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*Research Article*

# Hiding Without Cover? Defining Elk Security in a Beetle-Killed Forest

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**ABSTRACT** Recent mountain pine beetle (*Dendroctonus ponderosae*; pine beetle) outbreaks in the western United States have affected nearly 18 million ha of pine (*Pinus* spp.) forest and are unprecedented in spatial extent, severity, and duration, yet little is known about wildlife responses to large-scale insect outbreaks. Elk (*Cervus canadensis*) are important wildlife whose dominant management paradigm on public lands has focused on providing security habitat to increase survival during hunting seasons and to maintain elk presence on public lands to promote hunter opportunity. To assess the effect of pine beetles and associated changes in forest structure on elk security, we used a time series to characterize canopy cover pre- and post-pine beetle outbreak, characterized relative canopy cover among the dominant forest types in the study area post-pine beetle outbreak, and used global positioning system location data from male and female elk to define habitat relationships and security during the archery and rifle hunting seasons. Our study area was within the Elkhorn Mountains of southwest Montana, USA, 2015–2017, which experienced 80% mortality of lodgepole pine (*Pinus contorta*) forests during a pine beetle outbreak that peaked in 2008. We observed an 8.5% reduction in canopy cover within pine beetle-infested lodgepole pine forests, yet canopy cover remained relatively high among other forest types post-outbreak. The top-ranked habitat security models contained positive relationships with canopy cover, distance to motorized routes, terrain ruggedness, and slope with few notable differences among sexes and seasons. Across sexes and seasons, 75% and 50% of elk use was within areas with average canopy cover values $\geq 31 \pm 6.65$ (SD)% and $\geq 53 \pm 5.7$% that were an average of $\geq 2{,}072 \pm 187.93$ m and $\geq 3{,}496 \pm 157.32$ m from a motorized route, respectively. Therefore, we recommend fall elk security be defined as areas that meet these criteria for minimum canopy cover and distance from motorized routes in the Elkhorn Mountains and in other landscapes with similar forest characteristics and hunting pressures. Although we observed expected reductions in canopy cover within pine beetle-infested forests, defoliation alone did not appear to negatively affect elk security or reduce canopy cover below our management recommendations. Nonetheless, because of the prevalence of standing dead trees in our study area, we recommend future work that investigates the relationships with pine beetle-infested areas post-blowdown because changes in ground structure and costs of locomotion may affect elk habitat and security. © 2019 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

**KEY WORDS** *Cervus canadensis*, *Dendroctonus ponderosae*, elk, habitat, mountain pine beetle, resource selection function, security.

Recent mountain pine beetle (*Dendroctonus ponderosae*; pine beetle) outbreaks in the western United States have affected nearly 18 million ha of pine forest and are unprecedented in spatial extent, severity, and duration (Chan-McLeod 2006, Meddens et al. 2012, Ivan et al. 2018). Damage caused by pine beetles 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, Pfeifer et al. 2011, Simard et al. 2011, Saab et al. 2014). Wildlife responses to pine beetle outbreaks are dynamic and complex, and vary by taxa, sex, season, and the outbreak successional stage (Saab et al. 2014, Ivan et al. 2018). Understanding the effect of pine beetle 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). Although such changes can have profound effects on wildlife and are well

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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).

Elk (*Cervus canadensis*) have a broad distribution across western North America and can influence vegetation and plant communities (Frank and Evans 1997, Hobbs 2003) and provide economic benefits to regional communities through tourism and hunting (Duffield and Holliman 1988). 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 under 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 the increase in nontraditional private landowners that are more interested in natural amenities than livestock production and may have restricted public hunting opportunities on 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 that 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 pine beetle-killed forests across western North America. The loss of canopy cover is one of the first structural changes in forests after a pine beetle infestation and is arguably the biggest change affecting wildlife (Chan-McLeod 2006). Although specific management recommendations for security habitat have been set for patch size and distance to roads (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 recent work has provided quantitative recommendations for canopy cover based on a meta-analysis across southwest Montana, USA (Ranglack et al. 2017), the work did not include analyses of forest systems affected by pine beetles. The loss of cover after a pine beetle infestation may increase elk vulnerability and require updates to forest management guidelines regarding traditional security measures on public lands to maintain desired levels of survival and retain elk on public lands during the hunting seasons. Within the context of unprecedented pine beetle outbreaks throughout western North America forests, understanding how insect outbreaks and other disturbances that reduce canopy cover with respect to wildlife security is an important management objective.

