevation and slope) and climate data for each year and study area. From Natural Resource Conservation Service SNOTEL sensors (*http://www.wcc.nrcs.usda.gov/snotel*), we calculated 20-year and year-of-sampling averages of precipitation, temperature, and cumulative snow water equivalent (SWE) based on 3 sensors in the Elkhorn study area (mean elevation: 2,170 m ± 240 [SD]), 2 sensors in the Little Belt study area (2,128 m ± 186), 2 sensors in the North Sapphire (1,986 m ± 317), and 3 sensors in the South Bitterroot (2,011 m ± 364). We derived year-of-sampling climate metrics for a winter period (December – June) to characterize the moisture leading into the growing season and for a summer period (July – August) to characterize the additional moisture available throughout the growing season.

Results

We collected 12 composite pellet samples during the late summer in 2015 (n = 4) and 2016 (n = 8). A total of 16 species comprised 95% of the late summer diet (Table 6). Graminoids, forbs, and shrubs comprised 53.0%, 31.1%, and 14.2% of the diet, respectively. The most common graminoid forage species were *Poa* spp., *Festuca* spp., *Carex* spp., and *Pseudoroegnaria spicatum*, comprising 39.5% of the total diet. The most common forb forage species were *Lupinus* spp., *Astragalus* spp., *Lithospermum* spp., and *Equisetum* spp., comprising 21.1% of the diet. The most common shrub forage species were *Vaccinium* spp., *Artemisia frigida*, *Shepherdia canadensis*, and *Berberis repens*, comprising 11.9% of the diet.

We sampled vegetation at a total of 212 and 63 sites in the Elkhorn and Little Belt study areas, respectively (Table 7). Sampling varied across years such that the majority (89%) of

Table 6 – Percent composition, rank, and cumulative percent of the total late summer diet collected from composite pellet samples during July through September in the Elkhorn elk population in west-central Montana, USA, 2015 – 2016. We considered the species comprising 95% of the cumulative diet as late summer forage species.

Species	Common name	Lifeform	%	Rank	Cum. %
Lupinus spp.	Lupine spp.	forb	17.43	1	17.43
Poa spp.	Bluegrass spp.	graminoid	12.44	2	29.87
Festuca idahoensis	Idaho fescue	graminoid	9.59	3	39.46
Festuca campestris	Rough fescue	graminoid	8.9	4	48.36
Other forb*	--	forb	7.88	5	56.24
Vaccinium spp.	Heath spp.	shrub	6.08	6	62.32
Other grass*	--	graminoid	6.01	7	68.33
Carex spp.	Sedge spp.	graminoid	5.82	8	74.15
Artemisia frigida	Prairie sagewort	shrub	3.33	9	77.48
Pseudoroegneria spicatum	Bluebunch wheatgrass	graminoid	2.7	10	80.18
Agropyron spp.	Wheatgrass spp.	graminoid	2.29	11	82.47
Calamagrostis spp.	Reedgrass spp.	graminoid	1.93	12	84.4
Shepherdia canadensis	Russet buffaloberry	shrub	1.93	13	86.33
Dactylis glomerata	Orchardgrass	graminoid	1.88	14	88.21
Other shrub*	--	shrub	1.76	15	89.97
Astragalus spp.	Milkvetch/locoweed spp.	forb	1.57	16	91.54
Lithospermum spp.	Stoneseed spp.	forb	1.34	17	92.88
Composite hair*	--	---	0.75	18	93.63
Equisetum spp.	Horsetail spp.	forb	0.72	19	94.35
Mahonia repens leaf	Creeping Oregon grape	shrub	0.6	20	94.95

**General grouping category of unidentifiable species in diet analysis not included to filter the ground-sampled vegetation data to forage species.*

agriculture, grassland, shrubland, riparian, and forest landcover classes were sampled in 2016 and the majority (80%) of the 2 MPB infestation classes were sampled in 2017 (Figure 25). The majority (61%) of unaffected classes were sampled in the Little Belt study area. We additionally obtained vegetation data from 59 unaffected lodgepole sites sampled in the North Sapphire (n = 35) and South Bitterroot (n = 24) for comparisons with unaffected lodgepole sites sampled in the Little Belt study area.

Mean elevation and slope at vegetation sampling sites varied between the Elkhorn, Little Belt, North Sapphire, and South Bitterroot study areas (Table 8). As compared to the Little Belt study area, the unaffected and affected sites in the Elkhorn study area averaged higher in elevation and slope. Unaffected sites averaged lowest in elevation in the North Sapphire and South Bitterroot study areas.

Table 7 – Number of vegetation sampling sites in each landcover class by year for the Elkhorn and Little Belt study areas in west-central Montana, USA, 2016 – 2017.

Study area	Landcover	2016	2017	Total
Elkhorn	Agriculture	10	--	10
	Grassland	18	1	19
	Shrubland	24	4	28
	Riparian	10	2	12
	Forest	34	5	39
	Unaffected	7	5	12
	Affected	31	61	92
Little Belt	Unaffected	--	36	36
	Affected	--	27	27

Table 8 – Summary of elevation and slope in each mountain pine beetle (MPB) infestation class in the Elkhorn, Little Belt, North Sapphire, and Southern Bitterroot study areas in west-central Montana, USA, 2012 – 2017.

			Elevation (m)		Slope (°)	
Study area	MPB Class	No. plots	Mean	SD	Mean	SD
Elkhorn	Unaffected	12	2,286.0	81.8	17.95	6.22
	Affected	92	2,127.4	229.2	14.44	5.36
Little Belt	Unaffected	36	2,160.3	106.1	10.51	6.42
	Affected	27	2,075.1	191.59	10.61	6.29
N. Sapphire	Unaffected	35	2,011.0	149.5	13.45	6.46
S. Bitterroot	Unaffected	24	2,048.4	150.2	14.45	8.81

Climate varied between the Elkhorn, Little Belt, North Sapphire, and South Bitterroot study areas (Table 9). For the 20 years prior to each study, average annual SWE and precipitation were highest for the South Bitterroot and North Sapphire and lowest for the Elkhorn and Little Belt study areas. Average annual temperatures for January were highest for the Elkhorn and North Sapphire and lowest for the Little Belt and South Bitterroot study areas. Average annual temperatures for July were similar across all study areas, with the South Bitterroot study area marginally warmer.

In the Elkhorn study area, the average summer precipitation in 2016 was markedly higher than in 2017 by 66.3 mm, whereas differences in other climate metrics were modest (Table 10). In 2017, summer precipitation and temperatures were similar between the Little Belt and Elkhorn study areas; however, the Little Belt study area averaged higher winter precipitation by 31.8 mm and lower SWE by 32.3 mm. In the North Sapphire study area, climate metrics varied between 2014 and 2015, with substantially higher average summer and winter precipitation and SWE in 2014. In the South Bitterroot study area, climate metrics varied between 2012 and 2013, with substantially higher average winter precipitation and SWE in 2012. Average summer precipitation was similar between these years.

Table 9 – Historical (20-year summary) mean annual snow water equivalent (SWE), precipitation, and January and July temperature averaged across multiple SNOTEL sensors in the Elkhorn, Little Belt, North Sapphire, and Southern Bitterroot study areas in west-central Montana, USA.

	SWE (mm)		Precip. (mm)		Jan temp. (°C)		Jul temp. (°C)	
Study area	Mean	SD	Mean	SD	Mean	SD	Mean.	SD
Elkhorn	308.6	115.3	704.3	74.8	-5.0	1.2	14.1	1.2
Little Belts	354.7	62.9	862.4	57.2	-6.8	0.1	14.1	0.6
N. Sapphire	464.2	242.5	837.1	207.1	-5.4	0.8	14.0	1.0
S. Bitterroot	494.8	172.9	874.6	65.6	-6.4	1.3	14.4	0.5

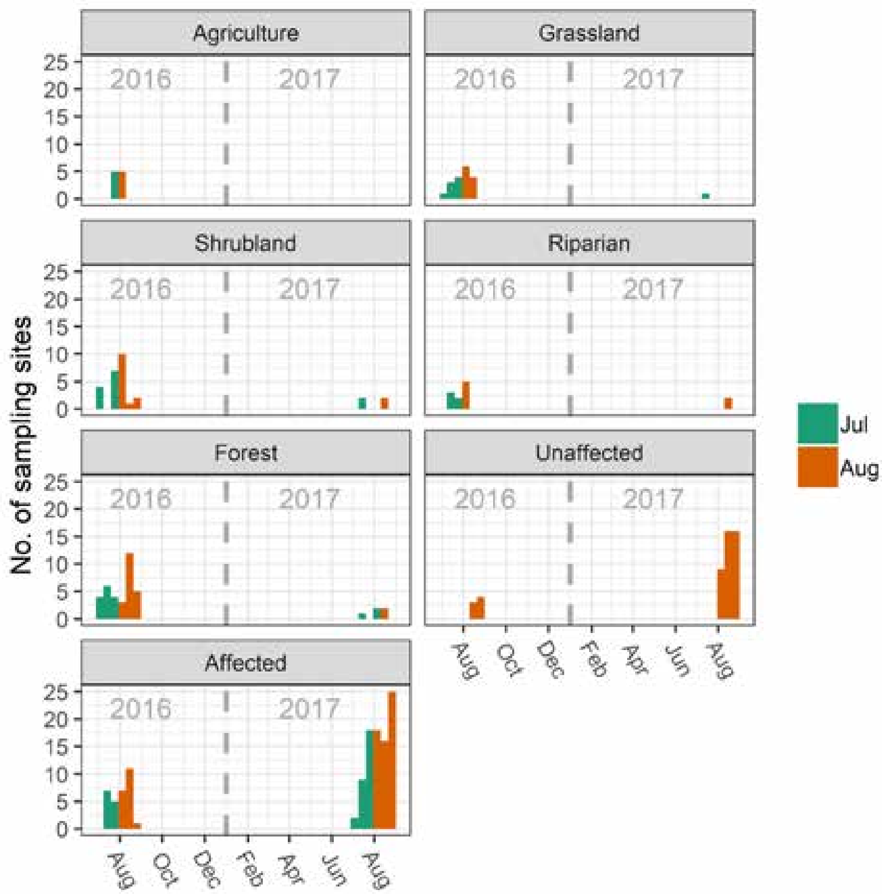

Figure 25 – Frequency distribution of vegetation sampling sites across time in each landcover class for the Elkhorn and Little Belt study areas in west-central Montana, USA, 2016 – 2017.

Table 10 – Summary of precipitation (mm), temperature (°C), and snow water equivalent (SWE; mm) for each season (winter: December – June; summer: July – August) and sampling year averaged across multiple SNOTEL sensors in the Elkhorn, Little Belt, North Sapphire, and Southern Bitterroot study areas in west-central Montana, USA.

		Winter						Summer			
		Precip.		Temp.		SWE		Precip.		Temp.	
Study area	Year	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Elkhorn	2016	455.7	56.7	1.4	1.5	258.0	100.4	81.0	11.1	13.0	1.3
Elkhorn	2017	463.7	71.0	-0.2	1.4	263.3	104.6	14.7	18.2	15.4	1.2
Little Belts	2017	495.5	77.1	-1.1	0.4	231.0	86.3	15.5	2.1	15.1	0.2
N. Sapphire	2014	674.0	192.3	-0.5	1.2	619.5	244.0	95.0	25.5	14.1	1.1
N. Sapphire	2015	429.5	157.7	2.1	1.0	345.5	187.4	54.0	31.1	13.6	1.2
S. Bitterroot	2012	632.0	64.5	0.1	1.1	492.7	150.9	37.3	19.2	15.8	0.5
S. Bitterroot	2013	493.7	22.7	0.1	1.4	397.0	149.0	32.3	4.0	16.3	0.9

Summary of general landcover classes

Within agricultural areas, the most common forage species included *Poa pratensis* (n = 5 plots). Within grasslands, the most common forage species included *Artemisia frigida* (n = 13), *Festuca idahoensis* (n = 10), and *Poa secunda* (n = 7). Within shrublands, the most common forage species included *Festuca idahoensis* (n = 21), *Artemisia frigida* (n = 20), and *Astragalus* spp. (n = 13). Within riparian areas, the most common species included *Equisetum arvense* (n = 1) and *Poa pratensis* (n = 1). Within forests, the most common species included *Festuca idahoensis* (n = 20), *Carex geyerii* (n = 17), and *Calamagrostis rubescens* (n = 11).

Mean forage abundance, cover, and species richness varied by lifeform and landcover class (Table 11; Figure 26 – Figure 28). Herbaceous forage abundance was highest and most variable in riparian areas and lowest and least variable in forests (Figure 26). Shrub forage abundance was highest and most variable in forests and lowest and least variable in

Table 11 – Summary of forage abundance (g/m²), cover (%), and species richness (no. of species) of lifeforms for each cover class estimated from sampling sites during late summer (July – August) in the Elkhorn Mountains of west-central Montana, USA, 2016 – 2017.

		Agriculture		Forest		Grassland		Riparian		Shrubland	
Metric	Lifeform	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Abundance	Herb.	11.10	14.43	7.40	10.99	17.79	36.61	49.90	52.71	14.65	21.86
	Shrub	0.00	0.00	5.47	10.45	1.57	2.26	0.26	0.89	1.59	3.48
Cover	Forb	0.74	2.34	0.44	1.12	1.56	3.34	1.90	6.33	1.66	2.76
	Gram.	9.00	12.57	10.69	12.92	15.04	19.58	33.70	27.09	11.58	12.02
	Shrub	0.02	0.06	7.86	12.85	2.41	3.14	0.58	2.02	1.49	2.27
Species richness	Herb.	0.90	1.10	2.15	1.11	2.53	1.84	2.58	1.44	2.46	1.48
	Shrub	0.10	0.32	0.59	0.55	0.68	0.48	0.08	0.29	0.71	0.46

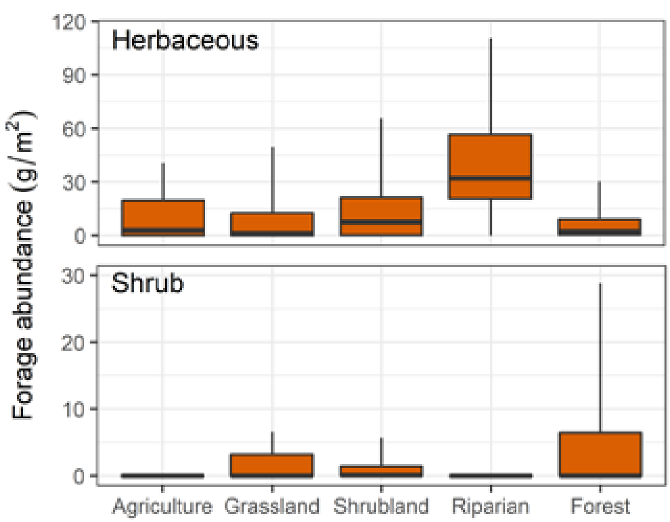

Figure 26 – Summary of mean herbaceous and shrub forage abundance (g/m²) estimated at sampling sites during late summer (July – August) for each cover class in the Elkhorn Mountains of west-central Montana, USA, 2016 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value. Note different y-axis scales.

agricultural areas. Forb and graminoid forage cover were highest and most variable in riparian areas (Figure 27). Forb forage cover was lowest and least variable in forests, and graminoid forage cover was lowest and least variable in agricultural areas. Shrub forage cover was highest and most variable in forests and lowest and least variable in agricultural areas. Herbaceous forage species richness was highest in riparian areas and lowest in agricultural areas (Figure 28). Herbaceous forage species richness was most variable in grasslands and least variable in agricultural areas. Shrub forage species richness was highest in shrubland and lowest in agricultural areas. Shrub forage species richness was most variable in forests and least variable in agricultural areas.

Forests were generally associated with low levels of herbaceous forage abundance and forage cover, but had the highest shrub forage abundance and forage cover relative to other landcover classes. Agricultural areas had only slightly higher levels of herbaceous forage abundance and forage cover than forests. Estimates of forage in grasslands and shrublands were generally similar within each forage metric and lifeform and were associated with moderate levels of forage relative to other landcover classes. Forb forage cover was highest in these landcover classes, but only modestly. Riparian areas had the highest herbaceous forage abundance, graminoid forage cover, and herbaceous forage species richness. All riparian sampling sites were located in higher elevation, montane areas, and therefore do not represent valley bottom riparian areas.

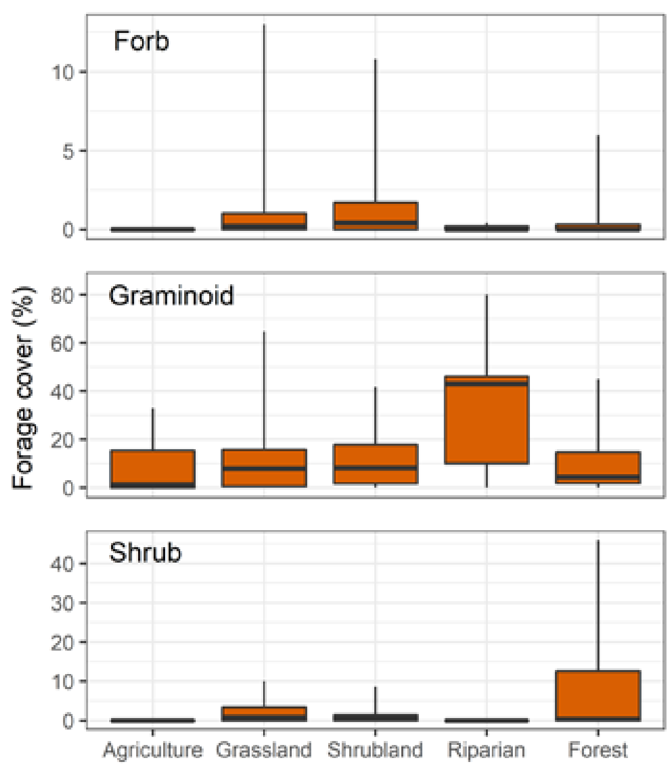

Figure 27 – Summary of mean forb, graminoid, and shrub forage cover (%) estimated from sampling sites during late summer (July – August) for each cover class in the Elkhorn Mountains of west-central Montana, USA, 2016 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value. Note different y-axis scales.

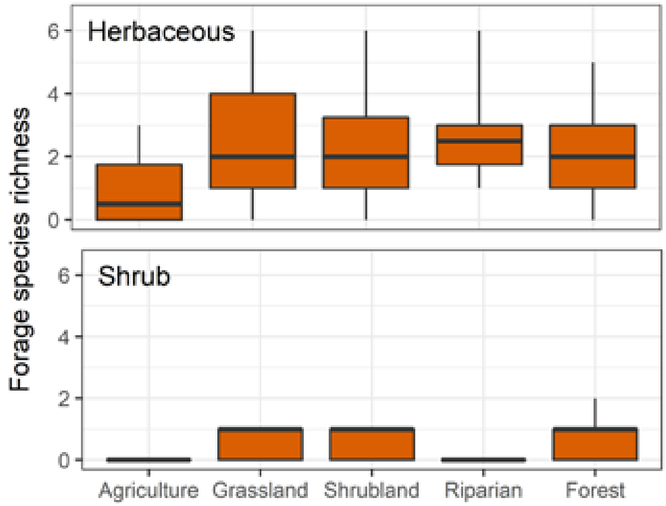

Figure 28 – Summary of herbaceous and shrub forage species richness (total number of forage species) measured at sampling sites during late summer (July – August) within each cover class in the Elkhorn Mountains of west-central Montana, USA, 2016 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value.

Due to the majority of sampling of the general landcover classes (i.e., agriculture, grassland, shrubland, riparian, and forest) occurring in 2016, estimates of forage metrics do not capture annual variation but are representative of years with similar weather (Table 10).

Summary of MPB infestation classes

Within areas unaffected by the MPB infestation, the most common forage species included *Vaccinium scoparium* (n = 43), *Vaccinium membranaceum* (n = 34), and *Carex geyerii* (n = 28). Within areas affected by the MPB infestation, the most common forage species included *Vaccinium scoparium* (n = 76), *Carex geyerii* (n = 67), and *Calamagrostis rubescens* (n = 57).

Mean forage abundance, forage cover, forage species richness, herbaceous quality, and canopy cover varied by lifeform, MPB infestation class, year, and study area (Table 12; Figure 29 – Figure 33). Herbaceous forage abundance was highest and most variable in affected areas across both years and study areas. Shrub forage abundance was highest in unaffected areas during 2017 across both study areas but highest in affected areas during 2016. Forb forage cover was highest and most variable in unaffected areas during 2016 but highest and most variable in affected areas during 2017 across both study areas. Graminoid forage cover was highest and most variable in affected areas across both years and study areas. Shrub forage cover was highest and most variable in affected areas across both years in the Elkhorn study area but highest and most variable in unaffected areas in the Little Belt study area. Herbaceous forage species richness was highest and most variable in unaffected areas in 2016 but highest and most variable in affected areas in 2017 across both study areas. Shrub forage species richness was highest in affected areas in the Elkhorn study area and highest in unaffected areas in the Little Belt study area.

Herbaceous quality was estimated from 18 unaffected (5 and 3 in the Elkhorn study area during 2016 and 2017, respectively, and 10 in the Little Belt study area) and 55 affected (26 and 29 in the Elkhorn study area during 2016 and 2017, respectively) sampling sites. Herbaceous quality was highest and most variable in affected areas during both years in the Elkhorn study area and highest and most variable in unaffected areas in the Little Belt study area. Overstory canopy cover was highest in unaffected areas during 2016 and highest in affected areas during 2017 in the Elkhorn and Little Belt study areas.

In both the Elkhorn (2016 and 2017 combined) and Little Belt study areas, herbaceous forage abundance slightly increased from the unaffected to affected class; however, values were generally similar across classes (Figure 29). In the Elkhorn study area, both shrub forage abundance and cover increased from unaffected to affected classes (Figure 30). In the Little Belt study area shrub forage abundance and cover decreased from unaffected to affected classes. In both the Elkhorn and Little Belt study areas, forb forage cover was generally similar and low across infestation classes, whereas graminoid forage cover showed a slight increase from unaffected to affected classes. In the Elkhorn study area, herbaceous forage species richness decreased from the unaffected to affected class, whereas in the Little Belt study area, herbaceous forage species richness increased from the unaffected to affected class (Figure 31). From the unaffected to affected class, shrub forage species richness increased in the Elkhorn study area and decreased in the Little Belt

Table 12– Summary of forage abundance (g/m^2), forage cover (%), forage species richness (number of species), herbaceous quality (DE [digestible energy]; kcal/g), and overstory canopy cover (%) within each mountain pine beetle (MPB) infestation class estimated from vegetation sampling sites during late summer (July – August) in the Elkhorn and Little Belt study areas of west-central Montana, USA, 2016 – 2017.

			Elkhorn				Little Belt	
			2016		2017		2017	
Metric	Lifeform	MPB Class	Mean	SD	Mean	SD	Mean	SD
Forage abundance	Herb.	Unaffected	6.3	6.1	0.0	0.0	8.1	10.9
		Affected	6.8	12.9	7.3	14.3	13.5	14.3
	Shrub	Unaffected	2.8	5.1	14.5	12.5	22.8	21.6
		Affected	11.9	15.9	12.5	16.0	9.0	12.7
Forage cover	Forb	Unaffected	3.2	4.7	0.0	0.0	0.9	2.8
		Affected	0.6	1.6	0.5	1.4	2.0	4.1
	Gram.	Unaffected	7.7	11.5	0.0	0.0	9.7	7.6
		Affected	14.3	18.0	11.6	16.6	15.9	10.9
	Shrub	Unaffected	9.0	13.9	16.0	6.2	31.1	16.0
		Affected	20.8	20.9	17.7	18.7	12.8	12.0
Forage spp. richness	Herb.	Unaffected	2.9	2.3	0.0	0.0	1.5	0.8
		Affected	1.7	1.3	1.5	1.0	2.3	1.4
	Shrub	Unaffected	0.7	0.8	1.0	0.0	1.9	0.3
		Affected	1.0	0.5	1.1	0.6	1.4	0.8
Quality (DE)	Herb.	Unaffected	3.19	0.11	2.99	0.05	3.32	0.09
		Affected	3.24	0.15	3.21	0.15	--	--
Canopy cover		Unaffected	76.5	20.7	3.2	1.1	16.4	10.3
		Affected	49.6	17.5	23.4	15.0	18.7	18.7

study area. Herbaceous forage quality increased from the unaffected to affected class in the Elkhorn study area. The Little Belt study area averaged higher in herbaceous forage quality in the unaffected class than in the Elkhorn study area (Figure 32). From the unaffected to affected class, overstory canopy cover decreased in the Elkhorn study area and increased in the Little Belt study area (Figure 33).

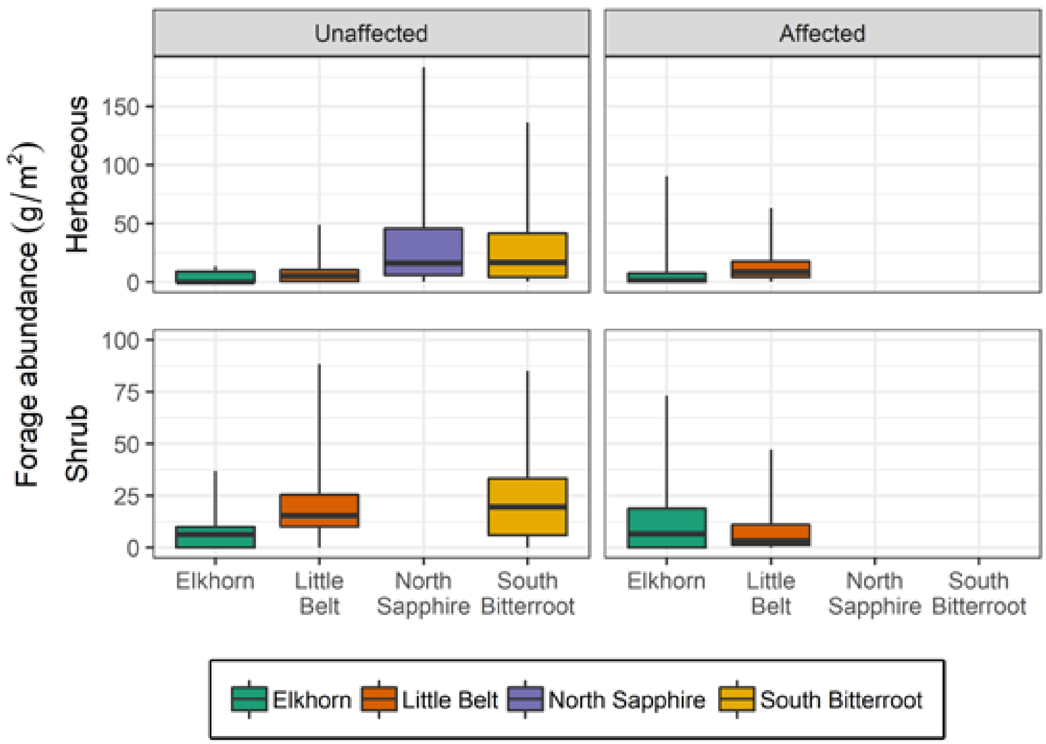

Figure 29 – Mean herbaceous and shrub forage abundance (g/m²) estimated from sampling sites during late summer (July – August) for each mountain pine beetle infestation class in the Elkhorn, Little Belt, North Sapphire, and Southern Bitterroot study areas of west-central Montana, USA, 2012 – 2017. Shrub abundance was not estimated for the North Sapphire study area due to imprecision in estimates. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value. Note different y-axis scales.