We used a multipronged observational approach to characterize the reductions in canopy cover associated with pine beetle outbreaks and the effect on elk security in the Elkhorn Mountains of southwest Montana. We expected to observe a decline in canopy cover in infested areas pre- and post-pine beetle outbreak and a general reduction in canopy cover in infested forests relative to uninfested forests. With respect to elk security, given the anticipated loss of canopy cover associated with the pine beetle outbreak, we expected elk to use 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).

## STUDY AREA

Our study area was broadly defined by the Elkhorn Mountains (2,600 $km^2$; 1,141–2,866 m elevation), a relatively isolated mountain chain in southwest Montana (Fig. 1). The climate was characterized by short, cool summers (17.4°C mean Jul temperature) and long, cold winters (−4.8°C mean Jan temperature) with mean annual precipitation ranging from 263 mm to 959 mm (PRISM Climate Group 2016). The core of the study area consisted of public lands (46%) predominantly managed by United States Forest Service (USFS) and Bureau of Land Management, which were surrounded by low elevation private lands (54%). We conducted our study between 2015 and 2017, 7–10 years after the peak of the pine beetle infestation in 2008. In total, the pine beetle outbreak killed approximately 190 $km^2$ (80%) of lodgepole pine forests in the study area.

Lower elevations were dominated by a mixture of open sagegrassland (e.g., big sagebrush [*Artemisia tridentata*], bluebunch wheatgrass [*Pseudoroegnaria spicata*], Idaho fescue [*Festuca idahoensis*], rough fescue [*Festuca scabrella*], bluegrasses [*Poa* spp.]) and patches of timber (primarily Rocky Mountain juniper [*Juniperus scopulorum*] or Douglas fir [*Pseudotsuga menziesii*]). Additionally, cultivated crops (pasture grasses and leguminous forbs) bordered the northern and southwestern portions of the study area. Upper elevations were dominated by dry coniferous forests (e.g., lodgepole pine, Douglas fir, ponderosa pine [*Pinus ponderosa*]) with small interspersed meadows (USFS et al. 1993). Sympatric ungulates included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), and a small population of bighorn sheep (*Ovis canadensis*). Carnivores included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and American black bear (*Ursus americanus*). Grey wolves (*C. lupus*) were transient in the study area.