Herbaceous forage abundance in unaffected areas in the Elkhorn (2016 and 2017 combined) and Little Belt study areas averaged lower and varied less than in the North Sapphire and South Bitterroot study areas (Figure 29). In unaffected areas, mean shrub forage abundance in the Elkhorn study area was lower than and in the Little Belt study area was similar to the South Bitterroot study area. Forb forage cover in unaffected areas in the Elkhorn and Little Belt study areas averaged lower and varied less than in the North Sapphire and South Bitterroot study areas (Figure 30). Graminoid forage cover in unaffected areas averaged similarly between the Elkhorn and North Sapphire study areas and between the Little Belt and South Bitterroot study areas, with the former study areas averaging lower and varying less. Shrub forage cover in unaffected areas averaged similarly in the Little Belt, North Sapphire, and South Bitterroot study areas, and lower in the Elkhorn study area. Herbaceous forage species richness in unaffected areas averaged lower in the Elkhorn and Little Belt study areas than in the North Sapphire and South Bitterroot study areas (Figure 31). Shrub forage species richness in unaffected areas averaged highest in the Little Belt study area and lowest in the Elkhorn study area.

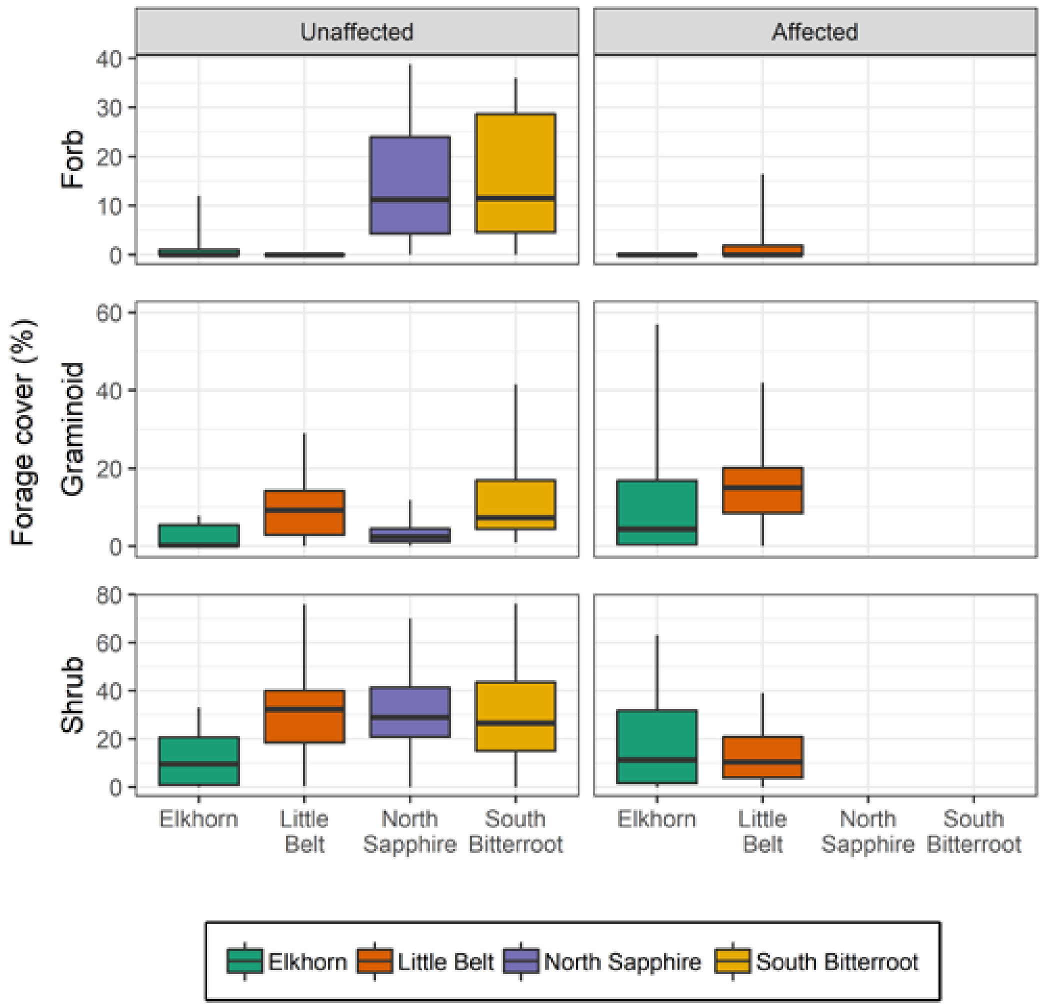

Figure 30 – Mean forb, graminoid, and shrub forage cover (%) estimated from sampling sites during late summer (July – August) for each mountain pine beetle infestation class in the Elkhorn, Little Belt, North Sapphire, and Southern Bitterroot study areas of west-central Montana, USA, 2012 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value. Note different y-axis scales.

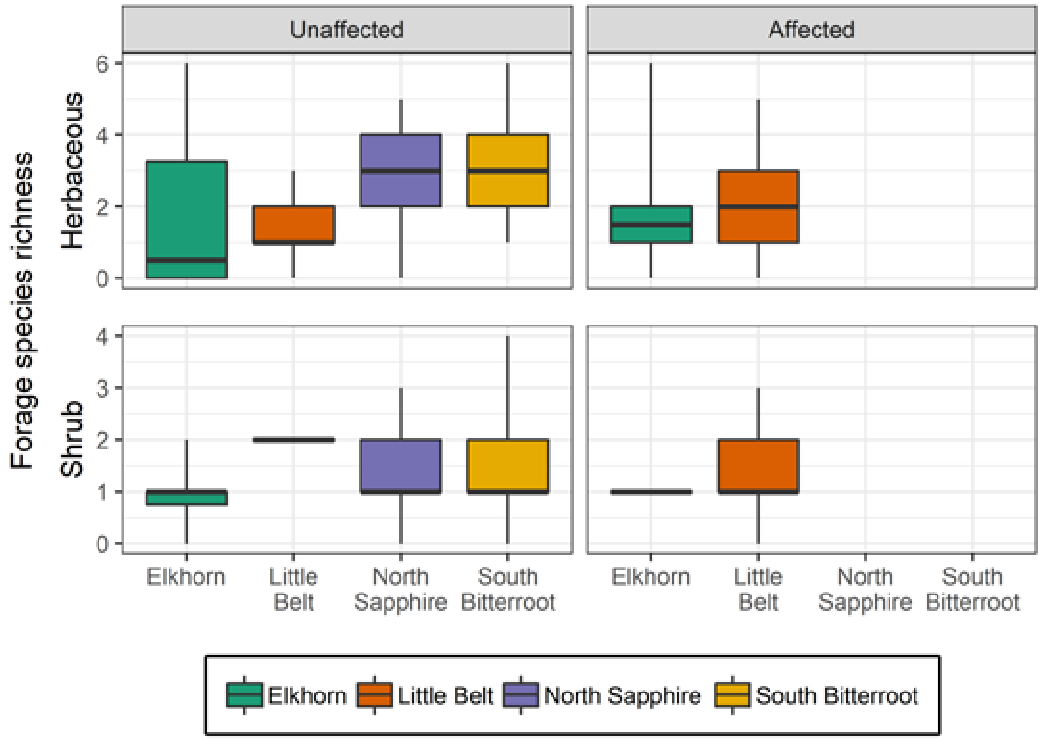

Figure 31 – Herbaceous and shrub forage species richness (total number of species) measured at sampling sites during late summer (July – August) for each mountain pine beetle infestation class in the Elkhorn, Little Belt, North Sapphire, and Southern Bitterroot study areas of west-central Montana, USA, 2012 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value. Note different y-axis scales.

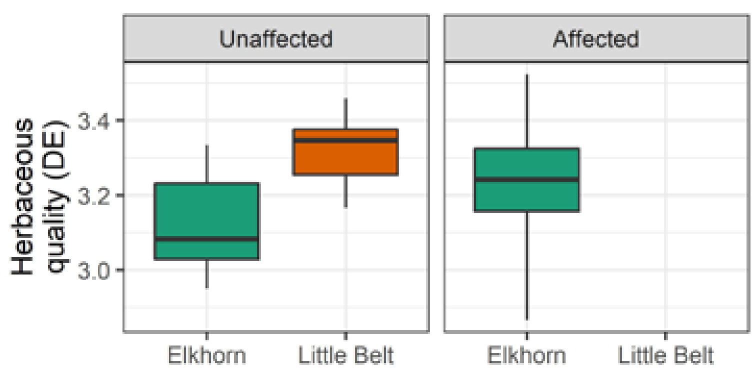

Figure 32– Herbaceous quality (DE [digestible energy]; kcal/g) measured at a sample of sampling sites during late summer (July – August) for each mountain pine beetle infestation class in the Elkhorn and Little Belt study areas of west-central Montana, USA, 2016 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value.

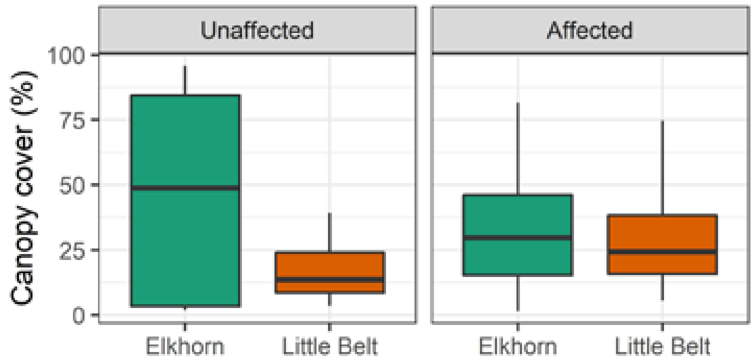

Figure 33– Overstory canopy cover (%) measured at sampling sites during late summer (July – August) for each mountain pine beetle infestation class in the Elkhorn and Little Belt study areas of west-central Montana, USA, 2016 – 2017. Box-and-whisker plots represent the minimum, first quartile, median, third quartile, and maximum value.

Discussion

We found modest variation in measurements of late summer elk forage (i.e., forage abundance, cover, and species richness) across landcover classes in the Elkhorn study area (Table 11; Figure 26 – Figure 28). Generally, the most abundant and species-diverse herbaceous forage occurred in riparian areas followed by grasslands and shrublands, with forage graminoids comprising the majority of the understory cover in all landcover classes. Forests had the lowest forage abundance but higher levels of forage cover and forage species richness than agricultural areas. Levels of forage in agricultural areas may be under-estimated, however, due to Medicago sativa (alfalfa) being excluded from species considered as forage (i.e., ranked 95.5% in the cumulative diet; Table 6) and recorded at only 1 sampling site. Levels of shrub forage were relatively insubstantial across the landcover classes but are likely not as important as herbaceous forage given that shrubs comprise a small portion of the elk late summer diet. We caution, however, that our results are primarily representative of climate conditions during 2016, given the substantially larger sampling effort during this year as compared to 2017 (Table 8; Figure 25). The Elkhorn study area experienced below average SWE and total (winter and summer) precipitation during both years of sampling, with lower SWE and precipitation experienced in 2017 (Table 9 – Table 10).

We found modest variation in forage metrics and overstory canopy cover between MPB infestation classes of lodgepole pine forest. Generally, levels of herbaceous forage abundance, forage cover, forage species richness, and quality increased and shrub forage abundance and forage species richness decreased from the unaffected to affected class. Overstory canopy cover generally decreased from the unaffected to affected class, although we found large variation in unaffected areas in the Elkhorn study area. The increase in herbaceous forage is likely due to the opening of the forest canopy. Understanding the effect of MPB infestation on elk forage in the Elkhorn study area, however, is hindered by the small sample size of unaffected sites in the Elkhorn study area from which to make direct within study area comparisons. The sampling in the Little Belt study area was intended to bolster sample size and improve inference of forage characteristics in mature unaffected lodgepole pine forests. The Little Belt study area occasionally differed in patterns of forage across the infestation classes as compared to the Elkhorn study area, even within the same year, likely indicating sample sizes are insufficient or the Little Belt study area is not representative of forage conditions typified in the Elkhorn study area. The Little Belt study area received greater annual average SWE and precipitation (Table 9) and averaged lower in elevation and slope than the Elkhorn study area, supporting the latter. Notwithstanding consideration of the Little Belt study area, caution should be made when interpreting the effect of MPB infestation on elk forage in the Elkhorn study area given the small sample size of the unaffected class.

Lastly, we found that the Elkhorn study area generally had lower levels of forage abundance, cover, and diversity in unaffected areas as compared to the North Sapphire and South Bitterroot study areas. These differences may be explained by the North Sapphire and South Bitterroot study areas averaging lower in elevation and greater in annual average and year-of-sampling SWE and precipitation. Given the climatic and topographic differences between these study areas and the Elkhorn study area, considering forage conditions in unaffected areas in the North Sapphire and South Bitterroot as representative of unaffected sites for further comparison with affected areas in the Elkhorn study area is likely not reasonable.

Section 5 – Effects of Mountain Pine Beetle on Elk Habitat Use

Introduction

Understanding the effect of MPB outbreaks is critical to land and wildlife managers tasked with promoting and conserving wildlife populations where widespread tree mortality has drastically altered historic forest structure, vegetation communities, and nutrient flow (Chan-McLeod 2006). While such changes can have profound effects on wildlife and are well studied when associated with other natural or managed disturbances (e.g., wildfire, prescribed fire, and timber management), little is known about wildlife responses to large-scale insect outbreaks (Martin et al. 2006, Saab et al. 2014, Lamont et al. 2019). Wildlife responses to MPB outbreaks are dynamic and complex, and can vary by taxa, sex, season, and the outbreak successional stage (Saab et al. 2014). Changes to forest structure and vegetation associated with MPB outbreaks are well documented and follow three principle successional stages: 1) standing dead trees with needles, 2) standing dead trees without needles after defoliation, and 3) blowdown of dead trees (Chan-McLeod 2006).

Assessing the impact of natural disturbances on wildlife is often limited by the lack of pre-disturbance data. Indeed, collecting pre- and post-disturbance datasets is complicated by the spatial and temporal unpredictability of natural disturbances. The Elkhorn Mountains study region provides a rare opportunity to study elk habitat use pre- and post-MBP-infestation. The region was first designated as a Wildlife Management Unit (WMU) by the U.S. Forest Service (USFS) in the mid-1980's and has remained a popular elk hunting district, especially for mature bulls. In conjunction with the WMU designation, Montana Fish, Wildlife & Parks (MFWP) initiated a long-term elk study spanning 1981 to 1992 and instrumented 323 individual elk (male = 180, female = 143) with VHF (very high frequency) collars over the 11-year period. MPB outbreaks in the Elkhorn Mountains began in the early 2000's, peaked in 2009, and affected approximately 190 km^2 of pine forests (see *Mountain pine beetle infestation* in *Section 2 – Study Area*). Following the MPB outbreaks, MFWP and partners initiated the Elkhorn Mountains Elk Project to provide managers and interested public with information and recommendations for managing elk habitat in areas impacted by MPB infestations and identify what types of habitat enhancement projects may benefit elk occupying areas affected by MPB infestations. This information may also be useful in helping to guide future harvest regulation recommendations. As part of this effort MFWP instrumented 60 individual elk (male = 25, female = 35) with GPS collars to collect movement and habitat use data (see *Section 3 – Elk Capture, Sampling, Survival, & Distributions*).

Our primary objective was to characterize changes in elk habitat use patterns between the pre- and post-MPB-infestation periods. We were specifically interested in changes in use of areas that were affected by MPB, as well as other general landcover classes and public and private lands. We characterized changes in habitat use patterns separately for males and females and for the winter, spring, summer, archery, and rifle seasons.

Methods

Pre- and post-MPB infestation

There was a total of 323 individuals (male = 180, female = 143) instrumented with VHF collars between 1981 and 1992 (i.e., pre-MPB). Collared individuals were relocated at approximately 3-week intervals, resulting in a total of 11,557 locations. Individuals were monitored for an average of 23.1 (± 18.9 SD) months with an average of 35.8 (± 32.7) locations per individual. Between 2015 and 2017 (i.e., post-MPB), 59 individuals (male = 24, female = 35) were instrumented with GPS collars which collected a total of 41,067 GPS locations after censoring locations with a DOP > 10 (D'Eon and Delparte 2005). An additional male was captured in 2015 but died from predation prior to the collection of locations by the GPS collar. There was an average of 696 (± 426) locations collected from each individual over an average of 22.1 (± 11.7) months. To match the daytime sampling of the VHF aerial monitoring we subset both location datasets to the daylight hours between 0700 and 1500 hours, resulting in 8,962 VHF and 11,806 GPS locations. The spatial extent of the VHF and GPS datasets broadly overlapped each other and the MPB-affected areas within the Elkhorn Mountains (Figure 34).

Areas affected by mountain pine beetles

The USFS conducted annual Insect and Disease Detection Surveys from 1997 to 2017 and delineated areas affected by MPB, as observed by tree canopy discoloration. The surveys did not track forest patches through time to document transitions between successional

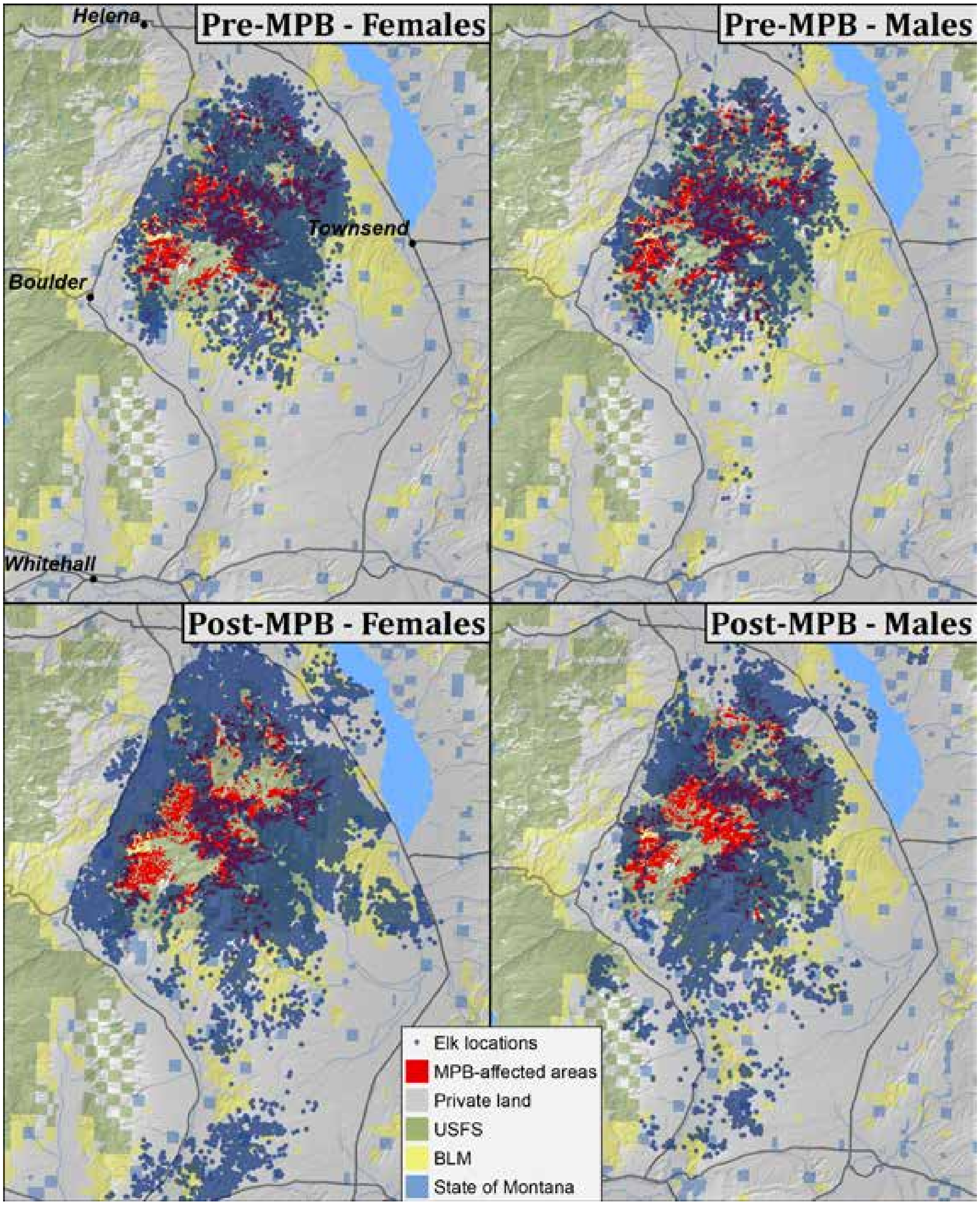

Figure 34 – Pre- and post-mountain pine beetle (MPB) locations for male and female elk (blue) overlain MPB affected areas within the Elkhorn Mountain study area in west-central Montana, USA, 1981 – 1992 and 2015 – 2017.

stages post-MPB-infestation. However, the majority of the pine forest in the Elkhorn Mountains was infested between 2007 – 2009, 7 years prior to the beginning of the post-MPB study in 2015. Although the transition from standing dead to downfall is often spatially and temporally variable, most of the affected areas within the Elkhorn Mountains have not passed the threshold typical of transitioning to downfall observed in other MPB-killed forests (Chan-McLeod 2006). Assuming 3 and10 years since infestation as the temporal transitions from standing dead with needles to standing dead without needles and then to downfall (Lewis and Hartley 2005, Chan-McLeod 2006), there was little downfall in the Elkhorn Mountains during the post-MPB study (Figure 35). Consequently, we did not delineate between the three transitional classes when contrasting elk habitat use pre- and post-MPB-infestation. Rather, we pooled all affected areas under a single classification which contained mostly standing dead trees without needles. Lastly, annual survey polygons of MPB affected areas tended to aggregate across landcover classes and included landcover classes where no MPB tree mortality occurred such as meadows and fir forests, which were patchily distributed across the landscape. We subset the annual MPB polygons to include only the areas that overlapped the PICO (*Pinus contorta*; i.e., dominated by lodgepole) and PICO-IMIX (i.e., dominated by a mix of lodgepole and shade-intolerant species) VMap landcover classifications to more explicitly depict lodgepole pine forests affected by MPB (see *Appendix A – Development & Accuracy of Landcover Classifications*).

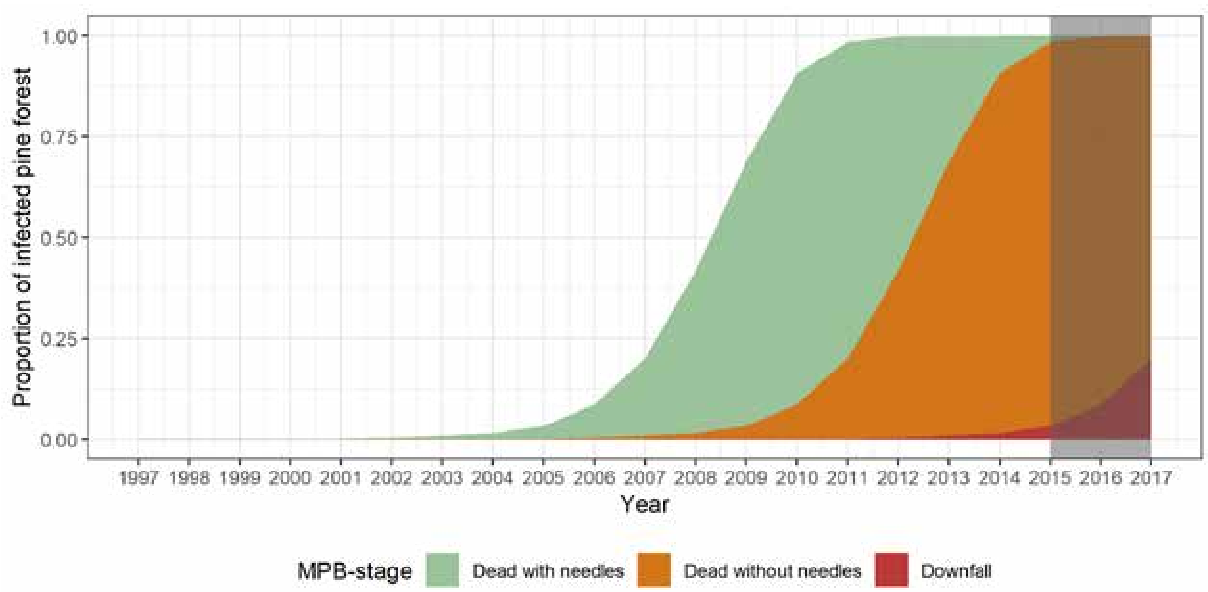

Figure 35 – Cumulative proportion of the forest successional stages after mountain pine beetle (MPB) infestation within the Elkhorn Mountain study area in west-central Montana, USA, 1997-2017. The grey shaded region denotes the post-MPB study period from 2015-2017.

Comparison of pre- and post-MPB-infestation habitat use by elk

We used the proportion of GPS and VHF locations (proportional use) as our measure of habitat use to accommodate the varying sample sizes among study periods (i.e., pre- and post-MPB), sexes, and seasons. Seasons included spring, summer, archery hunting season, rifle hunting season, and winter. We defined spring (i.e., calving) as May 20 – June 15, summer as July 1 to 1 week prior to the opening of archery season, and winter as 1 week after the close of rifle season to May 1. We defined the archery and rifle hunting seasons according to historic and current annual Montana general elk archery and rifle season dates, where the 6-week archery season starts on the 1st Saturday in September and the 5-week rifle season starts 5 weeks prior to the Saturday after Thanksgiving. We characterized the proportional use of MPB-affected areas, general landcover classes, and public and private land ownership pre- and post-MPB-infestation. Non-MPB-affected landcover classes were aggregated from classifications identified in the study area (see *Appendix A – Development & Accuracy of Landcover Classifications*) and included agriculture (i.e., cultivated and other agriculture), grassland, shrubland, riparian (i.e., valley and upland wetland riparian), and forest (i.e., low and high elevation conifer). In all instances, the VHF locations characterized habitat use prior to MPB-infestation and the GPS locations characterized habitat use post-MPB-infestation. We generated separate comparisons for each sex-season grouping.

Results

There was an average reduction in the proportional use of MPB-affected areas of 11% (± 7.2% SD) from the pre- to post-MPB-infestation study periods across both sexes and all seasons. The reduction in use of affected forests was more pronounced for females than for males, which had respective average reductions of 13.6% (± 6%) and 8.9% (± 8.3%). Among the sex-season groupings, the reduced use of affected forests was variable but most pronounced during the summer and archery seasons for females and the archery and rifle seasons for males (Figure 36). The winter season had the least proportional change for both sexes and was characterized by a slight increase in use for males.

Table 13 – Proportional use of the general landcover classes for the GPS and VHF datasets pooled across sexes and seasons in the Elkhorn Mountain study area, west-central Montana, USA, 1981-1992 and 2015-2017. Landcover classes are listed from least to most used within each data type.

Study period	Landcover class	Proportion
Pre-MPB	Agriculture	0.0004
	Riparian	0.0137
	Non-habitat	0.0179
	Shrubland	0.1064
	Grass	0.3037
	Forest	0.5579
Post-MPB	Non-habitat	0.0057
	Agriculture	0.0130
	Riparian	0.0285
	Shrubland	0.1222
	Grass	0.3638
	Forest	0.4669

Excluding the affected areas as a landcover classification, intact conifer forests were the most used landcover class pre- and post-MPB-infestation (Table 13). When pooled across sexes and seasons, 56% and 47% of the pre- and post-MPB locations, respectively, were within intact conifer forests. Grasslands and shrublands were the 2nd and 3rd most used landcover class in both the pre- and post-MPB-infestation periods. When partitioned into sex-season groupings, we observed only slight differences in use patterns from the pre- to post-MPB-infestation period (Figure 37). During the post-infestation period, females showed increase use of grasslands in all seasons which was offset by a reduction in the use of forested areas, although the magnitudes varied by season. Males had a similar trend towards increasing use of grasslands in the archery and rifle seasons during the post-infestation period, although to a lesser extent than females.

We observed an increase in the use of private lands from the pre- to post-MPB-infestation study periods with 17% and 43% of the pre- and post-MPB locations occurring on private lands, respectively. The general trends were largely driven by females which showed a decrease in use of public lands in all seasons (Figure 38). Males had a similar trend, but the different use patterns were less notable. Across all seasons there was an average of a 30% (± 3.9%) reduction in the number of locations that occurred on public lands from the pre-MPB-infestation to post-MPB-infestation periods for females and a 12% (± 6.7%) reduction for males.

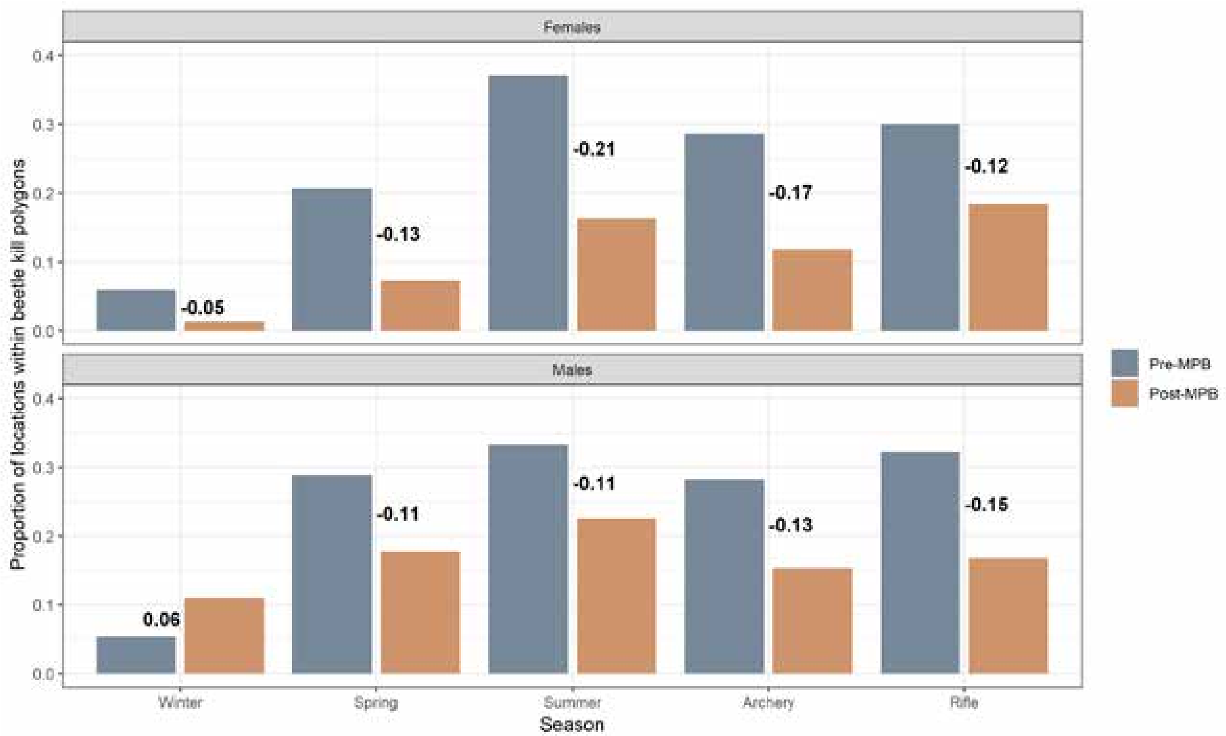

Figure 36 – Proportional use of areas affected by mountain pine beetle (MPB) between the pre- and post-MPB study periods for the sex-season groupings within the Elkhorn Mountain study area in west-central Montana, USA, 1981-1992 and 2015-2017.

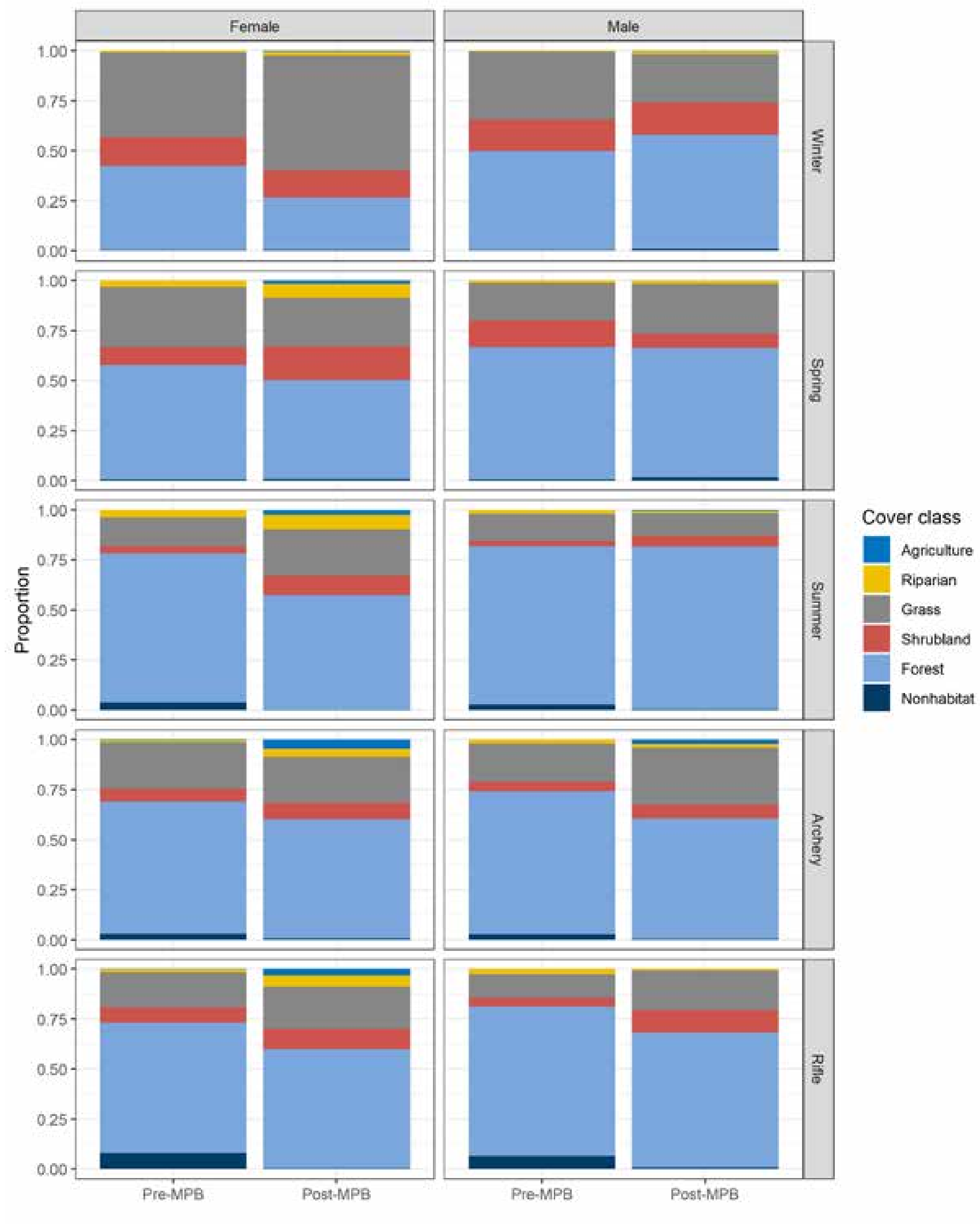

Figure 37 – Cumulative proportional use of the general landcover classifications other than lodgepole pine affected by mountain pine beetle (MPB) within the Elkhorn Mountain study area in west-central Montana, USA, 1981-1992 and 2015-2017. Elk sex is delineated across the columns and the 5 season are delineated down the rows.

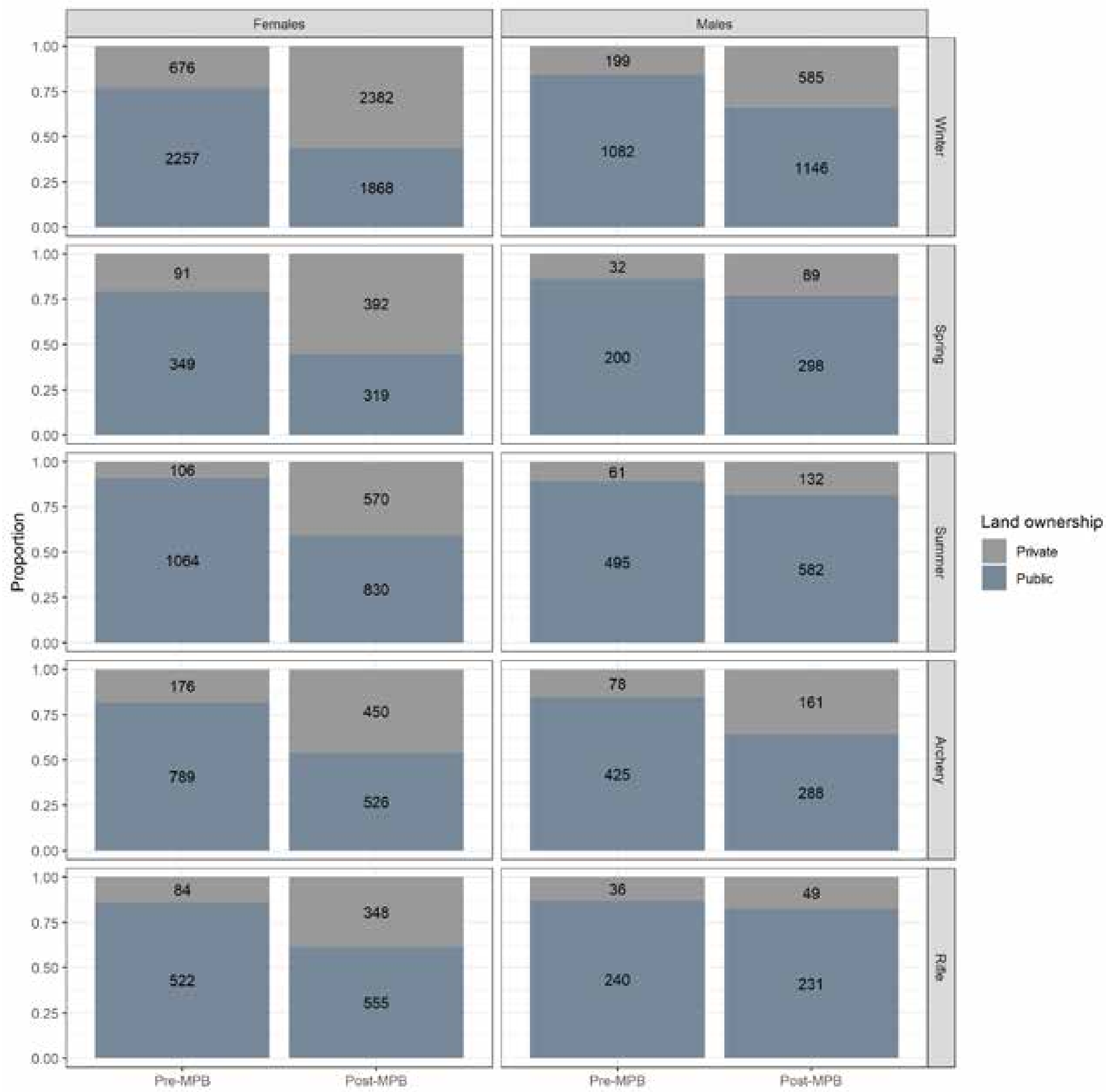

Figure 38 – Changes in the proportion of elk locations within public and private lands between the pre- and post-mountain pine beetle (MPB) study periods, Elkhorn Mountain study area, west-central Montana, USA, 1981-1992 and 2015-2017. The sample size for each group is shown in the center of each barplot.

Discussion

Our results show a reduction in use of areas affected by MPB between the pre- and post-MPB-infestation study periods in the Elkhorn Mountains. The pattern was consistent for both sexes and in all seasons apart from males in winter but was more pronounced for females than for males. Although the use of intact conifer forests showed a slight decline post-MPB-infestation which was offset by increased use of grasslands, the use of intact conifer forests remained relatively high post-MPB-infestation for all sex-season groupings with the exception of females in winter (Figure 37). The differing responses to MPB-affected and intact conifer forests between the pre- and post-MPB-infestation periods may be explained through the loss of thermal cover post-defoliation in affected forests. Recent work by Lamont et al. (2019) in south-central Wyoming documented avoidance of MPB-killed forests by elk during all parts of the day in summer while intact conifer forests were strongly selected for during the daylight hours, presumably for thermal cover. While we were not able to characterize hourly patterns of use with the temporal resolution of our data, the decreased use of MPB-affected areas may result from the loss of thermal cover after defoliation (Lamont et al. 2019). Given the timeframe between the MPB infestation and our post-MPB study, the loss of needles is likely the primary change in forest structure currently affecting elk habitat use in the Elkhorn Mountain study area. However, as MPB-affected forests transition to blowdown we expect the relationship with elk use may change, potentially resulting in increased use of affected areas due to the increased security offered by the down trees, or continued avoidance due to the increase in locomotion costs required to navigate the fallen timber.

We observed an increase in the use of private lands over the 40 years between the pre- and post-MPB study periods that was congruent with the changing use patterns with respect to MPB infestation and general landcover classes. We were unable to characterize or quantify the changes in private parcel ownership, changing views of elk hunting and elk tolerance, or changes in land use practices on private lands in the study area. Regionally, public hunting access and opportunity on private lands has been greatly reduced (Haggerty and Travis 2006). Changes in land use and increased security from harvest on private lands has resulted in a broad redistribution of elk from public to private lands through changes in resource selection (Proffitt et al. 2013) and migratory behaviors (Barker et al. 2019).

Within the Elkhorn Mountains, much of the public lands are forested and contain the majority of the MPB-affected areas. Consequently, the broad redistribution of elk from public to private lands that is associated with changing perceptions of elk tolerance may mask the response to MPB infestation. For example, both changes in land use on private lands and MPB infestation on public forested lands have the potential to result in decreased use of forested areas which are predominantly public, receive increased hunter pressure, and have been affected by MPBs. While our results indicated a decrease in use of lodgepole pine forests after MPB-infestation which is consistent with recent studies (i.e., Lamont et al. 2019), we were unable to disentangle the confounding effects associated with changing private land use and the broad redistribution of elk to private lands regionally. While we cannot rule out a MPB effect, we are not able to attribute the changes in landscape use to MPB alone. Rather, we suspect that both the MPB infestation and reduced willingness of private land owners to allow public access for hunting are working in tandem to influence changes in elk land use patterns between the pre- and post-MPB study periods in the Elkhorn Mountains.

Section 6 – Male & Female Elk Security during the Fall Hunting Seasons

Introduction

Understanding the effect of MPB outbreaks is critical to land and wildlife managers tasked with promoting and conserving wildlife populations where widespread tree mortality has altered wildlife-habitat relationships through changes to forest structure, vegetation communities, and nutrient flow (Chan-McLeod 2006). Elk management on public lands has traditionally focused on providing adequate cover and forage while minimizing motorized routes as the dominate attributes of habitat quality (Hillis et al. 1991, Lyon and Canfield 1991). The management goals with this paradigm are to provide security areas to increase elk survival during the hunting seasons and to maintain elk presence on public lands to promote hunter opportunity (Hillis et al. 1991). However, the traditional management paradigm has been complicated by changes in land use practices and restricted public hunting opportunities on some parcels that are privately owned (Haggerty and Travis 2006). This results in non-hunted parcels that function as security areas but do not follow the traditional management paradigm on public land and challenge management strategies in areas which strive to maintain or reduce elk population sizes through regulated harvest of adult females (Proffitt et al. 2010, 2013).

Providing additional security areas on public lands through policy changes (i.e. road closures) or habitat improvement projects, has been highlighted as an important management objective to retain elk on public lands and reduce the redistribution of elk to private lands with reduced or eliminated hunting opportunity (Proffitt et al. 2013, Ranglack et al. 2017, DeVoe et al. 2019). Although management paradigms have shifted to accommodate changes in land use practices and attitudes towards elk on private lands, managing for security areas on public lands has remained an important management objective (Ranglack et al. 2017). However, the availability of elk security areas with ample canopy cover may be at odds with the increasing prevalence of MPB-killed forests across western North America. The loss of canopy cover is one of the first structural changes in forests post-MPB-infestation and is arguably the biggest change impacting wildlife (Chan-McLeod 2006). While specific management recommendations for security habitat have been set for both patch size and distance to roads (i.e., Hillis et al. 1991), management recommendations for canopy cover have been more varied across the western United States, often relying on general descriptive measures (i.e. 'heavy cover'; Christensen et al. 1993). Although more recent work has provided quantitative recommendations for canopy cover based on a meta-analysis across southwest Montana (Ranglack et al. 2017), the work did not include analyses of forest systems impacted by MPBs. The loss of cover post-MPB-infestation may increase elk vulnerability and require updates to forest management guidelines regarding traditional security measures on public lands to both maintain desired levels of survival and retain elk on public lands during the hunting seasons. Within the context of unprecedented MPB outbreaks throughout western North America forests, understanding how insect outbreaks impact canopy cover with respect to wildlife security is an important management objective.

We used a multipronged approach to characterize the reductions in canopy cover associated with MPB outbreaks and the impact on elk security in the Elkhorn Mountains. This area experienced 80% mortality of lodgepole pine (*Pinus contorta*) forests during a MPB outbreak that peaked in 2008 (see *Mountain pine beetle infestation* in *Section 2 – Study Area*). We characterized canopy cover in MPB-infested areas using a time series spanning pre- and post-MPB outbreak to assess changes in canopy cover through time. We then characterized canopy cover for the dominant forest types in the study area post-MPB outbreak to assess the relative differences in current canopy cover among infested and uninfested forests. For these two components, we expected to observe a decline in canopy cover through time and a general reduction in canopy cover in infested forests relative to uninfested forests. Lastly, we used GPS location data from male and female elk to characterize habitat relationships and security during the archery and rifle hunting seasons. Given the anticipated loss of canopy cover associated with the MPB outbreak, we expected elk to utilize security areas characterized by large roadless areas (i.e., security patches) and rugged terrain, and we expected to observe an increase in selection for covariates associated with the traditional security paradigm for both sexes across the gradient of relative risk associated with the archery and rifle hunting seasons (Ranglack et al. 2017, DeVoe et al. 2019).

Methods

Canopy cover characterizations

We used aircraft survey data collected by the U.S. Department of Agriculture Forest Health Protection Aviation Program to delineate MPB-affected areas as observed by tree canopy discoloration indicating mortality (U.S. Forest Service 2017, 2018). However, the MPB delineations generated from aerial flights did not strictly mirror the patchy mosaic on the landscape and occasionally included grassland meadows or other landcover classifications not affected by MPBs. To reduce the contamination of non-beetle-killed areas, we clipped the polygons delineating MPB-infestations to include only the areas that overlapped with lodgepole pine or lodgepole pine shade-intolerant mixed forest classifications as defined by the Vegetation Mapping Program (VMap; U.S. Forest Service 2014).

We characterized canopy cover in MPB-infested forests using a time series from the Rangeland Analysis Platform (RAP; Jones et al. 2018) spanning 1990–2017, inclusive of the MPB outbreak in the Elkhorn Mountains. The RAP uses a combination of remotely sensed and ground-based data to predict per-pixel (30m by 30m) percent canopy cover across the western United States. Although developed for rangelands, the RAP model is an effective tool for describing changes in canopy cover through time with a fine-scale (annual) time series not available in other canopy cover layers (i.e. LANDFIRE, National Land Cover Database). To assess, changes in canopy cover within MPB-infested forests over time, we characterized the percent change from historic canopy cover levels prior to the MPB outbreak (1990–2000) within the 3 largest MPB polygons in the study area, which totaled 111 km^2 and accounted for nearly 60% of the lodgepole pine forests infested by MPB.

To assess changes in canopy cover between MPB-infested forests and uninfested forests, we summarized the percent canopy cover in infested and uninfested lodgepole pine forests as well as ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forest classifications. In aggregate, these forest types contained 99% of the forested landscape within the study area. We characterized the mean (± SD) percent canopy cover in each forest type using VMap canopy cover estimates from 2013 (U.S. Forest Service 2014). These estimates represented a mean response of canopy cover defoliation associated with MPB outbreaks approximately 5 years after peak infestation and were the most recent estimates for the Elkhorn Mountains post-MPB-infestation. Moreover, the VMap methods used to estimate canopy cover were specifically developed to note changes in canopy cover associated with MPB outbreaks (S. Brown, USFS, personal communication).

Security habitat modeling

During the winters of 2015 and 2017, we captured adult elk and deployed remote-upload GPS collars programmed to transmit 1 location every 23 hours (see *Section 3 – Elk Capture, Sampling, Survival, & Distributions*). Our primary objective was to evaluate the degree to which reductions in canopy cover associated with MPB outbreaks may impact forest management practices on public lands. Accordingly, we focused our security habitat modeling on individuals that remained on public lands during the archery and rifle hunting seasons and censored individuals that primarily occupied private lands with varying levels of hunter access restrictions. We retained in our dataset only individuals that had > 50% of their locations on lands that were open to public hunting (i.e., public lands or private lands enrolled in Montana Fish, Wildlife, and Parks hunter access program). To further target the periods when hunting pressure most strongly influenced elk behavior, we restricted our analyses to the daytime periods when hunting was allowed and censored all nighttime locations. Following regulations for legal hunting times, we defined daytime as starting 0.5 hours prior to sunrise and 0.5 hours after sunset.

We developed separate sex-season resource selection functions using a used-available design (Manly et al. 2002) and generalized linear mixed-effect models with a random intercept for each individual to account for autocorrelation within an individual and unequal sample sizes among individuals (Gillies et al. 2006). Our used dataset was defined by the locations collected from GPS collars while availability was sampled at a 1:15 used to available ratio within each individual's annual minimum convex polygon (MCP). The 1:15 ratio ensured a sufficient sample to avoid numerical integration error and convergence issues given the single location per day fix rates of the deployed GPS collars (Northrup et al. 2013). We characterized resource selection separately for the archery and rifle hunting seasons, which reflected varying degrees of perceived risk from high to low. Following the legal definitions, the archery season was the 6-week period starting on the 1st Saturday in September, and the 5-week rifle season started 5 weeks prior to the Saturday after Thanksgiving.

We evaluated multiple landscape attributes associated with elk security including 3 definitions of security patches, percent canopy cover, and distance to motorized routes (Table 14). Our criteria for defining security patches were based on current USFS security habitat management standards and were defined as contiguous areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route (Hillis et al. 1991). To evaluate the importance of canopy cover in definitions of elk security, the 2 additional security patch covariates included contiguous areas that contained at least 50% coverage of ≥ 15% and 30% canopy cover. In addition to the covariates associated with the traditional management paradigm, we evaluated the importance of terrain covariates associated with security: slope and ruggedness. For ruggedness we used the Vector Ruggedness Measure (VRM), a unitless measure of landscape ruggedness integrating variation in slope and aspect (Table 14, Sappington et al. 2007). Following a large body of literature from regional studies modeling seasonal habitats and security areas for elk and other ungulates, we used a pseudothreshold (natural log) functional form for canopy cover, distance to motorized routes, and ruggedness, and a quadratic functional form for slope (Sawyer et al. 2007, Proffitt et al. 2010, 2013, Ranglack et al. 2017, DeVoe et al. 2019).

We used a tiered approach to progress from univariate to multivariate models evaluating the traditional security metrics and landscape attributes. In each tier we identified the top-ranked model for each sex and season using AICc (Burnham and Anderson 2002). In the first tier, we fit univariate models for each of the security patch covariates (with and without canopy cover) to evaluate the importance of canopy cover in defining security patches. In the second tier, we fit 5 candidate models containing multiple combinations of covariates associated with the traditional management paradigm on public lands. Lastly, in the third tier, we added slope and terrain ruggedness as a paired combination to evaluate the addition of landscape covariates. With the final model we generated predictive plots for each continuous covariate while holding all other covariates at their mean value.

To provide management recommendations for covariates with a pseudothreshold form, we calculated the cumulative area under the curve from the right-hand side to target the covariate range with the highest relative probability of use for each sex and season. We then identified the range of covariate values that corresponded to 75% and 50% of the area under the curve and used the minimum values within the range to define thresholds for security and preferred security areas, respectively. These values served as the basis for our management recommendations and reflect the narrowest covariate range associated with 75% (i.e., security) and 50% (i.e., preferred security) of elk use. For quadratic covariates (i.e., slope), we noted the covariate value that maximized the relative probability of use for each sex and season.

Table 14 – Covariates used in male and female elk security habitat modeling, Elkhorn Mountains, southwest Montana, USA, 2015–2017.