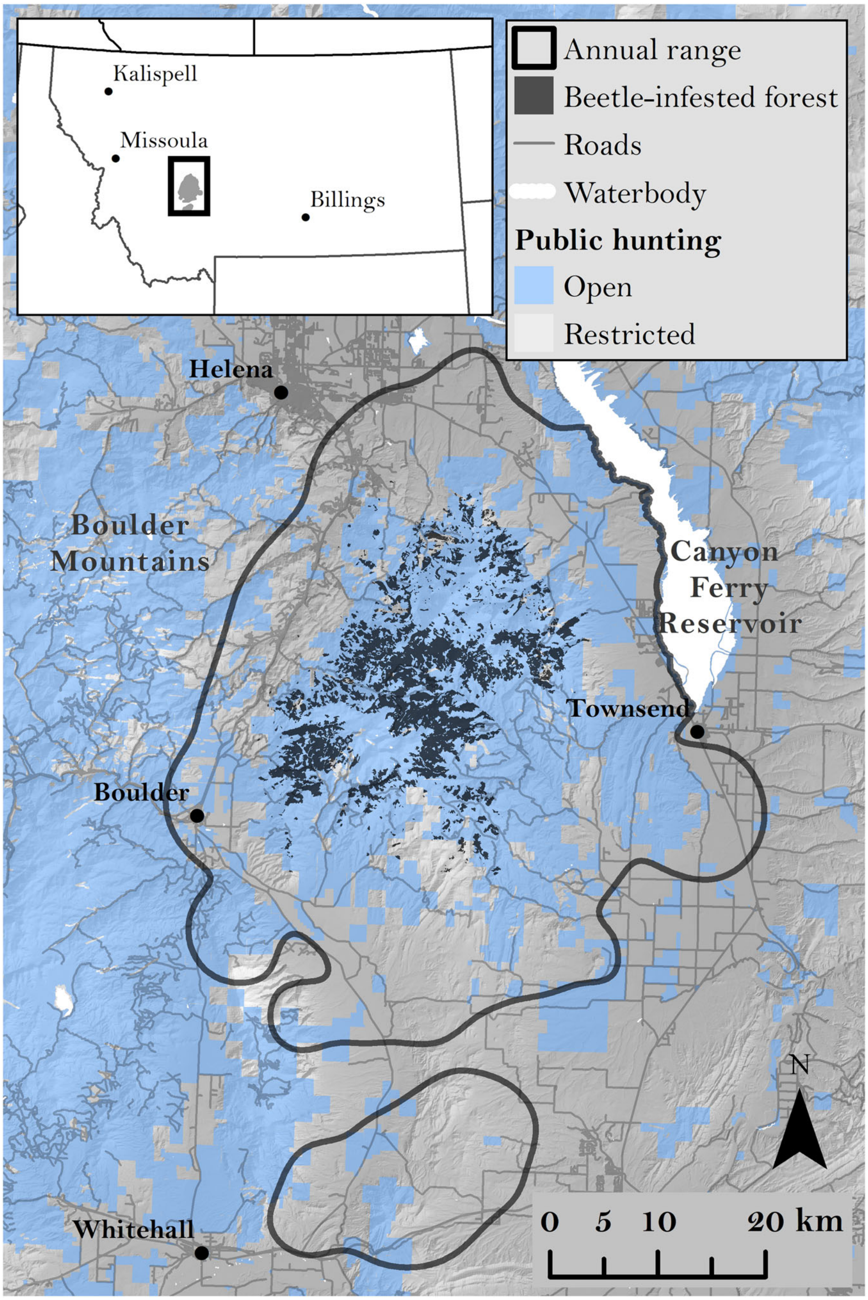


**Figure 1.** Elkhorn Mountain study area defined by the population-level elk annual range of collared individuals, southwest Montana, USA, 2015–2017. Dark shading in the core of the study area depicts the forests infested by mountain pine beetles. Blue shading depicts lands open to public hunting.

The Elkhorn Mountains are within Montana Fish, Wildlife and Parks hunting district (HD) 380, one of Montana's most popular hunting areas since the early 1960s (DeSimone and Vore 1992, Montana Fish Wildlife and Parks 2018). Estimated hunter effort has continued to increase since the 1960s with record highs of 3,936 hunters and 31,786 hunter days in 2015. Male elk hunting in this region is particularly popular because of a unique spike regulation that generates a relatively high male:female ratio and a mature male age structure. When this study occurred (2015–2017), anyone with a general hunting license could harvest a spike or antlerless elk during the archery season. During the rifle season anyone with a general hunting license could harvest a spike, and youth hunters could harvest an antlerless elk. For each year of the study, the number of limited either-sex permits was 120. The number of limited B licenses (antlerless elk) valid for either the entire hunting district or a portion of the hunting district was 700 in 2015, 800 in 2016, and 800 in 2017.

## METHODS

### Canopy Cover Characterizations

We used aircraft survey data collected by the United States Department of Agriculture Forest Health Protection Aviation Program to delineate pine beetle-affected areas as observed by tree canopy discoloration indicating mortality

(USFS 2017, 2018). However, the pine beetle 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 pine beetles. To reduce the contamination of non-beetle-killed areas, we clipped the polygons delineating pine beetle 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; USFS 2014).

We characterized canopy cover in pine beetle-infested forests using a time series from the Rangeland Analysis Platform (RAP; Jones et al. 2018) spanning 1990–2017, inclusive of the pine beetle outbreak in the Elkhorn Mountains. The RAP uses a combination of remotely sensed and ground-based data to predict per-pixel (30 m × 30 m) 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 pine beetle-infested forests over time, we characterized the percent change from historical canopy cover levels prior to the pine beetle outbreak (1990–2000) within the 3 largest pine beetle polygons in the study area, which totaled 111 $km^2$ and accounted for nearly 60% of the lodgepole pine forests infested by pine beetle.

To assess changes in canopy cover between pine beetle-infested forests and uninfested forests, we summarized the percent canopy cover in infested and uninfested lodgepole pine forests and ponderosa pine and Douglas fir 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 (USFS 2014). These estimates represented a mean response of canopy cover defoliation associated with pine beetle outbreaks approximately 5 years after peak infestation and were the most recent estimates for the Elkhorn Mountains after the pine beetle infestation. Moreover, the VMap methods used to estimate canopy cover were specifically developed to note changes in canopy cover associated with pine beetle outbreaks (S. R. Brown, USFS, personal communication).

## Security Habitat Modeling

During the winters of 2015 and 2017, we captured adult (>1.5 yr) elk by helicopter net-gunning and darting in accordance with an approved animal welfare protocol (Institutional Animal Care and Use Committee Project Number: FWP09-2014, FWP10-2017). We deployed remote-upload collars (Lotek Wireless model LifeCycle, New Market, Ontario, Canada) programmed to transmit 1 location every 23 hours through the Globalstar satellite network, the exact timing of which varied across collars. Average fix success excluding data transmission gaps was 96 ± 3%, indicating negligible landcover-induced fix bias (Johnson and Gillingham 2008). Collars on adult females remained on the animal for life and on adult males were programmed to automatically release after 4 years. We censored all locations with positional dilution of precision >10 to reduce spatial imprecision (D'eon and Delparte 2005).

Our primary objective was to characterize elk selection to define elk security habitat and inform land management practices on public lands. We focused our security habitat modeling on individuals that remained on lands open to public hunting and retained in our dataset only individuals that had >50% of their GPS locations on lands 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 legal hunting hours defined as 0.5 hours before and 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). We fit mixed-effect models using the lme4 R package (Bates et al. 2015) and the inverse link function. Our used dataset was defined by the locations collected from GPS collars, whereas we sampled availability at a 1:15 used to available ratio within each individual's annual 100% minimum convex polygon. 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 low to high. Following the legal definitions, the archery season was the 6-week period starting on the first 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 vulnerability including 3 definitions of security patches, percent canopy cover, and distance to motorized routes (Table 1). Although commonly used in elk security models, we did not include a covariate that described public or private land ownership because our analyses were restricted to individual elk that predominantly used lands that allowed public hunting. We derived our criteria for defining security patches from Hillis et al. (1991), which has been widely incorporated into USFS security habitat management standards, and defined security patches as contiguous areas of ≥100 ha located ≥0.8 km from an open motorized route. To evaluate the importance of canopy cover in definitions of elk security, the 2 additional security patch covariates included contiguous areas that contained ≥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

**Table 1.** 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), Christenses 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 2 different covariates. | Binary | Hillis et al. (1991), Christenses et al. (1993), DeVoe et al. (2019) |
| Canopy cover | Percent canopy cover. | 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 or quadratic, binary signifies categorical covariate for which we did not consider functional forms.

aspect (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 corrected Akaike's Information Criterion ($AIC_c$; 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 cumulative elk use as the cumulative area under the curve starting with the largest probability value 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% (security) and 50% (preferred security) of elk use. To minimize the influence of extreme outliers on the area under the curve and corresponding management thresholds, we removed from the available dataset covariate values that were well beyond the distribution of values observed in the used dataset. For quadratic covariates (i.e., slope), we noted the covariate value that maximized the relative probability of use for each sex and season.

We preformed model validation using a k-fold cross-validation within an iterative process where we withheld the locations for each 5 folds, fit an exponential resource selection function (RSF) with the data that were retained, and then predicted the fitted values for the observations that were withheld (Boyce et al. 2002). We then summed the occurrence of used locations within 10 equal-area RSF bins and evaluated the correlation between the frequency of occurrence and the relative RSF score using the Spearman's rank correlation (Boyce et al. 2002). The adjusted frequencies should be highly correlated with the relative RSF if the model performs well (Boyce et al. 2002). We conducted all analyses and data processing in the R environment for statistical computing (R Core Team 2018) in combination with the sf (Pebesma 2018) and raster (Hijmans 2017) packages for spatial analysis and the tidyverse suite (Wickham 2017) for data manipulation and visualization.