Covariate	Description	Functional forms[a]	Reference
Security patch	Contiguous areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route	Binary	Hillis et al. (1991), Christensen et al. (1993), DeVoe et al. (2019)
Security patch with canopy cover	Contiguous areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route and with at least half of the security patch containing 15% and 30% canopy cover as two different covariates	Binary	Hillis et al. (1991), Christensen et al. (1993), DeVoe et al. (2019)
Canopy cover	Percent canopy cover VMap 2013	Ps	USFS 2014, Ranglack et al. (2017), DeVoe et al. (2019)
Distance to motorized route	Distance (m) to motorized 2-track, dirt, or paved road designated as open to public use within each respective hunting season	Ps	McCorquodale et al. (2003), Ranglack et al. (2017)
Ruggedness	Vector Ruggedness Measure (VRM): a unitless measure of landscape ruggedness integrating variation in slope and aspect	Ps	Hillis et al. (1991), Sappington et al. (2007), DeVoe et al. (2015), Lamont et al. (2019)
Slope	Slope in degrees	Sq	Hillis et al. (1991), Ranglack et al. (2017), DeVoe et al. (2019)

[a] Ps = Pseudothreshold, Sq = Squared/Quadratic, Binary = categorical covariate for which functional forms were not considered.

Results

Canopy cover

The reductions in percent canopy cover below historic levels prior to the MPB outbreak (1990 – 2000) mirrored the MPB outbreak timeline with a 2 – 3 year lag after the initial infestation (Figure 39). Between the peak MPB outbreak in 2008 and the following 2 years, there was an average 8.5% (± 2.5%) reduction in canopy cover within the MPB-infested areas we evaluated. Post-MPB outbreak and associated canopy cover declines, canopy cover began to increase in 2010 and 2011, nearly approaching historic averages by 2015, 7 years after peak infestation.

Within forested portions of the study area, forests classified as uninfested lodgepole pine had the highest values for canopy cover post-MPB infestation with a mean of 77% (± 14.6; Figure 40). Similar to the trends described in the canopy cover time series, there was an 8% reduction in canopy cover in infested lodgepole forests (mean = 69 ± 15%). Interestingly, canopy cover in MPB-infested lodgepole forests remained higher than canopy cover in Douglas fir and ponderosa pine forests, which had 54% (± 18.9) and 27% (± 8.7%) canopy cover, respectively.

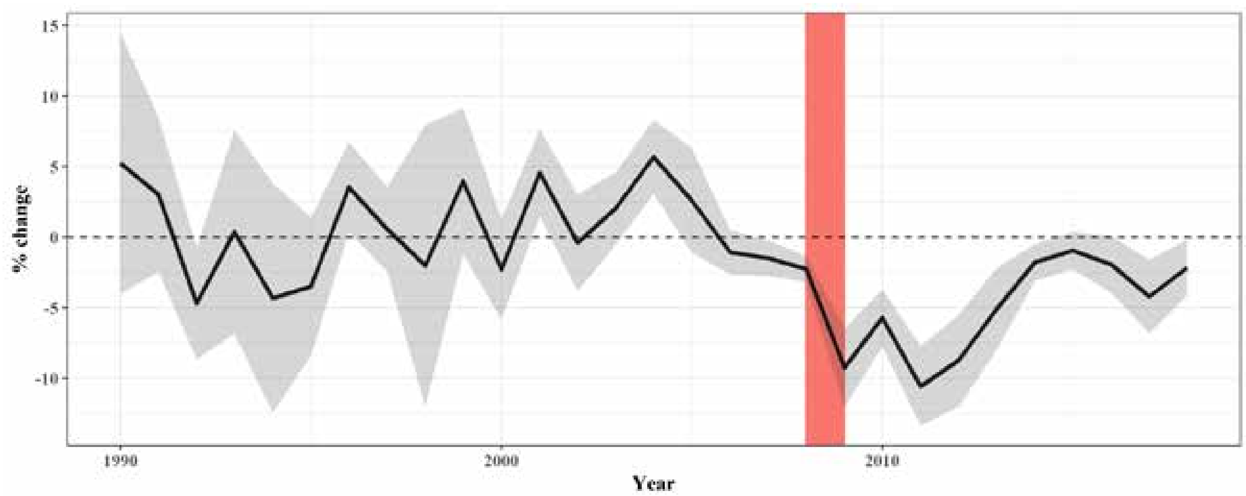

Figure 39 – Twenty-seven year (1990–2017) time series of the mean (± standard deviation) % change in canopy cover from the historic average (1990–2000) for the 3 largest patches of MPB-infested forest within the Elkhorn Mountain study area, southwest Montana, USA, 2015–2017. The year of peak MPB-infestation (2008) is shaded in red.

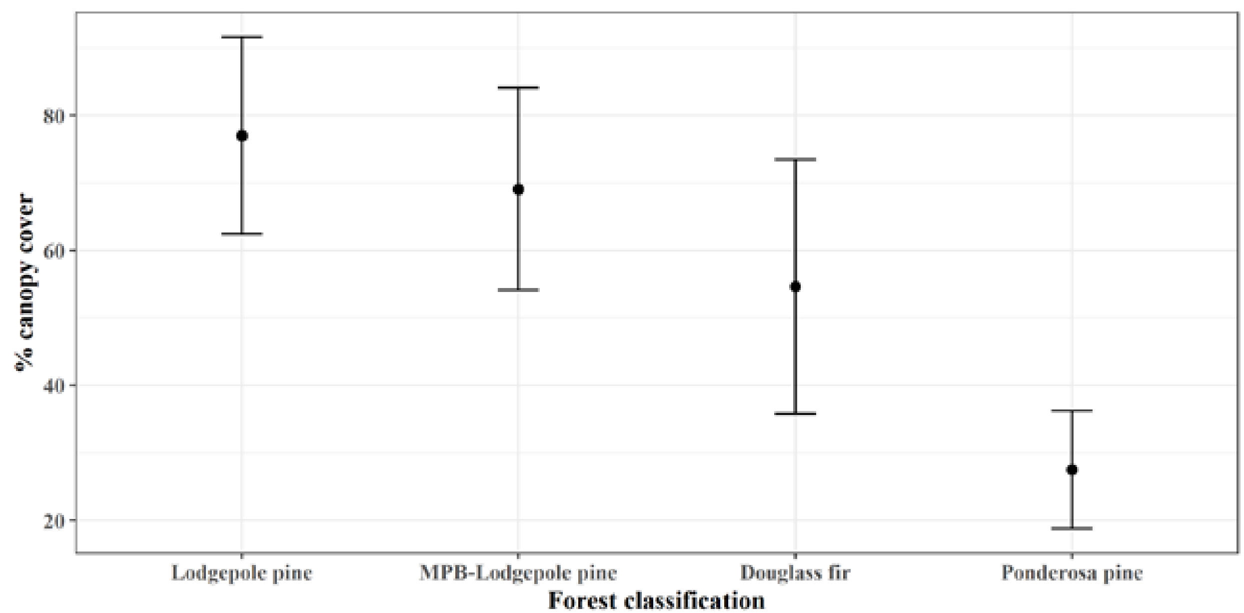

Figure 40 – Average canopy cover percentages (± standard deviation) within uninfested and infested lodgepole pine, Douglas fir, and ponderosa pine forest classifications, Elkhorn Mountains, southwest Montana, USA, 2015–2017.

Security habitat modeling

We captured a total of 59 adult (male = 24, female = 35) elk during the winters of 2015 and 2017. To evaluate security on public lands, we censored 4 males and 12 females that had > 50% of their GPS locations on private lands that restricted hunting during the archery and rifle seasons. We censored 3 individuals (males = 2, females = 1) without any daytime locations within a hunting season. Among the remaining 40 (male = 18, female = 22) individuals, there were 72 animals-years with an average of 30 (± 20.5) GPS locations for each individual-season and an average of 572 (± 235) GPS locations for each sex-season grouping.

In the first tier of model selection, where we evaluated the addition of 15% and 30% as canopy cover thresholds to define security patches, security patches defined without a canopy cover threshold were top-ranked for males in both seasons and for females during the archery season (*Appendix B – Habitat Security Models & Coefficient Estimates*). The one exception was females during the rifle season where security patches with 30% canopy cover were top-tanked. Nonetheless, there was a large degree of uncertainty in the top-ranked model and a small difference in ranking among the 3 univariate models. Because there was not a clear top-ranked model for females during the rifle season, and to have continuity among the second tier sex-season models with respect to security patch definitions, we selected security patches defined without canopy cover as the top model for all sex-seasons.

In the second tier, we evaluated 5 univariate and multivariate combinations of the traditional security metrics (i.e., distance to motorized routes, canopy cover, and security patches defined without a canopy cover threshold from the first tier). In all sex-seasons, the multivariate model containing distance to motorized routes and canopy cover was top-ranked (*Appendix B – Habitat Security Models & Coefficient Estimates*). In general, there was relatively more support for multivariate models than for univariate models and the least support for security patches as a single predictor of elk security. In the third tier, the inclusion of slope and ruggedness improved ranking in all sex-seasons, resulting in the same model structure in the final model for all sex-seasons which contained canopy cover, distance to motorized routes, ruggedness, and slope covariates.

With only a few exceptions, the top-ranked habitat security model produced similar results for both sexes and seasons (Figure 41). There was a positive pseudothreshold relationship with canopy cover, indicating increased selection for areas that had relatively more canopy cover, and the relationship was stronger for females than for males. Males during the archery season had the weakest relationship with canopy cover and a coefficient estimate that was nearly 0 (estimate = 0.009, standard error = 0.05; *Appendix B – Habitat Security Models & Coefficient Estimates*), resulting in a flat prediction line across the observed values of canopy cover (Figure 41). Although between season differences in selection for canopy cover were modest, both sexes selected for higher canopy cover values in the rifle season than in the archery season. The stronger relationship for females resulted in higher canopy cover thresholds associated with security and preferred security areas in both seasons. Females during the rifle season had the highest management recommendations with security areas containing canopy cover values ≥ 39% and preferred security areas containing canopy cover values ≥ 60%.

The relationship with distance to motorized routes was positive in all top-ranked season-sex models, indicating increasing selection for areas farther from roads. This relationship was steeper for females than for males and similar across the rifle and archery hunting seasons (Figure 41). There was strong overlap in covariate values delineating security and preferred security among both sexes and seasons. The most conservative values were for males during the archery season where security areas were defined as being ≥ 2,303 m from a road and preferred security areas were ≥ 3,679 m from a road.

The ruggedness covariate had the most varied results among sexes and seasons. Females had a positive association with ruggedness during the archery season and a negative relationship during the rifle season (Figure 41). In contrast, the relationship was positive for males with little difference between the rifle and archery season, both of which had a stronger relationship relative to females. The stronger relationship for males resulted in relatively high ruggedness thresholds associated with security and preferred security areas, which occurred in areas with ruggedness values ≥ 0.05 and ≥ 0.09, respectively. Lastly, the quadratic functional form for slope indicated an average optimal slope value of 18° (± 1.6°) with little variation among sexes or seasons (Figure 41).

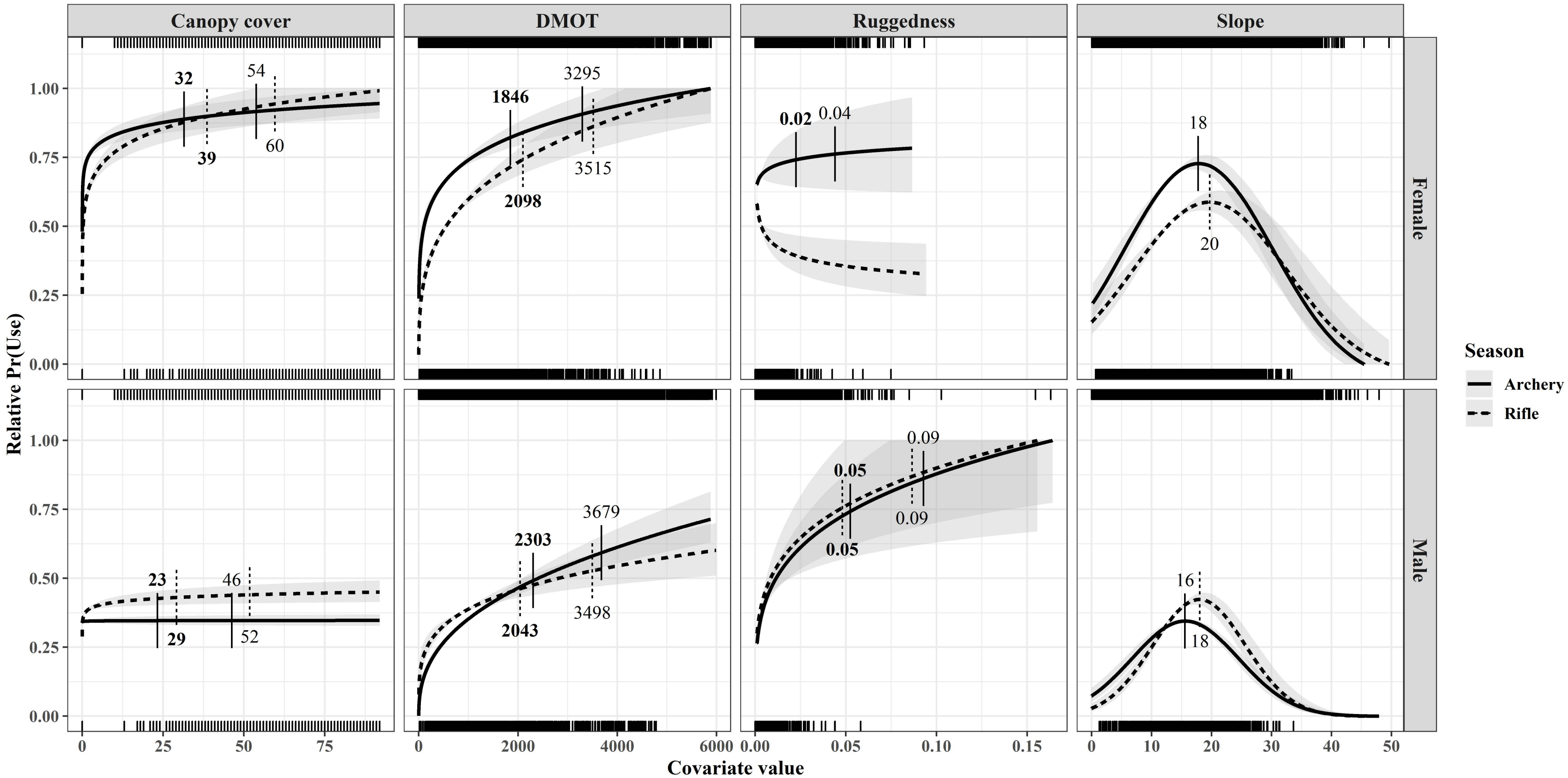

Figure 41 – Prediction plots showing the relationship with the relative probability of use [Relative Pr(Use); ± 95% CI] for each covariate (columns), sex (rows), and season (Archery = solid line, Rifle = dashed line) with all others held at their mean value, for elk in the Elkhorn Mountains, southwest Montana, USA, 2015–2017. The upper rug represents the available locations while the lower rug represents the used locations. Thresholds values for the archery (solid vertical lines) and rifle (dashed vertical lines) seasons represent the minimum covariate values for security and preferred security areas as defined by the 75% and 50% area under the curve thresholds, respectively. DMOT = distance to motorized route.

Discussion

Our study combined canopy cover characterizations with wildlife habitat modeling techniques to assess the impact of MPB-infestations on elk security through reductions in canopy cover. We observed an 8.5% reduction in canopy cover within MPB-infested lodgepole pine forests compared to historic levels prior to the MPB outbreak. Nonetheless, canopy cover in MPB-infested forests remained relatively high (mean = 69 ± 15% SD) and had higher cover values than Douglas fir and ponderosa pine forests by 15% and 42%, respectively. The presence of canopy cover was an important component in defining elk security and was retained within all sex-season habitat security models. However, given the relatively high degree of cover offered by lodgepole pine forests, including those impacted by MPBs, the changes in cover associated with defoliation post-MPB-infestation were relatively minor and did not result in a meaningful reduction in canopy cover below the thresholds used to define security and preferred security areas. Across sexes and seasons, elk security areas contained average canopy cover values ≥ 30% (± 6.7%) and contained 75% of elk use on the landscape. Preferred security areas, which contained 50% of elk use on the landscape, contained canopy cover values ≥ 53% (± 5.7). In general, although we observed expected reductions in canopy cover within MPB-infested forests, defoliation, which on average reduced canopy cover from 69 to 61%, was not predicted to reduce cover below security thresholds and negatively impact elk security through reductions in canopy cover.

In addition to the selection for areas with higher canopy cover, security habitat in the Elkhorn Mountains was characterized by positive associations with increasing distances from motorized routes, relatively rugged slopes, and moderate slope angles of 18°. In general, these findings corroborate with other studies characterizing elk security and habitat (Lyon and Canfield 1991, McCorquodale et al. 2003, Ranglack et al. 2017, DeVoe et al. 2019). Although the traditional definition of an elk security patch that has been broadly incorporated into forest management (i.e., contagious areas of ≥ 100 ha located ≥ 0.8 km from an open motorized route; Hillis et al. 1991) did not receive strong support among our candidate model set, our work lends credence to the importance of canopy cover and distance to motorized routes in defining elk security.

The importance of canopy cover in defining and managing for elk security on public lands is varied across the western U.S. In areas with expansive forest cover, elk security can be controlled through road management alone, yet where forest cover is limited or patchy, incorporating canopy cover into definitions of elk security is also important (Christensen et al. 1993, Unsworth et al. 1993). In contrast to the definitions for distances to motorized routes and patch size which have largely followed the Hillis paradigm (e.g., Hillis et al. 1991), the varied importance of canopy cover has resulted in a variety of arbitrary cover definitions used to define elk security (Christensen et al. 1993). A recent meta-analysis incorporating data from 325 female elk in southwest Montana that occupied both public and private lands recommended managing for areas with ≥ 13% canopy cover that are ≥ 2,760 m from motorized routes when defining elk security (Ranglack et al. 2017). Their recommendations were based on analysis of elk that occupied both public and private lands, and the covariate value that corresponded to half (e.g., 0.5) of the total change in the relative probability of use over the observed covariate range (Ranglack et al. 2017). Rather than provide a single minimum value, our approach provided a range for canopy cover and distance to motorized routes based on the cumulative area under the curve (i.e., cumulative probability of use) and our definitions of security and preferred security areas (i.e., 75% and 50% area under the curve, respectively). Our results suggest that minimum canopy cover values between 23% and 60% and distances to routes between 1,846 m and 3,679 m define the majority of elk use areas within the Elkhorn Mountains for both sexes in both the archery and rifle hunting seasons. Rather than provide a single minimum recommendation, the range of covariate values and their relationship with elk use provides an alternative approach to providing management recommendations that meaningfully translates to elk use.

In addition to different methodologies for defining threshold values, there were important differences between the study areas and study designs that may have contributed to the more conservative recommendations from this study compared to Ranglack et al. (2017) and Hillis et al. (1991). First, Ranglack et al. (2017) included female elk on public (i.e. hunted) and private (i.e., non-hunted) lands when defining elk security. In contrast, our recommendations are developed for male and female elk that predominately occupied public lands open to unrestricted public hunting and censored elk on private lands with restricted hunter access where elk may be less reliant on areas of dense canopy cover far from motorized routes due to relatively lower hunting pressure. Second, the Elkhorn Mountains hunting district 380 is the most heavily used in Montana with record highs of 3,936 hunters and 31,786 hunter days in 2015. Lastly, in contrast to Hillis et al. (1991), our study was located in southwest Montana where cover is patchily distributed. Given our focus on public lands in the most heavily hunted district in Montana with patchily distributed forest cover, one would expect stronger associations with forest cover and security areas than when pooling elk across areas with restricted and unrestricted access (e.g., Ranglack et al. 2017) or when working in systems that are largely forested (e.g., Hillis et al. 1991).

While our results indicated elk continued to use areas impacted by MPBs post-infestation during the hunting season, regionally there have been mixed results regarding elk use of MP-infested forests. In south-central Wyoming, Lamont et al. (2019) found that during summer, female elk avoided MPB-infested forests during nearly all parts of the day and selected for intact coniferous forests during the daytime. The selection for intact forests during the daytime in summer highlights the need for thermal refuge, which may be compromised in MPB-infested forests (Lamont et al. 2019). In contrast, Ivan et al. (2018) documented an increase in the use of MPB-infested forests by elk, mule deer, and moose during summer months across Colorado, presumably driven by increases in understory forage associated with the decrease in canopy cover post-defoliation. Given the host of dynamic factors that can influence wildlife response to MPB-infestations, many of which are spatially and temporally variable and difficult to quantify over broad spatial scales (i.e., number of downed trees), regional and taxonomic generalizations may prove difficult given the limited number of studies examining wildlife responses to MPB-infestations that have been completed currently (Saab et al. 2014).

An additional consideration in interpretations and applications of our work was the successional stage of MPB-infested forests in our study area. An increase in fallen trees is presumed to influence wildlife mobility in MPB-infested forests with a hypothesized reduction in use associated with increased costs in mobility (Saab et al. 2014, Lamont et al. 2019). Our study occurred between 2015 and 2017, 7–10 years after the peak of the MPB infestation in 2008, yet most of the infested trees were standing dead. Given the lack of downed trees during our study period, our results are specific to the period post-defoliation but prior to tree blowdown. Although Lamont et al. (2019) did document an increase in downed trees in MPB-infested forests, their study also occurred when trees were just beginning to fall, 3–7 years following the peak outbreak. Although downfall in infested areas was not widespread, the avoidance of MPB-infested areas during all parts of the day in their study area was suggestive of a down-tree effect and lends correlative support to elk avoiding MPB-infested areas and the associated increase in locomotion costs (Lamont et al. 2019). In Colorado, Ivan et al. (2018) did not describe the degree of downfall across their broad study region but did see increases in ungulate us of MPB-infested forest across three different severities (10%, 50%, and 90% mortality) spanning 0–11 years after initial outbreak.

As MPB-infested forests transition from standing dead to blowdown, understanding the impact on elk habitat and security is an important consideration. Given the large degree of canopy cover provided by lodgepole forests on public lands and the large percentages that have been impacted throughout the western U.S., relatively minor avoidance of these areas could result in a notable net loss of critical habitat that provides demographic benefits for elk through increased security and thermal cover. As MPB-infested forests continue to mature with increasing proportions of fallen trees, assessing the degree to which these forests are selected or avoided by elk and the impact on demography will be a management priority. Additionally, the management of adjacent or nearby intact forests may become increasingly important in providing elk security as infested stands mature and potentially become inadequate for providing elk security.

Section 7 – Effect of Mountain Pine Beetle on Hunter Effort, Harvest, & Success

Introduction

The extensive mortalities of pine (*Pinus* spp.) trees caused by mountain pine beetle (MPB; *Dendroctonus ponderosae*) infestations across western North America substantially altered forest community composition and structure, timber production, fuels and wildfire characteristics, and wildlife communities and habitat (Stone 1995, Chan-McLeod 2006, Page and Jenkins 2007, Jenkins et al. 2008, Klenner and Arsenault 2009, Pfiefer et al. 2011, Simard et al. 2011, Saab et al. 2014). The effects of the epidemic to elk, elk habitat, and its subsequent effects to hunting are much less known, however. Western Montana provides extensive coniferous forest habitat for elk as well as considerable elk hunting opportunities. Hunting district (HD) 380 in the Elkhorn Mountains, in particular, continues to be one of Montana's premier hunting destinations (DeSimone and Vore 1992, Montana Fish Wildlife & Parks 2018). During approximately 2006 – 2012, however, the MPB epidemic killed large expanses of lodgepole pine (*Pinus contorta*) forests throughout HD 380. Here, to understand if the MPB epidemic affected hunter opportunity in HD 380, we compare hunter effort, harvest, and success immediately prior to, during, and after the extensive tree mortalities.

Background

Hunting regulations: past & present

From 1960 – 1985, hunting regulations in HD 380 varied as the Elkhorn elk population continued to grow in size (see *Section 2 – Study Area: Elkhorn elk population*; DeSimone and Vore 1992, Montana Fish Wildlife & Parks 2004). Initial harvest regulations of antlerless elk were relatively restrictive (varying from a 1 – 3 day hunt window to 50 – 230 either-sex/antlerless permits issued), while regulations for antlered bulls were liberal (any bull could be harvested with a valid license). These regulations, however, resulted in low annual bull:cow ratios with bull counts that consisted almost entirely of spikes. Beginning in 1987, a "spike bull" regulation was introduced in HD 380 that allowed hunters with a valid general elk license the opportunity to harvest a spike bull, defined as having either unbranched antlers or a branch of less than 4 inches. More restrictive regulations were established for older bulls with branched antlers under a special permit drawing. This harvest strategy favored the recruitment of yearlings with greater than a four-inch branch into the older age class the following year and effectively produced older and more numerous bulls in the population. In 2005, the special permit drawing was changed to either-sex elk. This unique spike/either-sex harvest regulation has continued to the present and is implemented in only one other hunting district in Montana (HD 339).

In addition to the spike/either-sex regulation, antlerless elk permits and B-licenses have been issued in various forms (varying when and where valid) and at varying levels over time to help manage elk numbers in population segments and the overall elk population in HD 380. These harvest regulations have been effective in maintaining hunter opportunity while generally meeting elk population objective levels of 2,000 (± 300) total elk counted during post-season aerial surveys as guided by the State of Montana Elk Management Plan (Montana Fish Wildlife & Parks 2004). The elk management plan recommends maintaining ≥ 25 calves per 100 cows, ≥ 10 bulls per 100 cows, and an average age of bulls harvested on either-sex permits of ≥ 5.5 years old. Depending on the total number of elk, calf-cow ratios, and bull-cow ratios observed during post-season aerial surveys and the average age of brow-tine bulls harvested on the either-sex permits for 2 consecutive years, the elk management plan also identifies more liberal or restrictive regulations for implementation in subsequent years.

During this study (2015 - 2017), the general hunting license allowed for harvest of a spike or antlerless elk during the archery season. During the rifle season, the general hunting license allowed for harvest of a spike and youth hunters could harvest an antlerless elk. In 2015 and 2016, the number of limited either-sex permits was 120, while in 2017 the number increased to 135. The number of limited B licenses valid for the entire hunting district was 125 across all years of the study. In 2015, 250 and 325 B licenses were issued in southern and northern portions, respectively. In 2016 and 2017, 350 and 325 B licenses were issued in southern and northern portions, respectively.

Trends of hunter effort, harvest, & success

Hunting district 380 has been one of Montana's most popular hunting areas since the early 1960's and typically receives the greatest hunter effort (number of hunters and hunter recreation days) compared to all other Montana hunting districts (DeSimone and Vore 1992, Montana Fish Wildlife & Parks 2018). Estimated hunter effort has continued an increasing trajectory since the 1960's with record highs of 3,936 hunters and 31,786 hunter days in 2015 (panel B and C, Figure 42).