# RESULTS

## Canopy Cover

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

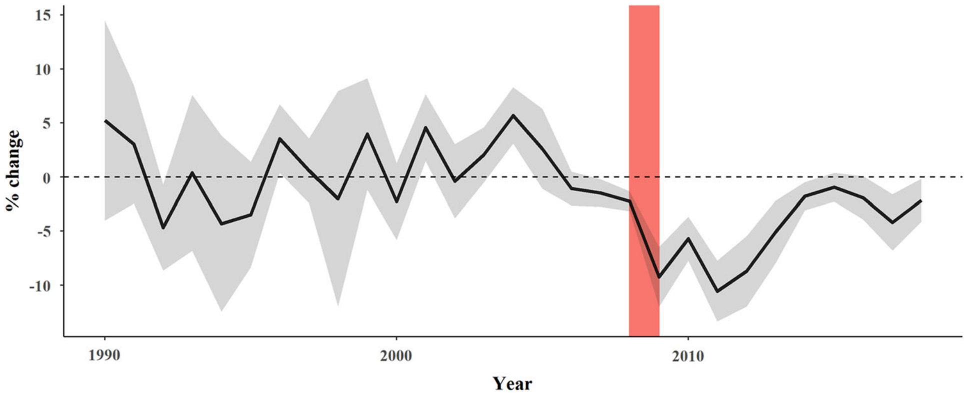


**Figure 2.** Twenty-seven-year (1990–2017) time series of the mean (±SD) percent change in canopy cover from the historical average (1990–2000) for the 3 largest patches of forest infested by mountain pine beetles within the Elkhorn Mountain study area, southwest Montana, USA, 2015–2017. The year of peak beetle infestation (2008) is shaded.

Within forested portions of the study area, forests classified as uninfested lodgepole pine had the highest values for canopy cover post-pine beetle infestation with a mean of 77 ± 14.6% (Fig. 3). Similar to the trends described in the canopy cover time series, there was an 8% reduction in canopy cover in infested lodgepole forests ($\bar{x} = 69 \pm 15\%$). Canopy cover in pine beetle-infested lodgepole forests remained higher than canopy cover in uninfested Douglas fir and ponderosa pine forests (including both infested and uninfested stands), which had 54 ± 18.9% and 27 ± 8.7% canopy cover, respectively.

## Security Habitat Modeling

We captured 59 adult (male = 24, female = 35, total excludes 3 individuals that died during capture) elk during the winters of 2015 and 2017. To evaluate security on lands open to public hunting, 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. Among censored elk, a mean of 74 ± 15% of male and female GPS locations were in areas with restricted hunting access. Lastly, 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 animal-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 (Table 2). The 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 difference of only 0.68 AIC$_c$ units 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 (Table 2).

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

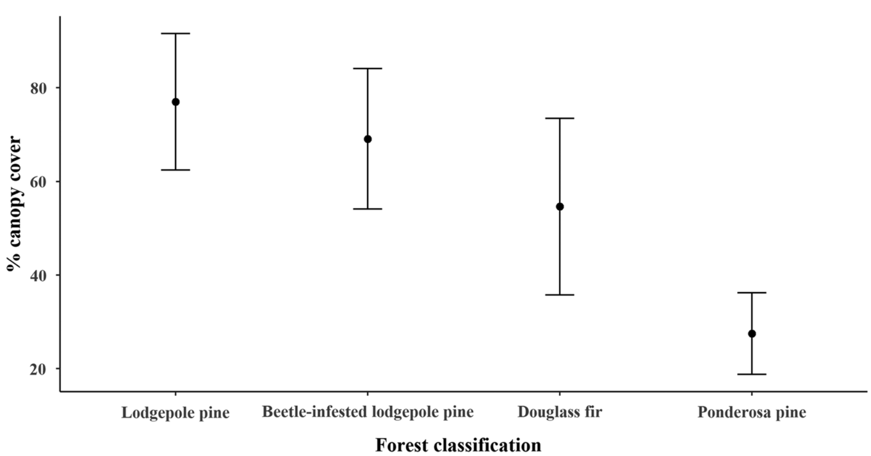


**Figure 3.** Average canopy cover percentages (±SD) within uninfested and pine beetle-infested lodgepole pine, Douglas fir, and ponderosa pine forest classifications, Elkhorn Mountains, southwest Montana, USA, 2015–2017.