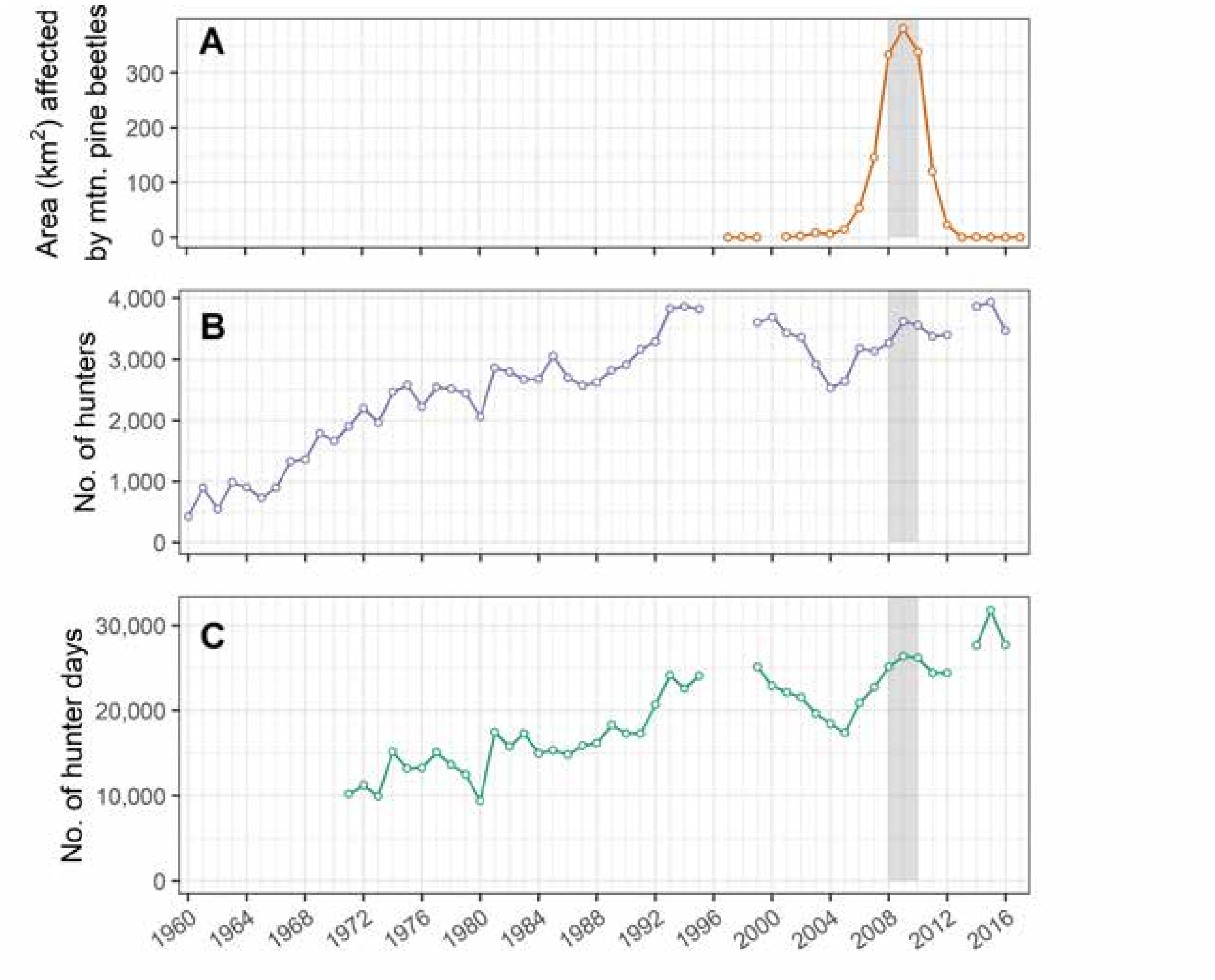

Figure 42 – Hunting district 380 estimates of area (km²) first affected by mountain pine beetles (panel A) and hunter effort as measured by estimates of the number of hunters (panel B) and hunter days (panel C) from 1960 to 2017. The gray shaded area indicates years (2008 - 2010) of peak beetle-killed tree mortality.

From 1960 to the early 1990's, total harvest of elk (comprised primarily of antlered elk) increased (panel A and B, Figure 43) as hunter effort and the elk population increased. With increases in antlerless harvest beginning in the late 1980's and a subsequent stabilizing of the elk population to levels within objective (Figure 5 in *Section 2*), the total harvest of elk generally stabilized from 1991 – 2017, averaging 641 (± 208) elk. During this same time period, similar numbers of antlered and antlerless elk were being harvested each year, averaging 318 (± 75) and 322 (± 154), respectively. Spikes comprised the majority of the antlered harvest from at least 2004 to 2017 with the annual harvest averaging 203 (± 49). During this time period, harvest of bulls with < 6 points and ≥ 6 points averaged 27 (± 11) and 71 (± 15), respectively.

Hunter success varied from 1960 – 2016 (panel C, Figure 43). During 1960 – 1970, hunter success rates were relatively high and averaged 18.3% (± 7.0%). Hunter success rates decreased to an average of 8.3% (± 2.5%) during 1971 – 1982 and then increased to an average of 15.2% (± 4.3%) during 1983 – 1991. In more recent years from 2004 – 2016, hunter success rates were relatively high and averaged 18.2% (± 3.5%).

The infestation: changes in hunter effort, harvest, & success?

MPBs affected approximately 1,431 km^2 of lodgepole pine forests in HD 380. Tree mortality was first observed in 1997 with only 0.5 km^2 of forest affected but increased by 2007 to 146.0 km^2. The peak of tree mortalities occurred in 2009 with 380.6 km^2 of newly affected forest (panel A, Figure 42). As the majority of the pine forest was affected, new tree mortality steeply declined in subsequent years, decreasing to only 0.1 km^2 of newly affected forest by 2013. To summarize the potential effect of tree mortality on hunter effort, harvest, and success, we classified years of tree mortality into 3 periods relative to

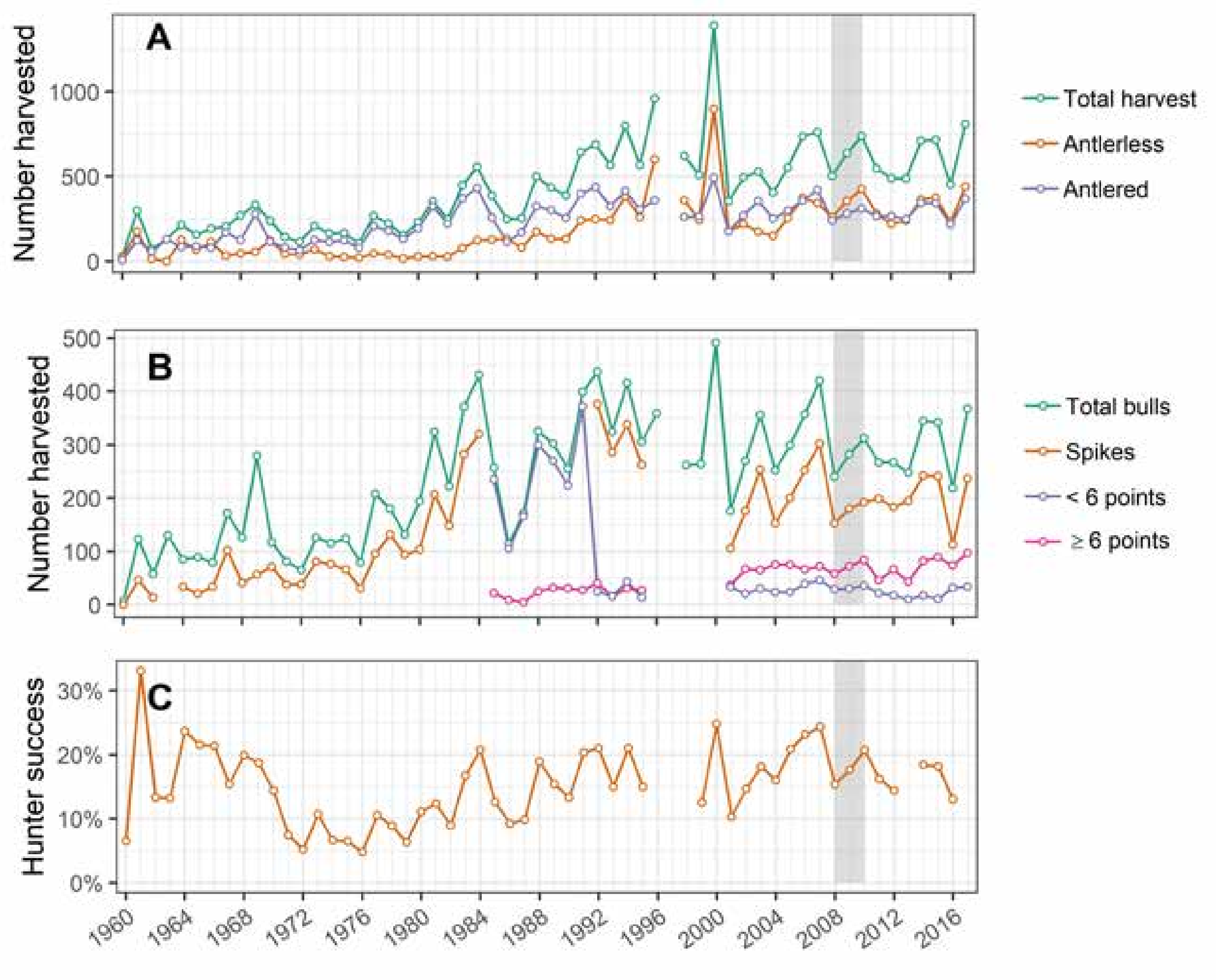

Figure 43 – Hunting district 380 estimates of hunter harvest of all (panel A) and bull (panel B) elk and hunter success (panel C) from 1960 – 2017. The gray shaded area indicates years (2008 – 2010) of peak beetle-killed tree mortality (refer to panel A in Figure 42). Note that methods of classifying bull elk changed in 1985 and 1992 such that spikes were included in the <6 points class during this period.

Table 15 – Average (± SD) levels of annual hunter effort, harvest, and success prior to peak (2001 – 2007), peak (2008 – 2010), and post peak (2011 - 2017) tree mortality caused by mountain pine beetle infestation in hunting district 380, Elkhorn Mountains, west-central Montana, USA.

Summary	Prior	Peak	Post
No. of hunters	3,026.3 (344)	3,480.3 (188.7)	3,605.4 (271.3)
No. of hunter days	20,404.7 (1981.5)	25,906.0 (653.0)	27,203.4 (3038.8)
Total harvest	547.6 (154.5)	626.0 (118.5)	601.3 (140.8)
Antlerless harvest	241.3 (87.3)	348.0 (82.3)	307.4 (85.3)
Antlered harvest	304.3 (80.9)	278.0 (36.2)	293.7 (57.1)
Spike	206 (67.4)	175.0 (20.0)	201.4 (46.0)
Bulls w/ <6 pts.	31.0 (9.1)	31.7 (3.8)	20.7 (9.4)
Bulls w/ ≥6 pts.	65.3 (13.1)	71.3 (13.0)	71.0 (20.7)
Hunter success (%)	18.2 (5.0)	17.9 (2.7)	16.1 (2.3)

peak tree mortality: prior, peak, and post. We defined peak tree mortality as 2008 – 2010, which included approximately 75% of the total tree mortality in HD 380. We defined the prior period as 2001 – 2007. Due to lack of data for hunter effort, harvest, and success and the likely association of these variables with other, unrelated factors preceding the infestation, we did not consider the years prior to 2001. We defined the post period as 2011 – 2017.

The total affected area during the prior, peak, and post periods was 232.3, 1,052.7, and 144.3 km^2, respectively. From the prior to the peak period, the average annual number of hunters and hunter days increased by 15.0% and 27.0%, respectively (Table 15; panel B and C, Figure 42). Across these periods, the average annual total harvest increased by 14.3%, harvest of antlerless elk increased by 44.2%, and harvest of antlered elk decreased by 8.6% (panel A, Figure 43). Across these periods, the average annual harvest of spikes decreased by 15.0%, while harvest of bulls with <6 points and bulls ≥6 points marginally increased, with increases ranging from 2.3 – 9.7% (panel B, Figure 43). The average annual hunter success decreased by 0.3% across these periods (panel C, Figure 43).

From the peak to the post period, the average annual number of hunters and hunter days further increased by 3.6% and 5.0%, respectively. Across these periods, the average annual total harvest decreased by 3.9%, harvest of antlerless elk decreased by 11.7%, and harvest of antlered elk increased by 5.6%. The average annual harvest of spikes increased by 15.1%, of bulls with <6 points decreased by 34.7%, and of bulls ≥6 points decreased by 0.4% across these periods. The average annual hunter success further decreased by 1.8% across these periods.

Discussion

Although we found changes in hunter effort (number of hunter and hunter days), harvest, and success across the periods before, during, and after peak MPB-caused tree mortality (Table 15; Figure 42 – Figure 43), the magnitude and direction of changes were within the range of variation typically observed for these metrics and are likely more strongly associated with changes in harvest regulations. For example, during peak tree mortality, the total number of available permits for antlerless and either-sex elk increased from 785 in 2008 to 1,010 in 2009 and 2010, corresponding to increases in the number of elk harvested and hunter success. Similar patterns were observed during the period after peak tree mortality; the total number of permits decreased to 605 in 2012 and increased to 645 in 2014 and 820 in 2015, corresponding to reduced and increased harvest and success rates, respectively.

Both metrics of hunter effort have been on an increasing trajectory since the 1960's, and further increases at the levels observed are not surprising. The levels of hunter harvest and success appeared to be within the normal range of values observed since the elk population stabilized within the population objective range of 1,700 – 2,300 elk (*Section 2 – Study Area: Elkhorn elk population*). Therefore, there is no evidence that the changes in levels of hunter effort, harvest, and success were associated with the MPB epidemic.

Section 8 – Elk Distributions in the Boulder Valley Area

Introduction

Since the previous 1981 – 1992 radio-collar study in the Elkhorn Mountains (see *Section 5 – Effects of Mountain Pine Beetle on Elk*), elk have expanded into the southern Boulder Valley area. Recurring annual aerial surveys of elk in the South Boulder Elk Herd Unit began in 2015 and counts have ranged from 143 – 163 since that time (see *Section 2 – Study Area*). Little information exists, however, about their distributions and interchanges with adjacent elk herds in the Elkhorn Mountains. Here, we estimate and describe annual and seasonal distributions of elk based on data from the previous and current study to understand how movement patterns of elk occupying the Boulder River Valley have changed through time.

Methods

We obtained historic elk location information collected as part of a previous study in the Elkhorn Mountains spanning 1981 – 1992 (DeSimone et al. 1996). In that study, adult female and male elk were instrumented with VHF (very high frequency) collars and aerially relocated approximately every 1-3 weeks. From this dataset, we included only locations from elk collared in the Prickly Pear, Elkhorn, and Devils Fence Elk Herd Units (EHU; see Figure 4 in *Elkhorn elk population*). Using the location data from GPS-collared adult female and male elk collected as part of the current study (see *Section 3 – Elk Capture, Sampling, Survival, & Distributions*), we included only locations from elk collared in the aforementioned EHU's in addition to the South Boulder EHU. Because our primary interest was on the effects of mountain pine beetle (MPB)-killed trees on elk in the Elkhorn Mountains, we only captured and collared 1 elk in the South Boulder EHU. We subsampled the GPS data to an acquisition rate of approximately 1 location every week to more closely accord with the VHF data for comparing within EHU population segments. We did not subsample the data for the more recently established South Boulder population segment to better approximate current distributions.

For each dataset (VHF and GPS), sex, and EHU population segment, we delineated annual and seasonal distributions across all years of location data using the adehabitatHR package in program R version 3.5.0 (R Core Team 2018) by estimating a 95% (i.e., home range) and 50% (i.e., core use range) kernel utilization distribution. Seasonal distributions included spring, summer, archery hunting season, rifle hunting season, and winter. We defined spring (i.e., calving) as May 20 – June 15, summer as July 1 to 1 week prior to the opening of archery season, and winter as 1 week after the close of rifle season to May 1. We defined the archery and rifle hunting seasons according to the annual Montana general elk archery and rifle season dates, where the 6-week archery season starts on the 1st Saturday in September and the 5-week rifle season starts 5 weeks prior to the Saturday after Thanksgiving. Annual distributions were defined as the spring season to the end of the winter season.

Results

From the previous VHF study, we obtained 2,384 locations from 78 individuals (1,539 and 845 locations from 31 females and 47 males, respectively) ranging from December 27, 1982 to April 15, 1992. Twelve females and 14 males were in the Prickly Pear, 4 females and 5 males in the Elkhorn, and 15 females and 28 males in the Devils Fence population segments. No individuals were in the South Boulder population segment. Per individual female, we obtained an average of 49.6 locations (range 3 – 110) over 987 days (range 33 – 1,907). Per individual male, we obtained an average of 18.0 locations (range 1 – 57) over 365 days (range 1 – 1,365). Estimated seasonal ranges varied for each population segment and sex (Table 16; Figure 45 – Figure 49). Due to low sample size or high dispersion of locations, we could not reliably estimate a summer, archery, and rifle seasonal range for males in the Elkhorn population segment.

From the current GPS study, we obtained 1,933 locations from 27 individuals (1,516 and 417 locations from 15 females and 12 males, respectively) ranging from January 30, 2015 to April 28, 2018. Six females and 3 males were in the Prickly Pear, 3 females and 1 male in the Elkhorn, 5 females and 8 males in the Devils Fence, and 1 female in the South Boulder population segments. Per individual female, we obtained an average of 41.4 locations (range 29 – 50) over 736 days (range 230 – 1,109). Per individual male, we obtained an average of 34.8 locations (range 12 – 47) over 434 days (range 155 – 934). Estimated seasonal ranges varied for each population segment and sex (Table 16; Figure 45 – Figure 49). Due to low sample size, we could not estimate a spring, summer, or rifle seasonal range for males in the Elkhorn population segment.

Estimated annual ranges for females and males indicated that, since the previous study, current distributions have expanded to areas farther south in the Devils Fence and South Boulder EHU's, as well as west into the adjacent HD 370 (Figure 44). In particular, the Devils Fence annual range for both females and males suggests substantial broadening of elk distributions to the south. Annual ranges for each population segment from the current study occurred across a greater diversity of private and public lands, including lands managed by the State of Montana, Bureau of Land Management (BLM), and U.S. Forest Service, as compared to the previous study. Compared to the previous study, the female annual range of the Elkhorn population segment occupied a broader area that included the Prickly Pear EHU. This distribution reflects the movements of two females captured in the

Table 16 – Number of locations and collared female and male adult elk for each Elkhorn population segment and season used in estimation of seasonal ranges from a previous VHF study (DeSimone and Vore 1992, DeSimone et al. 1996) *and the current GPS study, west-central Montana, USA. *Not used in estimation of seasonal ranges due to small sample size or high dispersion of locations.*

			1981 – 1992 (VHF)		2015 – 2018 (GPS)	
Sex	Elk pop. segment	Season	No. locations	No. elk	No. locations	No. elk
Female	Prickly Pear	Spring	39	12	20	6
		Summer	136	12	50	6
		Archery	101	12	32	6
		Rifle	63	12	29	6
		Winter	304	12	116	6
	Elkhorn	Spring	13	4	13	3
		Summer	38	4	24	3
		Archery	29	4	18	3
		Rifle	14	4	13	3
		Winter	83	4	53	3
	Devils Fence	Spring	36	12	18	5
		Summer	88	12	40	5
		Archery	58	12	28	5
		Rifle	48	11	16	4
		Winter	230	15	93	5
	South Boulder	Spring	--	--	78	1
		Summer	--	--	166	1
		Archery	--	--	123	1
		Rifle	--	--	108	1
		Winter	--	--	458	1
Male	Prickly Pear	Spring	19	12	11	3
		Summer	56	13	27	3
		Archery	45	12	19	3
		Rifle	28	10	16	3
		Winter	118	14	65	3
	Elkhorn	Spring	5	4	--	--
		Summer	11*	5	--	--
		Archery	7*	5	4*	1
		Rifle	7*	5	1*	1
		Winter	30	5	5	1
	Devils Fence	Spring	33	22	26	8
		Summer	74	23	60	8
		Archery	60	22	33	6
		Rifle	35	16	20	4
		Winter	154	28	125	8

Elkhorn EHU that spent subsequent winters in both the Elkhorn and Prickly Pear EHU's and the remainder of the year in the northern portion of the Prickly Pear EHU. The female core use area of the Prickly Pear and Elkhorn population segments extended farther toward and into the southwest corner of the Prickly Pear EHU adjacent to the town of Boulder, as compared to the previous study. In particular, the female range of the Prickly Pear population segment has contracted longitudinally along the east side of I-15, with elk remaining at low elevation year-round. The male range of the Elkhorn population segment appears to have contracted substantially; however, this may be largely due to the lack of locations obtained from the current study. The female annual range of the South Boulder population segment from the current study primarily occurred in the southern portion of the South Boulder EHU but also across State Highway (SH) 69 north of I-90. Additionally, the male core use area of the Devils Fence broadened to include more State of Montana and BLM lands to the south.

Spring and summer ranges and core use areas of females and males within each population segment were similarly distributed, respective to each study (Figure 45 – Figure 46). The female ranges of the Prickly Pear population segment occurred farther south and at lower elevation as compared to the previous study (Figure 50). The male ranges of the Prickly Pear population segment occurred farther north at the border of Sheep Creek and Prickly Pear EHU's as compared to the previous study. The female ranges of the Devils Fence population segment generally occurred in the same area as the previous study; however, elk were distributed farther south along the border of the Devils Fence and South Boulder EHU's. The male core use area of the Devils Fence population segment was generally similar, however, the ranges were more broadly distributed and occurred farther south as compared to the previous study. Compared to the previous study, the female ranges of the Elkhorn population segment were more broadly distributed across two regions in the Prickly Pear EHU and one region of the Elkhorn EHU with each region reflecting the distribution of one female. These females did not use the State of Montana lands within the Elkhorn EHU that were extensively used in the previous study. The spring and summer ranges of the South Boulder population segment in the current study occurred in the southwest portion of the South Boulder EHU. The summer range occurred partly across SH-69 in HD 370. The core use areas occurred adjacent to and north of I-90.

The female archery season ranges of the Prickly Pear and Elkhorn population segments, respective to each dataset, were generally similar to ranges described above for the spring and summer ranges (Figure 47). The female archery season range of the Devils Fence population segment was more contracted and occurred primarily in the northern portion of the Devils Fence EHU as compared to the broad distribution across the Prickly Pear, Elkhorn, and Devils Fence EHU's in the previous study. The archery season range of this population segment additionally extends farther south to the northern portion of the South Boulder EHU than in the previous study. The female archery season range of the South Boulder population segment shifted to primarily the east side of SH-69 and occurred in two regions of largely private land ownership. Male archery season ranges were generally located in areas similar to female ranges but were more broadly distributed. The male archery season range of the Prickly Pear population segment occurred farther north in the Prickly Pear EHU and east in the North and South Crow EHU's as compared to the previous study. Compared to the previous study, the male archery season range of the Devils Fence population segment was substantially larger in extent with core use areas that occurred broadly across the southern portion of the study area that included regions of the Sheep Creek, Prickly Pear, South Crow, Devils Fence, and South Boulder EHU's and of HD 370.

The female rifle season range of the Prickly Pear population segment generally occurred at lower elevations within the Prickly Pear EHU and extended farther south adjacent to I-15 to the town of Boulder (Figure 48). The male rifle season range of the Prickly Pear population segment generally occurred at higher elevations within the Prickly Pear EHU and were centered farther north and east as compared to the previous study. The female rifle season range of the Elkhorn population segment was more broadly distributed across the Elkhorn and Prickly Pear EHU's as compared to the previous study that occurred primarily within the Elkhorn EHU. The female rifle season range of the Devils Fence population segment was more contracted with core use areas occurring in similar areas as compared to the previous study. The male rifle season range of the Devils Fence population segment was also more contracted with three core use areas that included one similar to the previous study and two others occurring in the southeast corner of the Devils Fence EHU and on the border of the South and North Crow EHU's. A portion of the female rifle season range of the South Boulder population segment shifted back to the west side of SH-69 in HD 370, while a portion remained relatively broadly distributed across the southern region of the South Boulder EHU.

The female and male winter ranges of the Prickly Pear population segment occurred in similar locations to the previous study, but for females extended farther south towards the town of Boulder (Figure 49). In the previous study, a portion of the winter ranges occurred to the east in the South and North Crow EHU's. This portion was due to 3 females and 1 male that primarily wintered in the Prickly Pear EHU but occasionally switched wintering areas in some years. In the current study, one male spent about one month of one winter period in the southern Elkhorn EHU; otherwise, similar switching behaviors to the previous study were not observed. The female winter range of the Elkhorn population segment was more broadly distributed across the Prickly Pear, Elkhorn, and Devils Fence EHU's, reflecting distributions of one female occupying the Elkhorn and Devils Fence EHU's and two females occasionally overlapping in distribution in the Prickly Pear EHU. The male winter range of the Elkhorn population segment was more contracted and restricted to the Elkhorn EHU compared to the previous study that was broadly distributed across the Prickly Pear, Elkhorn, Devils Fence, North Crow, and South Crow EHU's. This difference may be likely due to the low sample size used to estimate the range in the current study, however. For the Devils Fence population segment, the female winter range was more broadly distributed in a north-south direction and the primary core use area was distributed farther to the east than the previous study. The male winter range of the Devils Fence population segment was more broadly distributed to the south and east extending to the border of the South Boulder EHU and into the North Crow EHU. Female core use areas of the South Boulder population segment indicated increased use of a small area west of SH-69.