Table 2. 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 corrected Akaike's Information Criterion ($AIC_c$) ranking. We also present the number of parameters (K) and model weight ($w_i$).

| Model tier | Sex-season | Model[a] | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|---|---|
| Tier 1: Security patch | Female-archery | Security.00 | 3 | 6,399.02 | 0.00 | 0.67 |
| | | Security.30 | 3 | 6,401.72 | 2.70 | 0.17 |
| | | Security.15 | 3 | 6,401.86 | 2.85 | 0.16 |
| | Female-rifle | Security.30 | 3 | 4,570.29 | 0.00 | 0.41 |
| | | Security.00 | 3 | 4,570.86 | 0.56 | 0.31 |
| | | Security.15 | 3 | 4,570.97 | 0.68 | 0.29 |
| | Male-archery | Security.00 | 3 | 3,916.05 | 0.00 | 1.00 |
| | | Security.15 | 3 | 3,984.58 | 68.53 | 0.00 |
| | | Security.30 | 3 | 3,984.68 | 68.62 | 0.00 |
| | Male-rifle | Security.00 | 3 | 2,132.94 | 0.00 | 0.96 |
| | | Security.30 | 3 | 2,140.85 | 7.91 | 0.02 |
| | | Security.15 | 3 | 2,140.85 | 7.91 | 0.02 |
| Tier 2: Traditional security | Female-archery | Canopy cover + DMOT | 4 | 6,267.63 | 0.00 | 1.00 |
| | | Canopy cover | 3 | 6,293.88 | 26.25 | 0.00 |
| | | Canopy cover + security.00 | 4 | 6,294.21 | 26.59 | 0.00 |
| | | DMOT | 3 | 6,366.89 | 99.26 | 0.00 |
| | | Security.00 | 3 | 6,399.02 | 131.39 | 0.00 |
| | Female-rifle | Canopy cover + DMOT | 4 | 4,328.85 | 0.00 | 1.00 |
| | | Canopy cover + security.00 | 4 | 4,363.95 | 35.10 | 0.00 |
| | | Canopy cover | 3 | 4,382.79 | 53.94 | 0.00 |
| | | DMOT | 3 | 4,527.33 | 198.49 | 0.00 |
| | | Security.00 | 3 | 4,570.86 | 242.01 | 0.00 |
| | Male-archery | Canopy cover + DMOT | 4 | 3,902.77 | 0.00 | 0.78 |
| | | DMOT | 3 | 3,905.31 | 2.55 | 0.22 |
| | | Canopy cover + security.00 | 4 | 3,913.24 | 10.47 | 0.00 |
| | | Security.00 | 3 | 3,916.05 | 13.29 | 0.00 |
| | | Canopy cover | 3 | 3,974.72 | 71.95 | 0.00 |
| | Male-rifle | Canopy cover + DMOT | 4 | 2,096.46 | 0.00 | 0.99 |
| | | Canopy cover + security.00 | 4 | 2,105.41 | 8.96 | 0.01 |
| | | Canopy cover | 3 | 2,110.71 | 14.25 | 0.00 |
| | | DMOT | 3 | 2,121.66 | 25.20 | 0.00 |
| | | Security.00 | 3 | 2,132.94 | 36.48 | 0.00 |
| Tier 3: Traditional and landscape security | Female-archery | Canopy cover + DMOT + Slope$^2$ + ruggedness | 7 | 6,233.22 | 0.00 | 1.00 |
| | | Canopy cover + DMOT | 4 | 6,267.63 | 34.41 | 0.00 |
| | Female-rifle | Canopy cover + DMOT + slope$^2$ + ruggedness | 7 | 4,305.30 | 0.00 | 1.00 |
| | | Canopy cover + DMOT | 4 | 4,328.85 | 23.54 | 0.00 |
| | Male-archery | Canopy cover + DMOT + slope$^2$ + ruggedness | 7 | 3,808.99 | 0.00 | 1.00 |
| | | Canopy cover + DMOT | 4 | 3,902.77 | 93.77 | 0.00 |
| | Male-rifle | Canopy cover + DMOT + slope$^2$ + ruggedness | 7 | 2,029.19 | 0.00 | 1.00 |
| | | Canopy cover + DMOT | 4 | 2,096.46 | 67.27 | 0.00 |

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

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 by a minimum of 2.55 ($\bar{x} = 18.21 \pm 15.06$) $AIC_c$ units (Table 2). 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 $AIC_c$ ranking in all sex-seasons by a minimum reduction of 23.5 ($\bar{x} = 57.74 \pm 31.97$) $AIC_c$ units (Table 2), 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 (Appendix A). Across all sex and season combinations, the Pearson's correlation coefficients were ≤0.4.