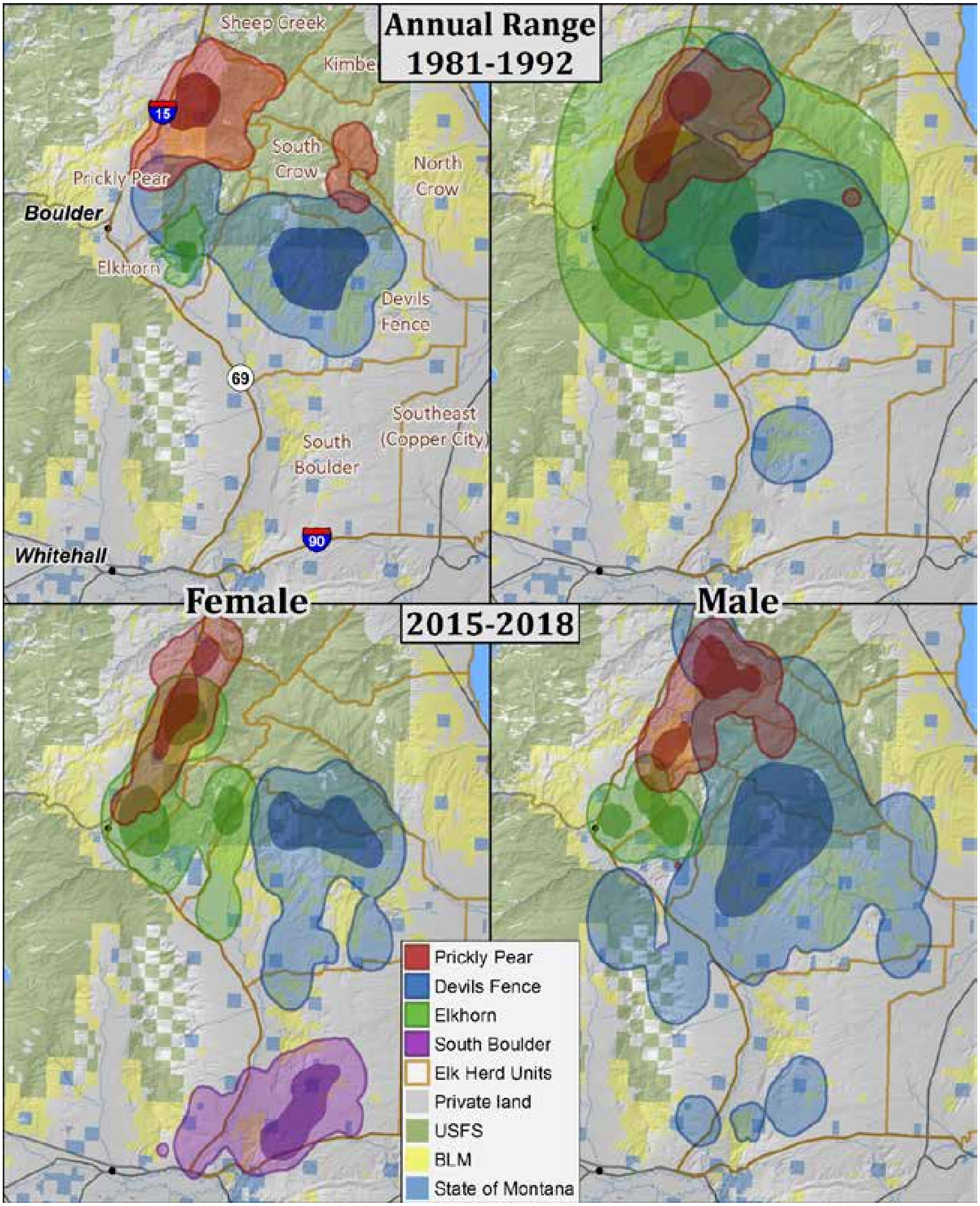

Figure 44 – Annual ranges of female (left panels) and male (right panels) elk based on data obtained from a previous VHF study (top panels) and the current GPS study (bottom panels) for population segments in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate core use areas.

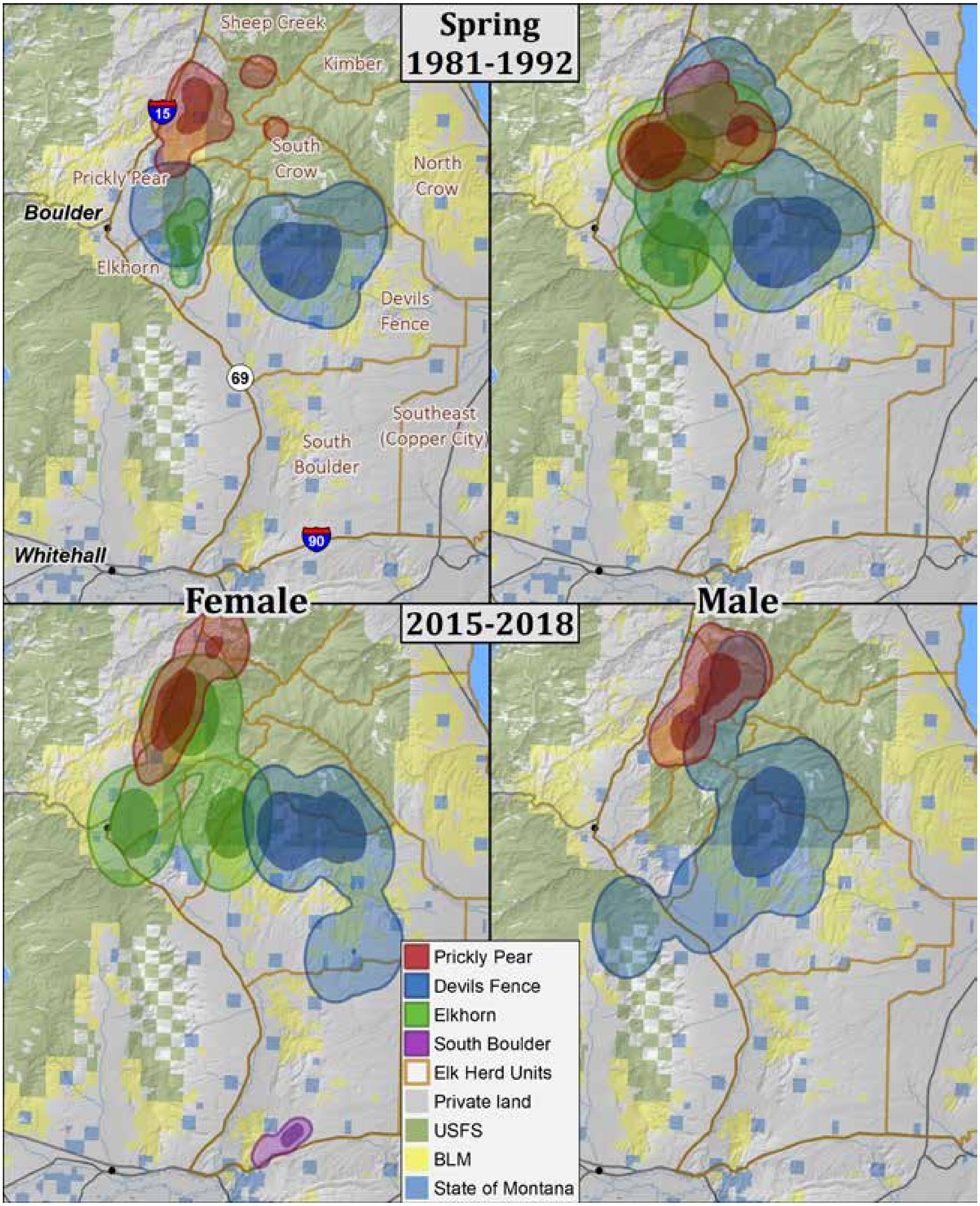

Figure 45 – Spring (May 20 – June 15) seasonal range of female (left panels) and male (right panels) elk based on data obtained from a previous VHF study (top panels) and the current GPS study (bottom panels) for population segments in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate core use areas.

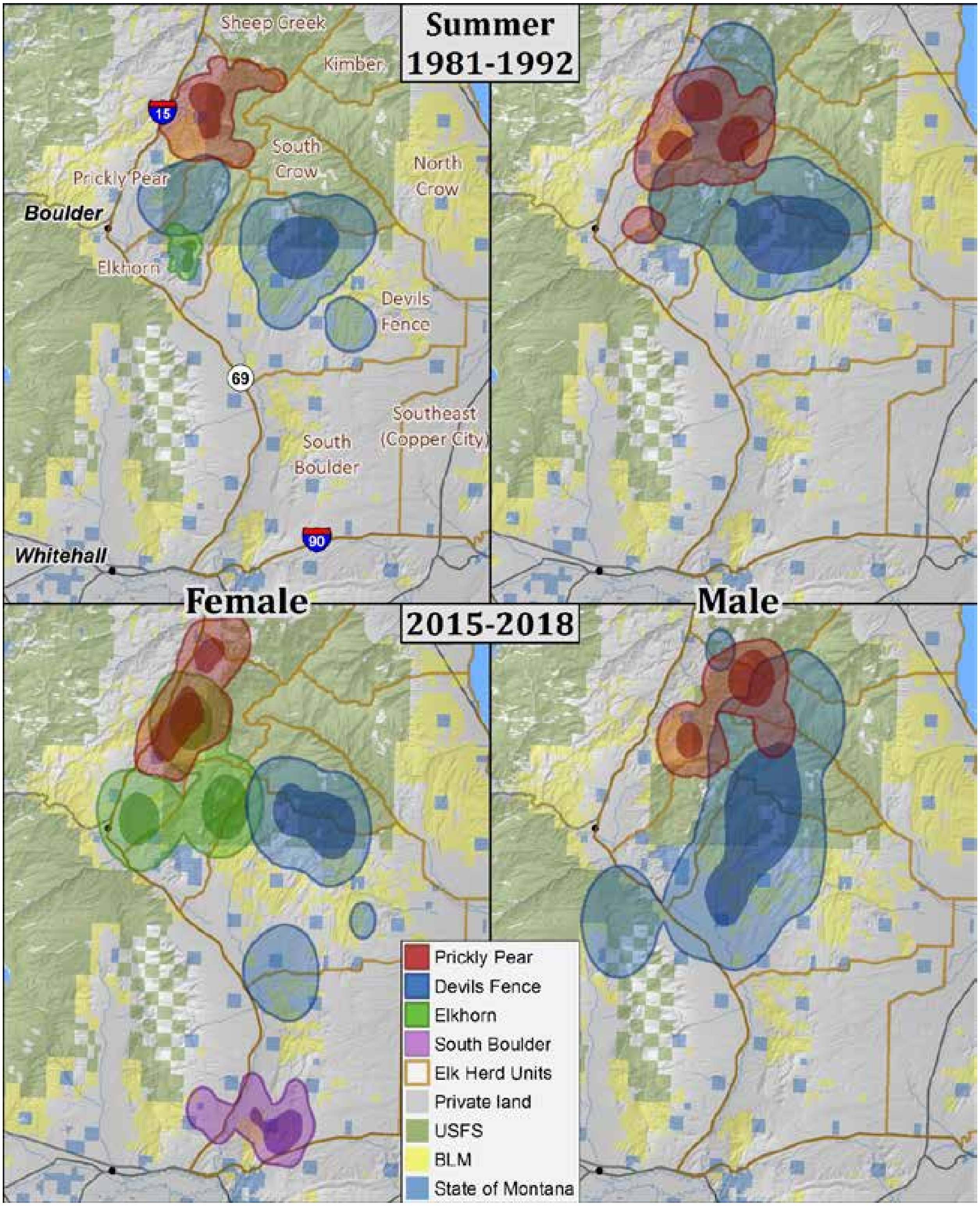

Figure 46 – Summer (July 1 – one week prior to archery season opening date) seasonal range of female (left panels) and male (right panels) elk based on data obtained from a previous VHF study (top panels) and the current GPS study (bottom panels) for population segments in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate core use areas.

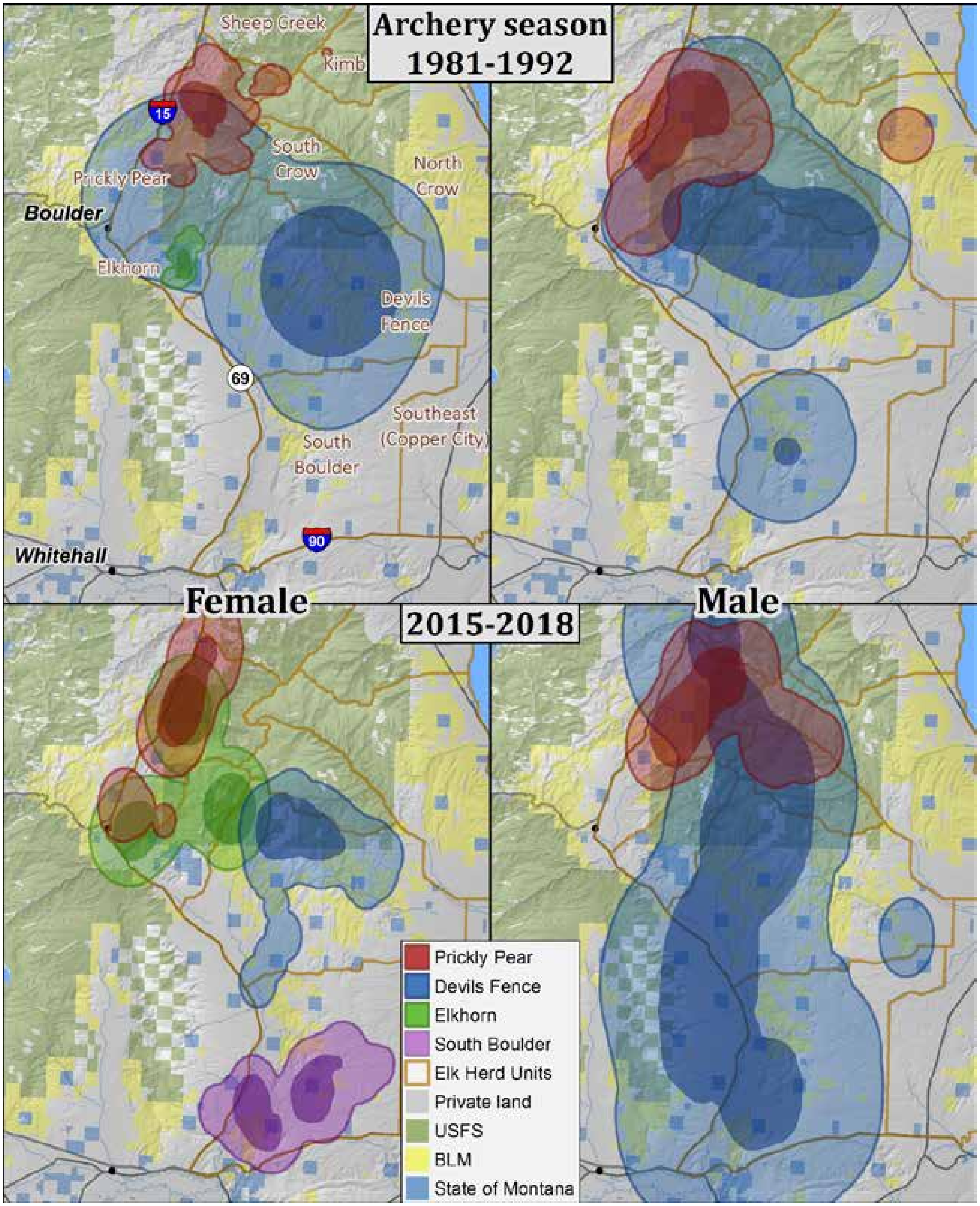

Figure 47 – Archery hunting season range of female (left panels) and male (right panels) elk based on data obtained from a previous VHF study (top panels) and the current GPS study (bottom panels) for population segments in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate core use areas.

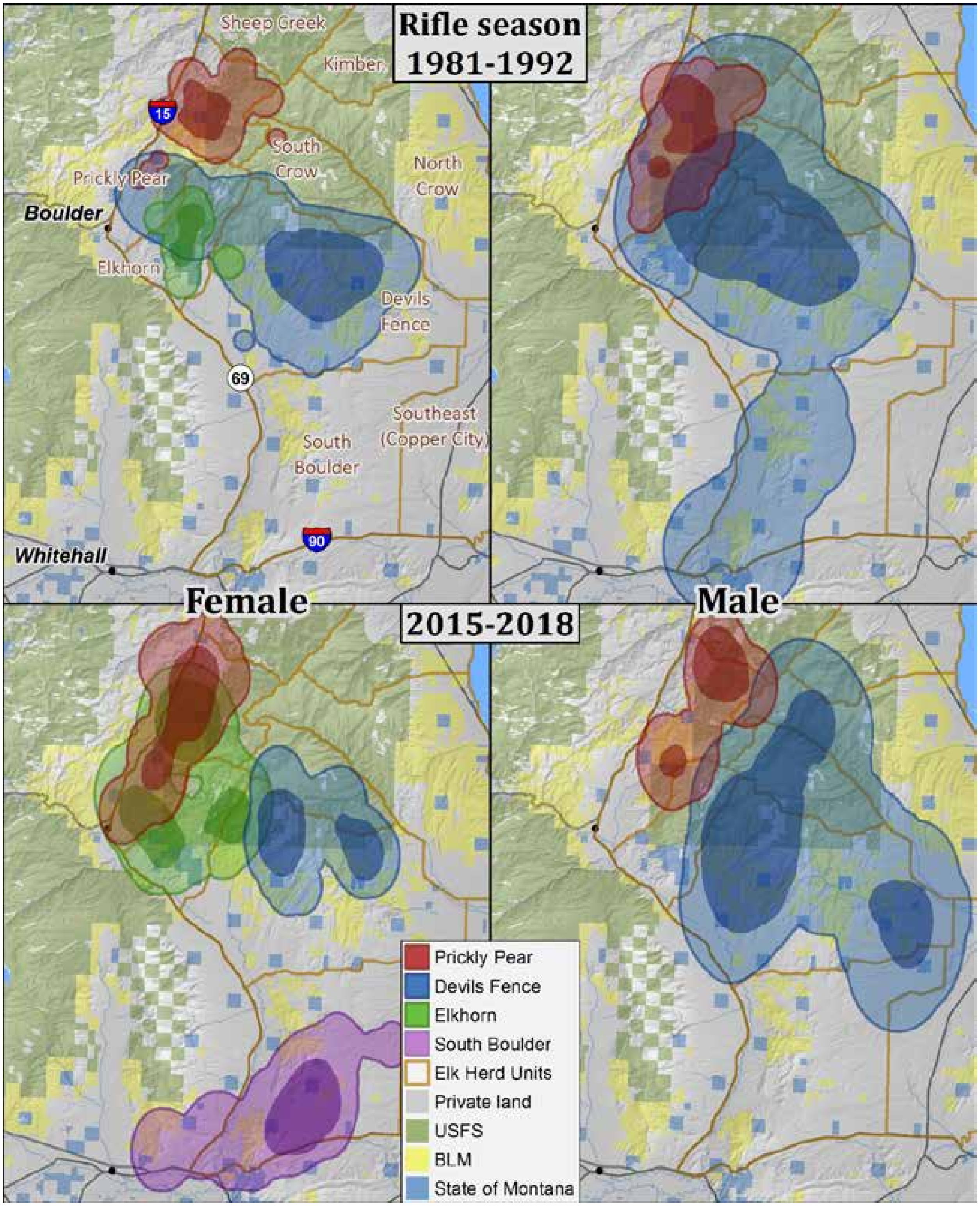

Figure 48 – Rifle hunting season range of female (left panels) and male (right panels) elk based on data obtained from a previous VHF study (top panels) and the current GPS study (bottom panels) for population segments in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate core use areas.

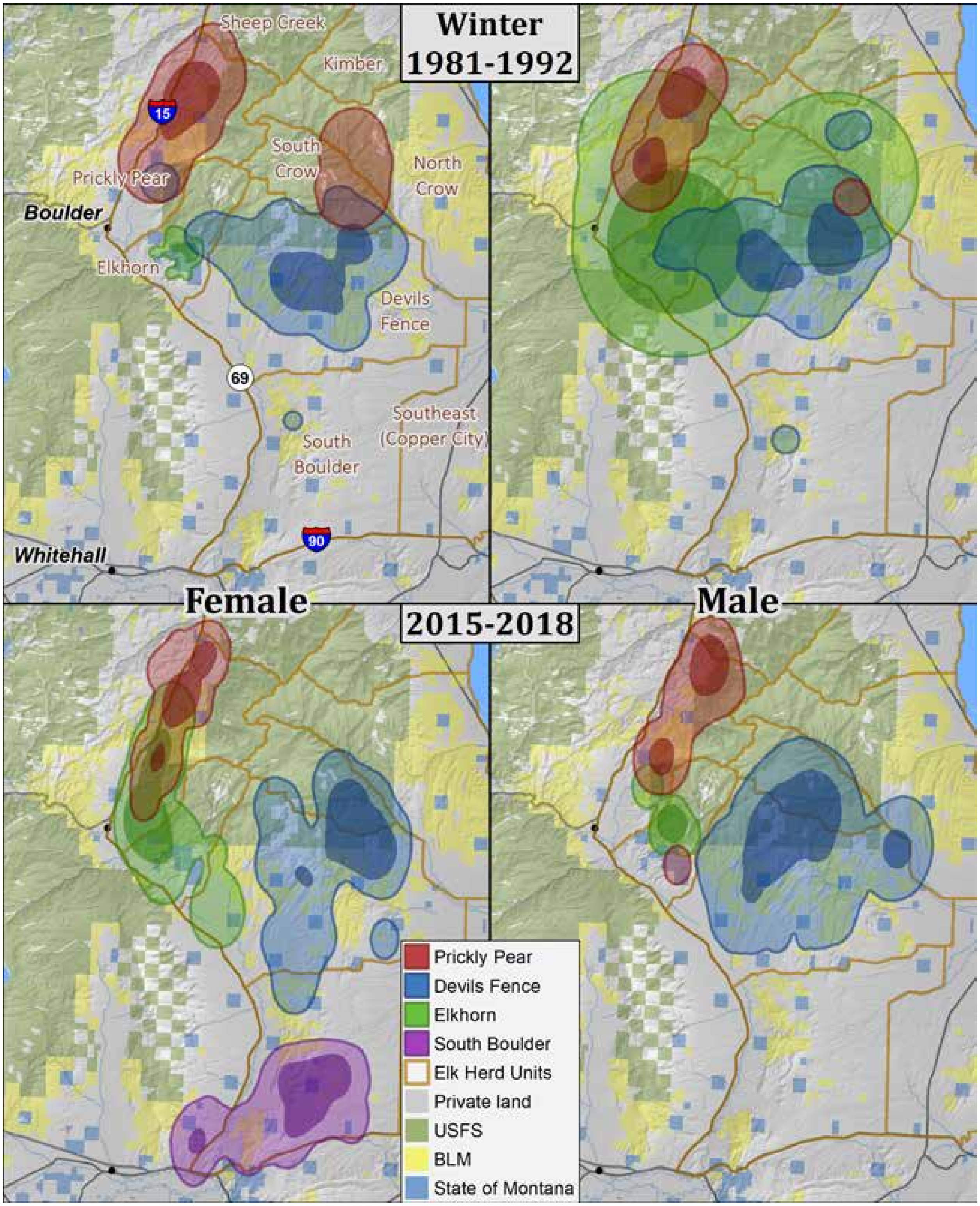

Figure 49 – Winter (one week after rifle season closing date – May 1) seasonal range of female (left panels) and male (right panels) elk based on data obtained from a previous VHF study (top panels) and the current GPS study (bottom panels) for population segments in the Elkhorn elk population of west-central Montana, USA. Darker regions indicate core use areas.

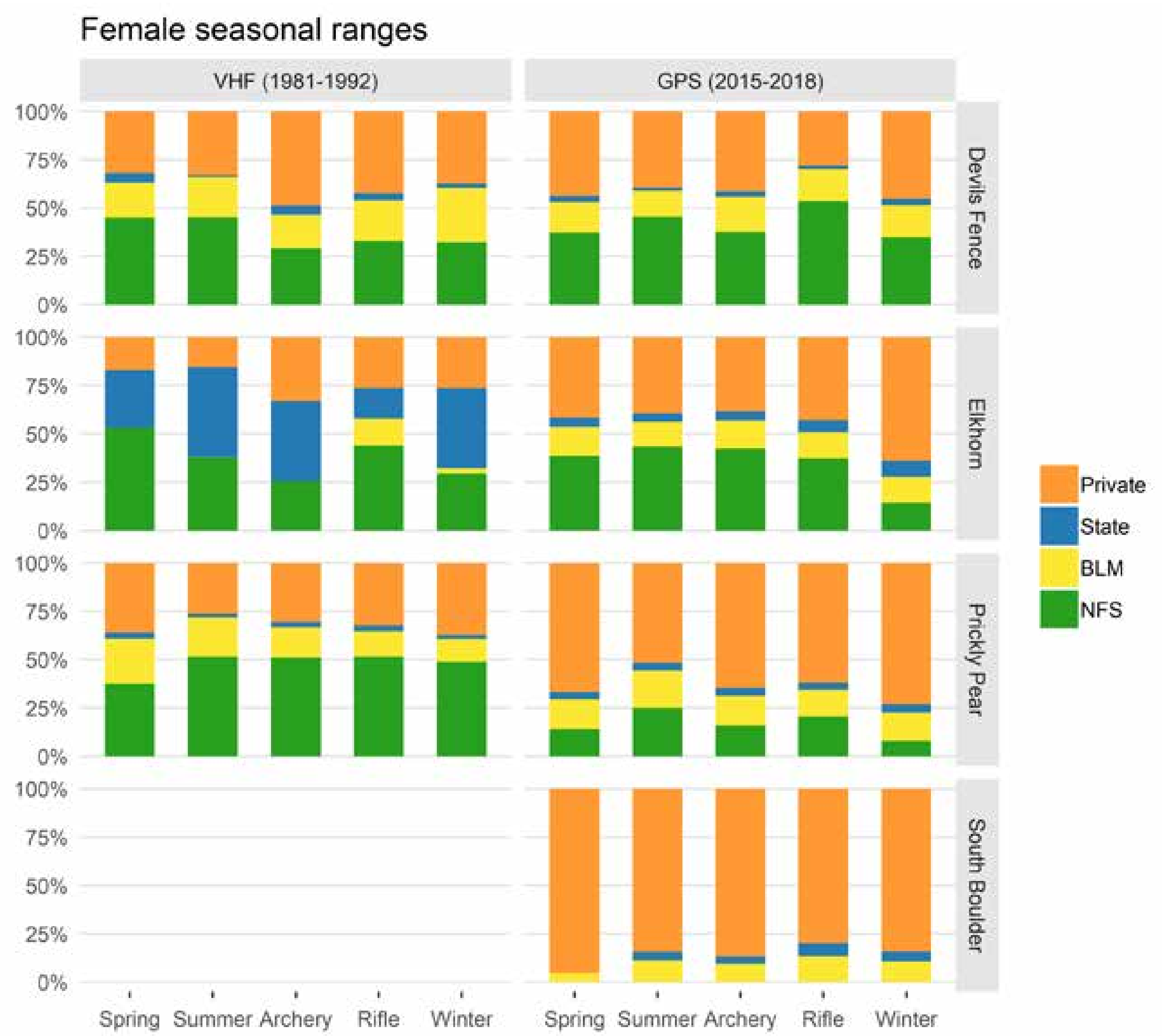

Figure 50 – Percent of private, state, Bureau of Land Management (BLM), and U.S. National Forest System (NFS) land ownership within adult female seasonal ranges for each Boulder Valley population segment in the VHF (1981 – 1992) and GPS (2015 – 2018) studies of the Elkhorn population in west-central Montana, USA. Percentages of other city, county, and federal ownerships were too small for display.

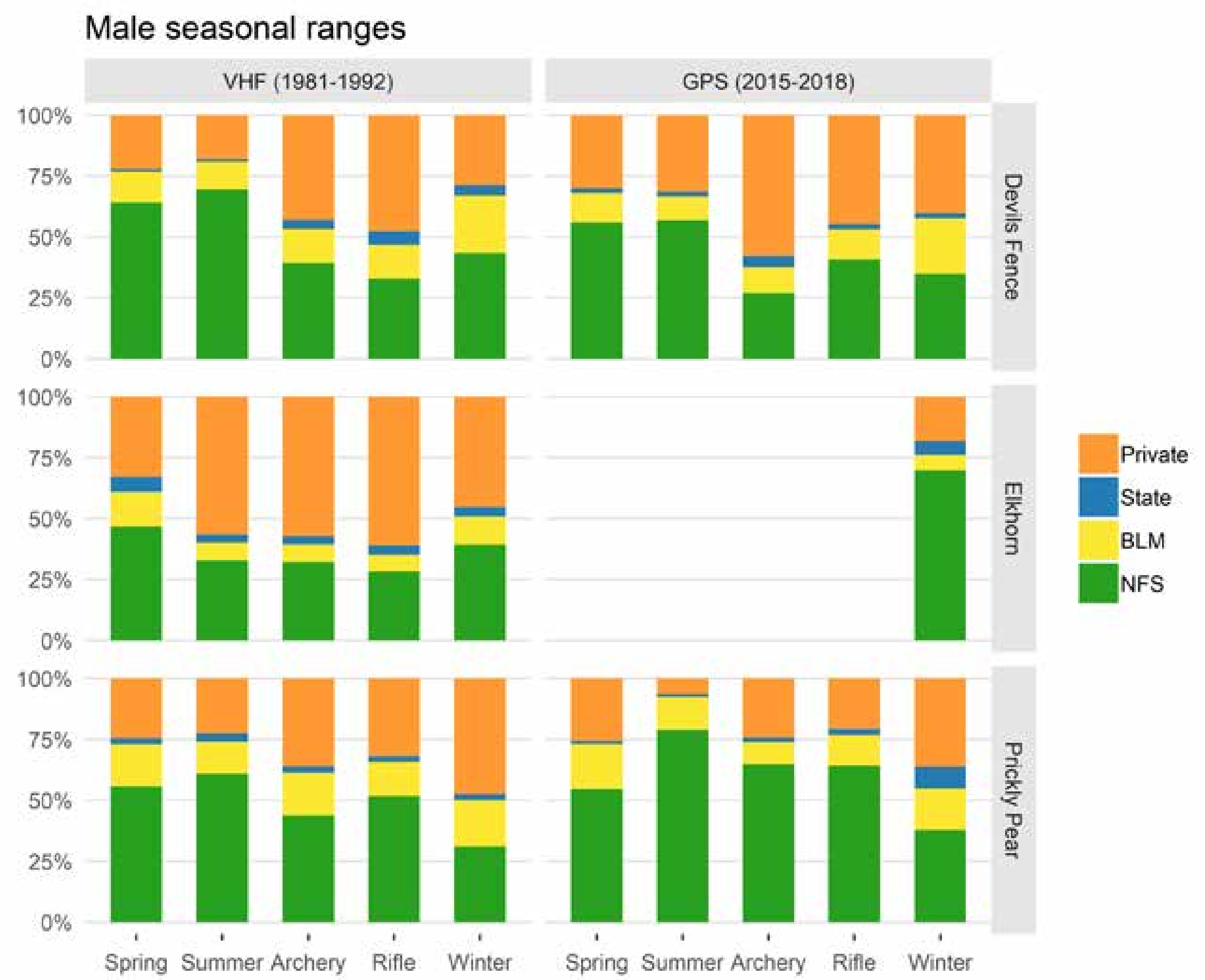

Figure 51 – Percent of private, state, Bureau of Land Management (BLM), and U.S. National Forest System (NFS) land ownership within adult male seasonal ranges for each Boulder Valley population segment in the VHF and GPS studies of the Elkhorn population in west-central Montana, USA. Percentages of other city, county, and federal ownerships were too small for display. Due to low sample sizes in the GPS data, only the winter range was estimable for the Elkhorn population segment.

Discussion

Since the initial VHF radio-collar study implemented 1981 – 1992, seasonal ranges of the elk in the Elkhorn Mountains appear to have expanded south into the South Boulder EHU of HD 380 and into the adjacent HD 370 (however, see limitations described below). In particular, we found that elk in the Devils Fence population segment occupied areas farther south than during the previous study and that elk in the more recently identified South Boulder population segment were year-long residents of the southern portion of the South Boulder EHU. Although elk in the South Boulder population segment may have originated from other regions, it is likely that the source is from the Devils Fence population segment due to the proximity and expanded seasonal ranges of these elk. Incidences of anecdotal observations of very low numbers of elk in the South Boulder EHU in the early 1990's, however, may suggest a longer presence or an earlier dispersal event in that area than revealed by our data.

During our GPS study, we found no movement of females into or away from the South Boulder population segment. Three males from the Devils Fence population segment seasonally occupied the South Boulder EHU; all 3 males spent some amount of time during the archery hunting season and 2 males spent one late-winter in the South Boulder EHU. While the seasonal ranges of the South Boulder population segment were based on one collared female, they were likely representative of at least a portion of the population segment. In addition, aerial counts during the winter indicate that approximately 150 elk occupy the South Boulder EHU suggesting that the population segment has become established. The most recent count for this population segment was 143, and the population appears to be stable since consistent counts began in 2015 (range 143 – 163; counts prior to 2015 were inconsistent and included in the Devil's Fence EHU).

Seasonal movements of the South Boulder population segment showed areas of use on both the west (HD 370) and east side of State Highway 69. These elk primarily used HD 370 during the summer and rifle seasons. While seasonal ranges of the South Boulder population segment encompassed portions of I-90, this was due to limitations of using kernel density estimates; no GPS locations occurred south of the interstate.

Public hunting access and therefore hunting pressure has been variable in the South Boulder EHU. Much of the area was private land, and public land areas, with the exception of the Doherty Mountain area, were generally only accessible through adjacent private land (Figure 51). Some private property in the area was enrolled in FWP's Block Management program, while other private property was generally restricted to friends and family only or no hunting was allowed at all. Elk were often found on those properties with the most limited hunting access during both the archery and rifle hunting seasons.

Generally, seasonal ranges and core use areas of the Prickly Pear, Elkhorn, and Devils Fence population segments have remained relatively consistent since the previous study. Some differences were apparent, however. First, female seasonal ranges in the Prickly Pear population segment suggest increased year-long residency patterns on lower elevation private lands along I-15. Second, male core use areas across all seasons in the Prickly Pear population segment generally occurred at higher elevations and included an area located farther to the north on the border of the Sheep Creek EHU. Lastly, female seasonal ranges in the Elkhorn population segment suggest reduced year-long use of State of Montana lands within the Elkhorn EHU. Few GPS locations occurred within these state lands and only during the rifle (primarily at night) and winter season. However, these locations were based on only 3 females and may not represent the entire population segment.

Our findings should be treated with some caution. Differences in study designs between the VHF and GPS studies may have influenced the results, including what, how many, and where animals were captured (e.g., VHF-collared animals were exclusively captured on U.S. Forest System lands and had larger representation for each season). Elk may have been present at very low numbers in the Boulder Valley EHU but were not collared as part of the VHF study. However, we did find some evidence that individuals from other populations used areas farther south during the GPS study as compared to the VHF study. Additionally, kernel density estimates can over-estimate the extent of seasonal ranges for low sample sizes and does not consider barriers such as development, roads, and water bodies. Lastly, changes between seasonal ranges may be due to mortalities of collared individuals, particularly during the archery and rifle seasons.

Section 9 – Effects of Vegetation Restoration Treatments on Elk Habitat Use

Introduction

Restoration efforts aimed at enhancing vegetation conditions can improve habitat for and aid in managing distributions of wildlife by altering important resources such as food and cover. For ungulates, restoration efforts have proven valuable for improving forage by using methods such as prescribed fire and thinning of conifers (Jourdonnais and Bedunah 1990, Peck and Peek 1991, Sachro et al. 2005, Vore et al. 2007, Long et al. 2008, Sittler et al. 2015). In the Elkhorn Mountains, restoration treatment projects focused on enhancing wildlife habitat and ungulate forage were implemented by the U.S. Forest Service (USFS) on National Forest System lands spanning 1994 – 2017 (U.S. Forest Service 1994, 1996, 2000, 2003, 2004, 2013). The treatments typically employed prescribed burning and thinning of conifers within forest and grassland land cover types. The response of elk to these treatments has not been evaluated, however. Using telemetry data, our objective was to assess the efficacy of these treatments by characterizing elk use patterns and changes in elk use patterns of the treated areas. To characterize post-treatment use patterns, we used GPS location data collected from 60 individual elk (see *Section 3 – Elk Capture, Sampling, Survival, & Distributions*), and to characterize changes in elk use patterns, we compared the post-treatment GPS locations with pre-treatment VHF location data collected from 323 individual elk (see *Methods* in *Section 5 – Effects of Mountain Pine Beetle on Elk Habitat Use*). We characterized elk use patterns separately for the winter, spring, summer, archery, and rifle seasons.

Methods

The treatment projects (Table 17, Figure 52) were initiated based on USFS Decision Memos and included: 1) the Crow Creek Vegetation Treatment, 2) the Bighorn Sheep and Elk Winter Range (that includes the Bighorn Sheep Habitat Enhancement and the Power Gulch

Bighorn Sheep Prescribed Burn treatments), 3) the Pole Creek Prescribed Burn, and 4) the 1988 Elkhorns Habitat Enhancement. Treatment dates for each project were inferred from the Decision Memos and spatial attribute tables but were not always available for individual polygons. Given this and that polygons within each project received similar types of treatments in a similar timespan, we aggregated polygons for each treatment project.

Table 17 – Vegetation restoration treatments implemented by the U.S. Forest Service spanning 1994 – 2017 in the Elkhorn Mountains, west-central Montana, USA. Map IDs correspond to Figure 52.

Map ID	Project name	Treatment date(s)	Area (km^2)	Project summary	Comments
1	Crow Creek Vegetation Treatment	1994 – 2017	34.21	Prescribed burning & thinning of conifers to improve wildlife habitat.	
2	Bighorn Sheep & Elk Habitat Projects	1996 – 2007	1.83	Prescribed burning & conifer reduction to improve bighorn sheep and elk habitat on winter range.	Includes the Bighorn Sheep Habitat Enhancement (1996 – 1999), Bighorn Sheep and Elk Winter Range Prescribed Burn (2000 – 2001), and the Power Gulch Bighorn Sheep Prescribed Burn (2004 – 2007) treatment projects.
3	Pole Creek Prescribed Burn	2003	0.69	Prescribed burning of grasslands to enhance elk forage.	
4	1988 Elkhorns Habitat Enhancement	2014	2.02	Aspen & willow regeneration, prescribed burning in lodgepole pine forest, & thinning of conifers to improve wildlife habitat.	Treatments in lodgepole pine forests were to promote diversity of tree species and stand age class following the 1988 Warm Springs fire.

The Crow Creek Vegetation Treatment project was jointly proposed by the USFS and Bureau of Land Management to treat grassland and conifer habitats in the Crow Creek drainage and Limestone Hills with a combination of prescribed burning and thinning (U.S. Forest Service 1994). These treatments began in 1994 and spanned 14 years. The Bighorn and Elk Habitat projects included treatments from 3 separate projects that overlapped spatially in the lower Crow Creek drainage: 1) the Bighorn Sheep Habitat Enhancement project (1996 – 1999; U.S. Forest Service 1996) aimed at enhancing forage and reducing conifer encroachment with prescribed burning in grassland areas on bighorn sheep winter range, with expected coincidental benefits to elk through forage improvement; 2) the Bighorn Sheep and Elk Winter Range project (2000 – 2001; U.S. Forest Service 2000) aimed at improving forage conditions for bighorn sheep and elk, reducing conifer encroachment and canopy cover, and regenerating aspen stands; and the Power Gulch Bighorn Sheep Prescribed Burn project (2004 – 2007; U.S. Forest Service 2004) intended to complete unfinished treatments from the previous treatments and treat an additional unit using prescribed burning and slashing of conifers.

The Pole Creek Prescribed Burn project was intended to revitalize grasslands to improve forage conditions and attract elk and cattle away from adjacent heavily grazed areas (U.S. Forest Service 2003). The treatment occurred in the Pole Creek drainages along the lower Beaver Creek area and was completed in 2003. The 1988 Elkhorns Habitat Enhancement project aimed to use thinning followed by prescribed burning to maintain and enhance wildlife habitat affected by the 1988 Warm Springs Fire located in the Jackson Creek, Staubach Creek, Crystal Creek, and Pole Creek drainages. The treatments were designed to reduce colonizing conifers for regenerating aspen and willow stands, maintain grasslands and shrublands, and promote age class and tree species diversity in homogenous lodgepole pine stands that regenerated after the fire. The treatments began in 2014 and were ongoing at the time of this study.

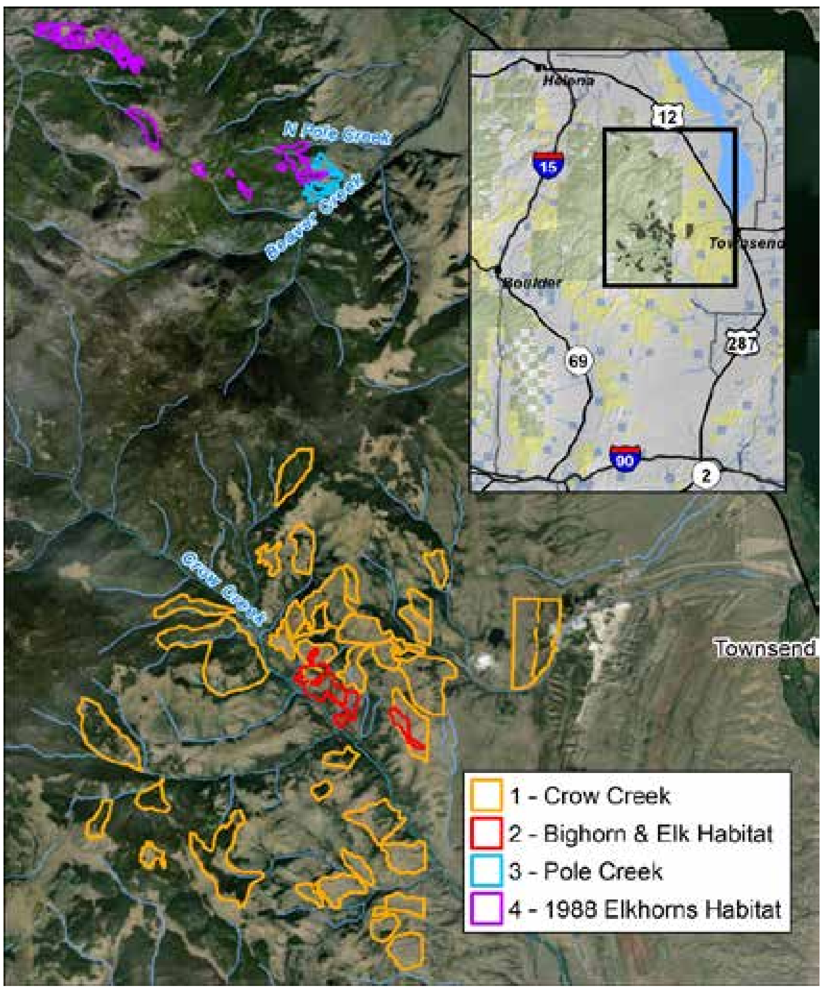

Figure 52 – Vegetation restoration treatments implemented by the U.S. Forest Service spanning 1994 – 2017 in the Elkhorn Mountains, west-central Montana, USA. Map IDs correspond to Table 17. In inset map, land ownership is colored as U.S. Forest System (green), Bureau of Land Management (yellow), state of Montana (blue), and private (light gray) and restoration treatment areas are indicated in dark gray.

To evaluate elk use patterns of treatment areas, we overlaid the pre- and post-treatment locations on the polygons. We summarized the number and proportion of pre- and post-treatment locations occurring within each treatment project and across seasons (i.e., spring, summer, archery hunting season, rifle hunting season, and winter). We defined spring (i.e., calving) as May 20 – June 15, summer as July 1 to 1 week prior to the opening of archery season, and winter as 1 week after the close of rifle season to May 1. We defined the archery and rifle hunting seasons according to historic and current annual Montana general elk archery and rifle season dates, where the 6-week archery season starts on the 1st Saturday in September and the 5-week rifle season starts 5 weeks prior to the Saturday after Thanksgiving. We lastly summarized the proportion of post-treatment locations within each treatment project for day (0700 – 1500) and night periods to assess timing of elk use.

Results

All treatment projects received elk use during both the pre- and post-treatment periods (Figure 53), with the Crow Creek Vegetation Treatment receiving substantially more proportional use, likely largely associated with the larger size of the project area. For all treatment projects and periods, however, proportional use was very low, with less than 6% of all locations occurring in the Crow Creek Vegetation Treatment and less than 0.5% of all locations occurring in each of the remaining treatment projects. Elk proportional use of treatment projects varied across seasons (Figure 54). During both the pre- and post-treatment periods, the Crow Creek Vegetation Treatment received elk use across all seasons, with most use occurring during the winter. All treatment projects received the most proportional use (pre- and post-treatment) during the winter excepting the 1988 Elkhorns Habitat Enhancement project that received most post-treatment proportional use during the summer.

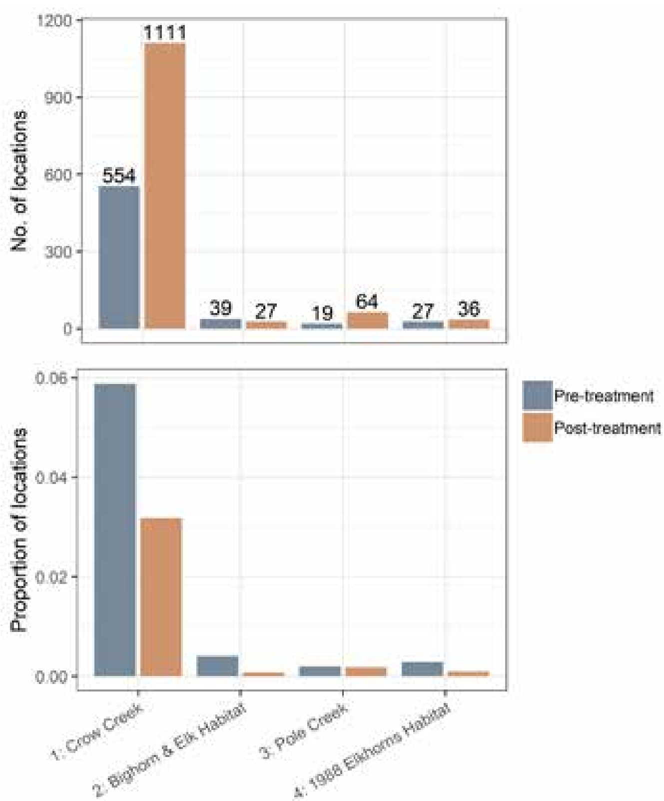

Figure 53 – Number and proportion of pre- and post-treatment locations within each restoration project treatment area in the Elkhorn Mountains, west-central Montana, USA, 1981-1992 and 2015-2017. Numbers in x-axis labels correspond to map IDs in Table 17 and Figure 52.

From the pre- to post-treatment periods, there was an overall reduction in proportional use of 2.7% in the Crow Creek Vegetation Treatment. Across all seasons in this treatment project, the reduction in proportional use averaged

2.0% (± 0.03% SD) with proportional use decreasing the most during winter (5.6%) and increasing only during the summer by 2.0%. In the Bighorn and Elk Habitat project, there was an overall reduction in proportional use of 0.3%. Across all seasons, the reduction in proportional use averaged 0.2% (± 0.3%) with proportional use decreasing the most during winter (0.7%) and increasing only during the summer by 0.02%. In the Pole Creek Prescribed Burn project, there was an overall reduction in the proportional use of 0.02%. The largest decrease in proportional use occurred during the winter (0.1%) and increases in proportional use occurred during both the archery (0.02%) and rifle season (0.5%). In the 1988 Elkhorns Habitat Enhancement project, there was an overall reduction in proportional use of 0.2%. Across all seasons, the reduction in proportional use averaged 0.2% (± 0.4%) with proportional use decreasing the most during the rifle season (0.6%) and increasing during the summer (0.3%) and archery season (0.07%).

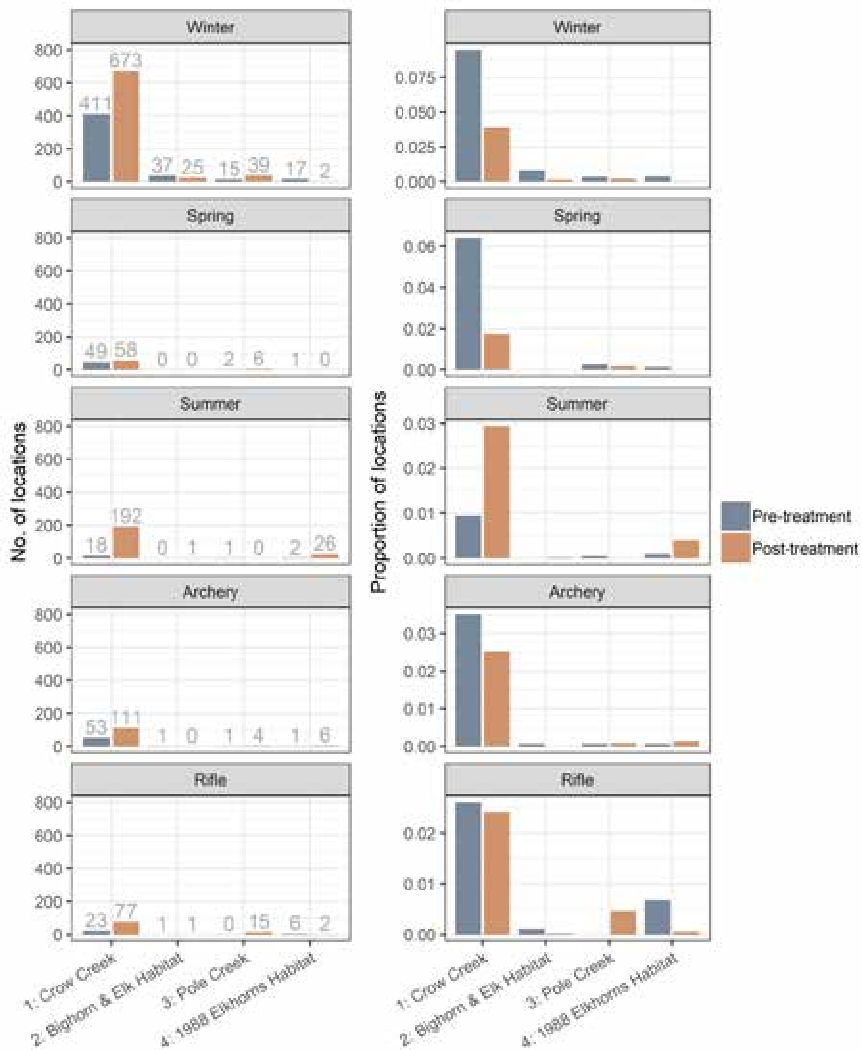

Figure 54 – Number and proportion of pre- and post-treatment locations for each season within each restoration project treatment area in the Elkhorn Mountains, west-central Montana, USA, 1981-1992 and 2015-2017. Numbers in x-axis labels correspond to map IDs in Table 17 and Figure 52.

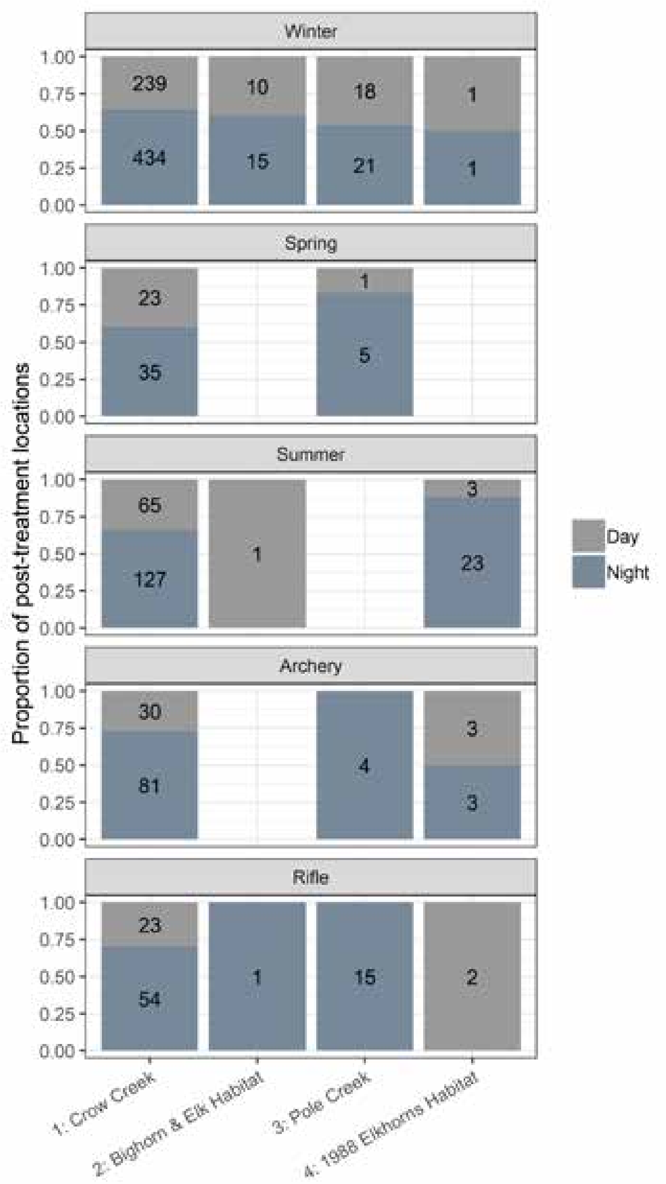

Figure 55 – Proportion of post-treatment locations for day (0700 – 1500) and night periods within each restoration project treatment area in the Elkhorn Mountains, west-central Montana, USA, 2015-2017. Numbers in x-axis labels correspond to map IDs in Table 17 and Figure 52.

Across nearly all seasons where elk use occurred, the proportion of post-treatment locations in the treatment projects occurred primarily (≥ 50%) during night (Figure 55); however, the number of locations during some seasons was extremely low. In the Crow Creek Vegetation Treatment, the average percent of locations that occurred during the night was 66.8% (± 4.9%). In the Bighorn and Elk Habitat project, 60.0% of locations during the winter occurred during night. The remaining seasons had very few (≤ 1) locations. In the Pole Creek Prescribed Burn project, 53.8% and 100% of locations during the winter and rifle season, respectively, occurred during the night. The remaining seasons had very few (≤ 6) locations that primarily occurred during night. In the 1988 Elkhorns Habitat project, 88.5% of locations during the summer occurred during the night. The remaining seasons had very few (≤ 6) locations.

Discussion

Our results show elk use in each of the vegetation treatment areas during both the pre- and post-treatment time periods. The majority of pre- and post-treatment locations in each of the treatment areas occurred during the winter excepting the 1988 Elkhorns Habitat Enhancement project where the majority of post-treatment locations occurred during the summer. The Crow Creek Vegetation Treatment project received elk use each season, whereas use was lacking or minimal during non-winter seasons in the Bighorn and Elk Habitat project area, during spring, summer, and archery in the Pole Creek Prescribed Burn project area, and during winter, spring, archery, and rifle seasons in the 1988 Elkhorns Habitat Enhancement project area. The vast majority of the post-treatment locations occurred during night when elk are likely to be foraging, indicating that elk may be benefiting from the forage improvements resulting from the restoration efforts.

Overall, however, our results show a reduction in elk use of treatment areas. Changes in use were most evident for the Crow Creek Vegetation Treatment project, due to larger sample sizes, with decreases in use during all seasons excepting summer. Treatments in this project included substantial removal of colonizing juniper in grasslands which may result in a decrease in cover that provides security and thermal benefits to elk. Decreases in elk use during the winter, spring, archery, and rifle seasons in this project area, as well as other project areas, may be a consequence of conifer removal, however other unknown factors may also play a role. Increases in use occurred during the summer in the Bighorn and Elk Habitat project, archery and rifle seasons in the Pole Creek Prescribed Burn project, and the summer and archery seasons in the 1988 Elkhorns Habitat Enhancement project.

However, the number and proportion of both pre- and post-treatment locations were extremely small in each project area (< 6% of locations), preventing or substantially limiting our ability to make interpretations of change in elk use of these areas. In addition, we could not account for a variety of changes occurring on the Elkhorn Mountains landscape, and therefore cannot directly associate changes in use with restoration efforts. For example, reductions in elk use in the Crow Creek Vegetation Treatment may be due to the increased popularity of archery, particularly given the greater concentration of roads open to motorized travel in this area. The reductions in elk use observed across all treatment areas during the winter may be due to factors that are similarly affecting the eastern portion of the Elkhorn Mountains, given all the restoration areas are located in this region. For example, displacement of elk may be due to increased antler hunting activity in this region during the winter. Additionally, changes to the USFS travel plan in 1995 may have contributed to observed changes in elk use.

Section 10 – Conclusions & Management Recommendations

The Elkhorn elk population continues to be relatively stable and within the population management objective of 2,000 elk, with good recruitment rates (range 25 – 36 calves per 100 adult females since 2012). In addition, the annual counts ($\bar{x}$ = 66.4) of yearling (spike) bulls have remained relatively constant since the late 1990's and recent (2017 – 2018) annual bull:cow ratios (22.3 bulls per 100 cows) and counts (198 – 246) of brow-tined bulls were high. Annual survival rates of female ($\bar{x}$ = 0.83, 95% CI = 0.72 – 0.90) and male ($\bar{x}$ = 0.61, 95% CI = 0.38 – 0.78) elk were near estimates of other harvested elk populations in Montana and western states, with the majority (75 – 78%) of mortalities caused by human harvest (Smith and Anderson 1998, Biederbeck et al. 2001, Hamlin and Ross 2002, Raedeke et al. 2002, Brodie et al. 2013).

Although evidently not constraining female pregnancy rates based on our data, nutritional resources on the Elkhorn Mountains landscape may be limited given the lower levels of body fat observed in females as compared to other elk populations in western Montana. Compared to similar assessments of the nutritional landscape in the northern Sapphire Mountains and southern Bitterroot Valley in western Montana, the Elkhorn Mountains landscape also had lower levels of summer-fall forage abundance, particularly in forested areas (Proffitt et al. 2016b, 2017, DeVoe et al. 2018). For example, in uninfected lodgepole pine forests in the northern Sapphire Mountains, mean herbaceous forage abundance was estimated as 31.9 g/m^2, whereas we found 3.7 g/m^2 in the Elkhorn Mountains. Within the Elkhorn Mountains, mountain pine beetle (MPB)-killed lodgepole forests had higher mean herbaceous forage abundance (7.1 g/m^2), graminoid forage cover (12.5%), and herbaceous quality (3.22 kcal/g) during the summer-fall relative to lodgepole forests that were unaffected by MPB's (3.7 g/m^2, 4.5%, and 3.12 kcal/g, respectively). We attribute this to changes in canopy cover in MPB-infected lodgepole forests permitting greater production of understory vegetation. Managers could use vegetation treatments, such as thinning and prescribed burning, or managing wildfires to enhance the availability of late summer and fall forage in unaffected forested areas (DeVoe et al. 2018, Proffitt et al. 2019).

The Elkhorn Mountains have experienced considerable change over the past 30 years. While many changes, such as grazing practices, private land use practices, and conifer encroachment, were beyond the scope of this study, we found some evidence that elk habitat use may have been influenced by the extensive MPB-killed lodgepole pine forests. Elk used areas impacted by MPBs less across nearly all seasons as compared to use prior to MPB-infestation, with the most substantial reductions in use for male elk during the archery and rifle seasons and for female elk during the archery season. However, we also found that elk selected strongly for areas with greater canopy cover during the hunting seasons and that levels of canopy cover in MPB-infested forests remained relatively high. MPB infected lodgepole forest canopy cover was 15% and 42% higher than uninfested Douglas fir and ponderosa pine forests, respectively. This suggests that although elk may use MPB-affected areas less than prior to infestation, these areas still provide valuable security cover during the hunting seasons. Incorporating our results that elk also selected strongly for areas farther from motorized routes, we recommend that managers aim to provide security areas during the archery and rifle hunting seasons for both sexes that are comprised of canopy cover values ≥ 23–60% and ≥ 1,846–3,679 m from motorized routes, which represent the thresholds for areas that contain 75% and 50% of the elk use on the landscape during hunting seasons, respectively.

While our results indicate that elk continued to use areas impacted MPBs post-infestation, a recent study in south-central Wyoming by Lamont et al. (2019) found strong avoidance of MPB-killed areas during the summer despite greater forage abundance in these areas. Lamont et al. (2019) suggested that the avoidance was driven by energetic costs of locomotion due to increased downed logs, conditions not currently present at a substantial level in the Elkhorn Mountains. Additionally, the study suggested avoidance of MPB-affected forests in summer may be due to lack of adequate thermal cover (Lamont et al. 2019). In the Elkhorn Mountains, we expect that as blowdown of dead trees increases, the relationships with elk use may change potentially resulting in decreased selection of affected areas due to altered security cover, thermal cover, and locomotive costs associated with fallen timber. In contrast, Ivan et al. (2018) documented an increase in the use of MPB-infested forests by elk, mule deer, and moose during summer months across Colorado, presumably driven by increases in understory forage associated with the decrease in canopy cover post-defoliation. Given the host of dynamic factors that can influence wildlife response to MPB-infestations, many of which are spatially and temporally variable and difficult to quantify over broad spatial scales (i.e., number of downed trees), regional and taxonomic generalizations may prove difficult given the limited number of studies examining wildlife responses to MPB-infestations that have been completed currently (Saab et al. 2014). Nonetheless, the management of adjacent or nearby intact forests may become increasingly important in providing security as infested stands mature and potentially become inadequate for providing elk security. We recommend that in the Elkhorn Mountains and other areas recently impacted by MPB, adjacent, intact forests be managed for elk security to ensure that elk have secure cover available as the infestation matures and trees fall.

Simultaneous with changes in elk use of MPB-affected forests, elk also increased use of private lands from the pre- to post-MPB infestation periods. We suspect that the MPB infestation, the continued increase in hunter effort and pressure, and the changing perceptions and land use of private landowners may have been working concurrently to influence changes in elk use patterns over the past 25 years. Out of the 4 Boulder Valley population segments (i.e., Devils Fence, Elkhorn, Prickly Pear, and South Boulder), we observed an increase in year-long residency on private lands along I-15 of females in the Prickly Pear segment. Additionally, female elk in the Elkhorn segment showed substantially reduced year-long use of State of Montana lands, favoring private lands along State Highway 69 instead. Movements to private lands were not as evident in the remaining population segments and the overall population seasonal ranges still indicated extensive use of public lands, even during the archery and rifle hunting seasons. However, if trends of elk distributional shifts to private lands continue in the Elkhorn population, as has occurred in other populations in Montana (Proffitt et al. 2010, 2013, 2017), retaining the same harvest regulations without broadening strategies to improve public hunter access on private lands or reducing harvest risk on public lands may fail to maintain the elk population within objective and result in undesirable elk distributions concentrated on privately owned lands. Levels of elk tolerance on private properties may be reduced if forage competition with livestock and crop or property damage by elk increase. Additional strategies for maintaining or encouraging public land use by elk may include enhancing summer-fall nutritional resources on public lands and working with private landowners to reduce elk access to high nutritional value forage or attractants on their properties. Although current harvest strategies have been successful in managing the overall population to date, these recommended strategies may help prevent distributional shifts to private lands from occurring prior to and during the fall hunting seasons by balancing harvest risk and forage availability across public and private lands and allow improved hunter access to elk and harvest in the future.

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Appendix A – Development & Accuracy of Landcover Classifications

Development of landcover classifications

The landcover classifications were developed from USDA Forest Service products that included landcover classifications from the Northern Region Vegetation Mapping Program (VMap) database (*https://www.fs.usda.gov/detailfull/r1/landmanagement/gis/?cid=stelprdb5331054&width=full*) and mountain pine beetle (MPB) infestation data from the Aerial Detection Survey (ADS) database (Johnson and Wittwer 2008, Barber and Vanderzanden 2009; *https://www.fs.usda.gov/detail/r1/forest-grasslandhealth/?cid=stelprdb5366459*). We integrated these datasets to identify general landcover classifications as well as lodgepole pine forests that were affected by MPB.

The landcover classifications were originally defined by Cascaddan (2018; see below for development methods and accuracy assessment) and included 13 classes: cultivated agriculture, other agriculture, grassland, shrubland, upland wetland riparian, valley wetland riparian, low elevation conifer, high elevation conifer, mature unaffected lodgepole, old infested lodgepole, recent infested lodgepole, early seral lodgepole, and non-habitat. For the purposes of this report and due to limited inference as a consequence of low sample sizes in landcover classes, these classes were further aggregated into 7 classes that included: agriculture (cultivated and other agriculture), grassland, shrubland, riparian (valley and upland wetland riparian), forest (low and high elevation conifer), mature unaffected lodgepole, and affected lodgepole (old and recent infested lodgepole).

To identify lodgepole pine forest and distinguish between old and recent infested stands, we first filtered VMap to include only the PICO and PICO-IMIX classes (*Pinus contorta* and *Pinus contorta*-shade intolerant mix, respectively) from the tree dominance group 6040 classification. This dominance group is based on two thresholds: 1) if the dominant tree species comprises at least 60% of the total abundance, the dominance group is designated as the dominant species plant code; and 2) if the dominant tree species comprises < 60% but ≥ 40%, the dominance group is designated as the dominant species plant code with a suffix of the tree lifeform subclass, such as -IMIX (i.e., shade intolerant mix; Barber and Vanderzanden 2009). We then integrated the MPB infestation data to outline areas of MPB-caused tree mortality (Johnson and Wittwer 2008). This was done by erasing the first year of detection from all subsequent overlapping survey years to retain the first year of infestation of lodgepole pine by MPB for assignment into one of the two temporal infestation classes. USDA Forest Service fire history data was used to remove lodgepole pine forest that was affected by wildfire within 30 years. This was done to avoid sampling early seral lodgepole pine forest that MPB does not infest.

To classify the remaining landcover types, we reclassified VMap into 10 additional classes. Some VMap classes were split into more than one new class, and we used visual assessment of aerial imagery to make the distinction into new classes (e.g., for reclassifying GRASS-WET into a new class, aerial imagery was used to distinguish if the polygon was valley wetland riparian or cultivated ag; Table A1). The classes included cultivated agriculture, other agriculture, grassland, shrubland, upland wetland riparian, valley wetland riparian, low elevation conifer, high elevation conifer, and non-habitat. High elevation conifer included *Pinus albicaulis, Abies lasiocarpa,* and *Picea engelmannii*. Low elevation conifer included *Pseudotsuga menziesii***,** *Pinus ponderosa*, and *Pinus flexilis*.

Assessment of landcover classification accuracy

To assess model accuracy, we compared the model derived landcover class to actual classes verified on the ground. We sampled a total of 290 independent sites that were randomly generated across the study areas from within the landcover classes. Trained personnel recorded the actual cover class at each site. We first used an error matrix (Table A2) to estimate the overall accuracy, producer's accuracy, and user's accuracy (Table A3; Congalton 1991). We then estimated the Kappa statistic as a multivariate measure of agreement for discrete data, between the model derived landcover classes and the ground-truthed cover classes (Landis and Koch 1977, Congalton 1991). In the error matrix and accuracy assessment statistics we evaluated the accuracy of 11 of the landcover classes (grassland, upland wetland riparian, other agriculture, shrubland, low elevation conifer, high elevation conifer, mature unaffected lodgepole, valley wetland riparian, MPB-killed forest, cultivated agriculture, and early seral lodgepole). It was impossible for personnel to distinguish between old and recent infested lodgepole pine forest, so these two classes were combined into the MPB-killed forest class for the accuracy assessment.

The overall accuracy was 0.64 (Table A3). The producer's accuracy rates averaged 0.64, ranging from a low of 0 in the other agriculture class to 100 in the valley wetland riparian and cultivated agriculture classes. The user's accuracy rates averaged 0.56, ranging from 0 in the other agriculture class to 100 in the mature unaffected lodgepole class. Based on these accuracy assessments, the landcover model performed moderately well for discriminating most landcover classes but was least accurate in predicting the other agriculture class. The Kappa statistic was estimated to be 0.54 ($p < 0.001$; 95% CI = 0.47, 0.61) indicating moderate agreement.

Table A1. The original Vegetation Mapping Program (VMap) landcover class code, class name, description and the reclassification code and name for the 13 landcover classes in the Elkhorn region, Montana.

VMap Code	VMap Name	Description	Reclassification Code	Reclassification name
3160	GRASS-DRY	Dry grass	1, 3, or 12	Grass, Other Agriculture, or Cultivated Ag
8170	POTR5	Aspen	2 or 9	Upland or Valley Wetland Riparian
3190	GRASS-WET	Wet grass	1, 3, 12, 2, or 9	Grass, Other Agriculture, Cultivated Ag, Upland or Valley Wetland Riparian
3330	SHRUB-MESIC	Mesic shrub species	2 or 9	Upland or Valley Wetland Riparian
8160	POPUL	Cottonwood and poplar	2 or 9	Upland or Valley Wetland Riparian
3320	SHRUB-XERIC	Xeric shrub species	4	Shrubland
8180	JUNIP	Juniper	4	Shrubland
8183	JUNIP-IMIX	Juniper shade-intolerant mix	4	Shrubland
8010	PIPO	Ponderosa pine	5	Low Elevation Conifer
8013	PIPO-IMIX	Ponderosa pine shade-intolerant mix	5	Low Elevation Conifer
8020	PSME	Douglas fir	5	Low Elevation Conifer
8023	PSME-IMIX	Douglas fir shade-intolerant mix	5	Low Elevation Conifer
8153	PIFL2-IMIX	Limber pine shade-intolerant mix	5	Low Elevation Conifer
8400	IMIX	shade-intolerant mix	5	Low Elevation Conifer
8123	PIAL-IMIX	Whitebark pine shade-intolerant mix	6	High Elevation Conifer
8060	ABLA	Subalpine fir	6	High Elevation Conifer
8064	ABLA-TMIX	Subalpine fir shade-tolerant mix	6	High Elevation Conifer
8074	PIEN-TMIX	Engelmann spruce shade-tolerant mix	6	High Elevation Conifer
8070	PIEN	Engelmann spruce	6	High Elevation Conifer
8050	PICO	Lodgepole pine	7, 10, 11, or 13	Mature Unaffected Lodgepole, Old Infested, Recent Infested, or Early Seral Lodgepole
8053	PICO-IMIX	Lodgepole pine shade-intolerant mix	7, 10, 11, or 13	Mature Unaffected Lodgepole, Old Infested, Recent Infested, or Early Seral Lodgepole
5000	WATER	Open water	8	Non-habitat
7000	SPVEG	Sparsely vegetated	8	Non-habitat
7100	URBAN	Urban	8	Non-habitat
8900	TRANS	Transportation	8	Non-habitat

Table A2. The error matrix showing the number of sample locations assigned to each landcover class and the actual category that was verified on the ground. Because age of infestation could not be determined in ground assessments, old infested and recent infested classes were combined into the mountain pine beetle (MPB)-killed forest class. Columns represent the ground verified class, and rows represent the assigned class from the landcover map.

	Grass	Upland Wetland Riparian	Other Ag	Shrub-land	Low Elev. Conifer	High Elev. Conifer	Mature Unaffect. Lodgepole	Valley Wetland Riparian	Cultivated Ag	Early Seral Lodgepole	MPB-killed Forest	Total
Grass	19	1	0	10	4	0	1	0	0	1	1	37
Upland Wetland Riparian	0	9	0	0	0	0	0	0	0	1	0	10
Other Agriculture	0	0	0	0	0	0	0	0	0	0	1	1
Shrubland	2	0	0	23	5	0	0	0	0	0	0	30
Low Elev. Conifer	0	0	0	0	25	0	0	0	0	1	10	36
High Elev. Conifer	0	0	0	0	1	7	0	0	0	0	11	19
Mature Unaffect. Lodgepole	0	0	0	0	0	0	3	0	0	0	0	3
Valley Wetland Riparian	0	0	5	0	0	0	0	2	0	0	0	7
Cultivated Ag	0	0	2	0	0	0	0	0	10	0	0	12
Early Seral Lodgepole	0	0	0	0	0	0	5	0	0	1	1	7
MPB-killed Forest	1	0	0	0	3	1	35	0	0	2	86	128
Total	22	10	7	33	38	8	44	2	10	6	110	290

Table A3. Producer's, user's, and overall accuracies (measured in proportions) for each landcover class comparing the landcover model class and the actual class as verified on the ground. Because the age class of infestation could not be distinguished on the ground, both the old and recent infested classes were combined into the mountain pine beetle (MPB)-killed forest class.

	Producer's Accuracy	User's Accuracy	
Grass	0.86	0.51	
Upland Wetland Riparian	0.90	0.90	
Other Agriculture	0.00	0.00	
Shrubland	0.70	0.77	
Low Elevation Conifer	0.66	0.69	
High Elevation Conifer	0.88	0.37	
Mature Unaffected Lodgepole	0.07	1.00	
Valley Wetland Riparian	1.00	0.29	
Cultivated Ag	1.00	0.83	
Early Seral Lodgepole	0.17	0.14	
MPB-killed Forest	0.78	0.67	
Average	0.64	0.56	
Overall			0.64
Kappa			0.54
Kappa 95% C.I.			0.47-0.61
Kappa p-value			<0.001

Appendix B – Habitat Security Models & Coefficient Estimates

Table B1 – Habitat security model selection results for tiers 1–3 comparing used and available locations for male and female elk in the archery and rifle hunting seasons, Elkhorn Mountains, southwest Montana, USA, 2015–2017. Models are arranged by AICc ranking. We also present the number of parameters (K) and model weight (w_i).

Model tier	Sex-Season	Model[a]	K	AICc	ΔAICc	w_i
Tier 1: Security patch	Female-Archery	Security.00	3	6399.02	0.00	0.67
		Security.30	3	6401.72	2.70	0.17
		Security.15	3	6401.86	2.85	0.16
	Female-Rifle	Security.30	3	4570.29	0.00	0.41
		Security.00	3	4570.86	0.56	0.31
		Security.15	3	4570.97	0.68	0.29
	Male-Archery	Security.00	3	3916.05	0.00	1.00
		Security.15	3	3984.58	68.53	0.00
		Security.30	3	3984.68	68.62	0.00
	Male-Rifle	Security.00	3	2132.94	0.00	0.96
		Security.30	3	2140.85	7.91	0.02
		Security.15	3	2140.85	7.91	0.02
Tier 2: Traditional security	Female-Archery	Canopy cover + DMOT	4	6267.63	0.00	1.00
		Canopy cover	3	6293.88	26.25	0.00
		Canopy cover + Security.00	4	6294.21	26.59	0.00
		DMOT	3	6366.89	99.26	0.00
		Security.00	3	6399.02	131.39	0.00
	Female-Rifle	Canopy cover + DMOT	4	4328.85	0.00	1.00
		Canopy cover + Security.00	4	4363.95	35.10	0.00
		Canopy cover	3	4382.79	53.94	0.00
		DMOT	3	4527.33	198.49	0.00
		Security.00	3	4570.86	242.01	0.00
	Male-Archery	Canopy cover + DMOT	4	3902.77	0.00	0.78
		DMOT	3	3905.31	2.55	0.22
		Canopy cover + Security.00	4	3913.24	10.47	0.00
		Security.00	3	3916.05	13.29	0.00
		Canopy cover	3	3974.72	71.95	0.00
	Male-Rifle	Canopy cover + DMOT	4	2096.46	0.00	0.99
		Canopy cover + Security.00	4	2105.41	8.96	0.01
		Canopy cover	3	2110.71	14.25	0.00
		DMOT	3	2121.66	25.20	0.00
		Security.00	3	2132.94	36.48	0.00
Tier 3: Traditional & landscape security	Female-Archery	Canopy cover + DMOT + Slope^2 + Ruggedness	7	6233.22	0.00	1.00
		Canopy cover + DMOT	4	6267.63	34.41	0.00
	Female-Rifle	Canopy cover + DMOT + Slope^2 + Ruggedness	7	4305.30	0.00	1.00
		Canopy cover + DMOT	4	4328.85	23.54	0.00
	Male-Archery	Canopy cover + DMOT + Slope^2 + Ruggedness	7	3808.99	0.00	1.00
		Canopy cover + DMOT	4	3902.77	93.77	0.00
	Male-Rifle	Canopy cover + DMOT + Slope^2 + Ruggedness	7	2029.19	0.00	1.00
		Canopy cover + DMOT	4	2096.46	67.27	0.00

[a] Security.00 = Security patch with no canopy cover requirement; Security.15 and Security.30 = Security patch with at least 50% coverage of 15% and 30% canopy cover; DMOT = distance to motorized route.

Table B2 – Coefficient estimates for the top-ranked habitat security models for male and female elk during the archery and rifle hunting seasons, Elkhorn Mountains, southwest Montana, USA, 2015–2018.

Sex-Season	Covariate	Beta	Std. Error
Female-Archery	Intercept	-2.629	0.047
	Canopy cover	0.294	0.040
	DMOT	0.196	0.039
	Slope	0.222	0.048
	Slope^2	-0.188	0.035
	Ruggedness	0.032	0.036
Female-Rifle	Intercept	-2.811	0.063
	Canopy cover	0.595	0.056
	DMOT	0.343	0.051
	Slope	0.285	0.060
	Slope^2	-0.169	0.041
	Ruggedness	-0.094	0.045
Male-Archery	Intercept	-2.471	0.075
	Canopy cover	0.009	0.050
	DMOT	0.479	0.063
	Slope	0.063	0.064
	Slope^2	-0.424	0.059
	Ruggedness	0.225	0.043
Male-Rifle	Intercept	-2.466	0.101
	Canopy cover	0.207	0.079
	DMOT	0.289	0.077
	Slope	0.491	0.099
	Slope^2	-0.533	0.087
	Ruggedness	0.189	0.059

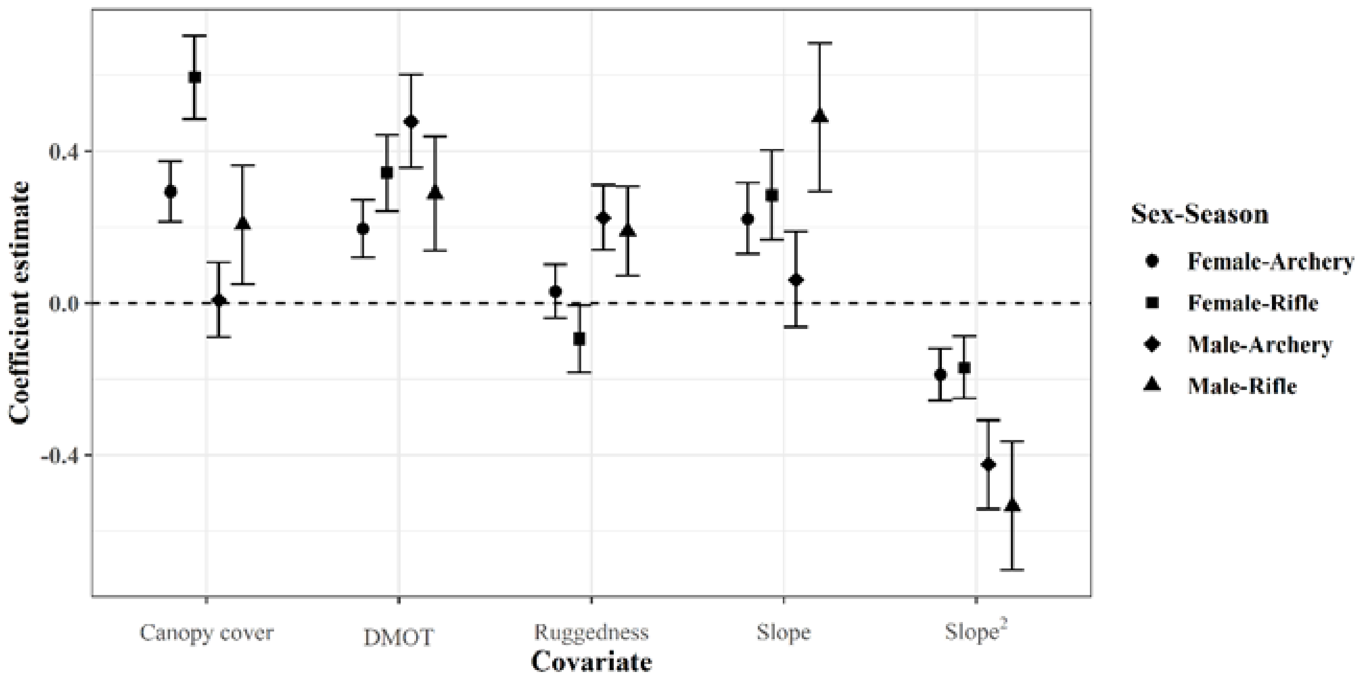

Figure B1 – Coefficient estimates (± standard error) for the top-ranked habitat security models for male and female elk during the archery and rifle hunting seasons, Elkhorn Mountains, southwest Montana, USA, 2015–2018. DMOT = distance to motorized road.