The top-ranked habitat security models performed well with a strong correlation between area-adjusted frequencies and the relative RSF for all sexes and seasons (female-archery: $r_s = 0.93$, $P < 0.001$, female-rifle: $r_s = 0.99$, $P < 0.001$, male-archery: $r_s = 0.97$, $P < 0.001$, male-rifle: $r_s = 0.91$, $P < 0.001$). Additionally, with only a few exceptions the top-ranked models produced similar results across sexes and seasons (Fig. 4). 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 zero (Appendix A), resulting in a flat prediction line across the observed values of canopy cover (Fig. 4). 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

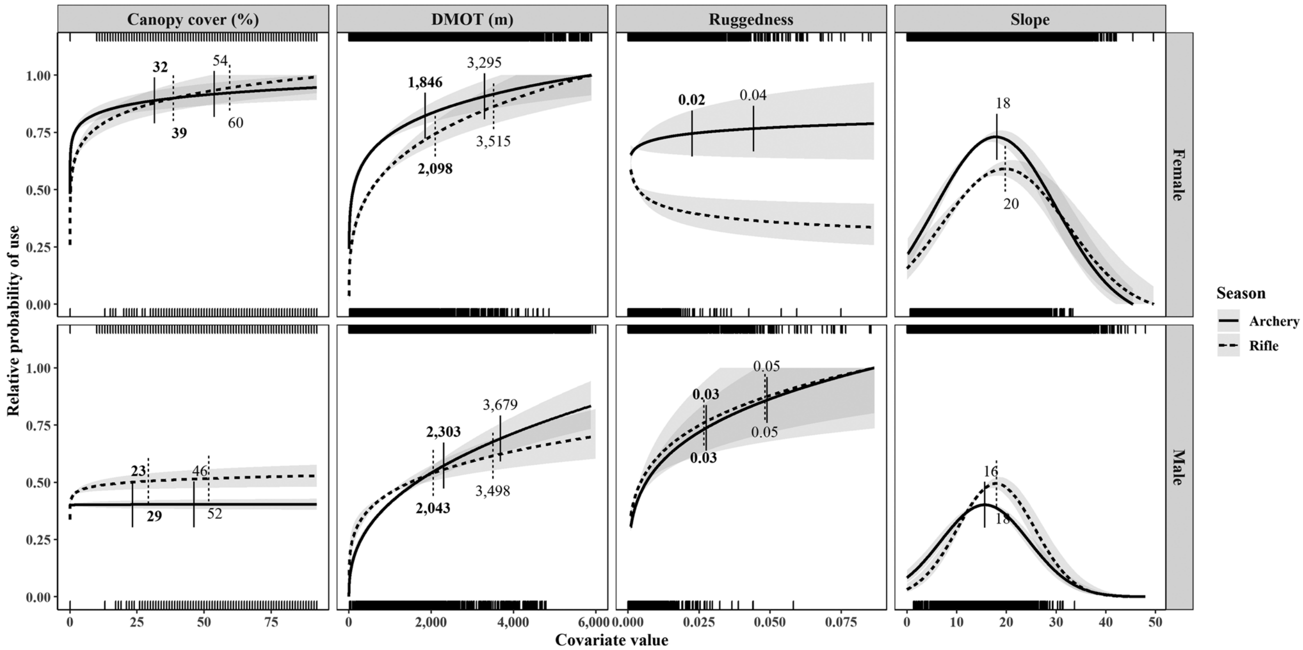


**Figure 4.** Prediction plots showing the relationship with the relative probability of use (±95% CI) for each covariate (columns), sex (rows), and season (archery = solid line, rifle = dashed line) with all others held at their mean value, for elk in the Elkhorn Mountains, southwest Montana, USA, 2015–2017. The upper rug represents the available locations, whereas 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% cumulative elk use thresholds, respectively. DMOT = distance to motorized route.

rifle season selected 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 (Fig. 4). 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 (Fig. 4). 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 ≥0.03 and ≥0.05, 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 (Fig. 4).

## DISCUSSION

Our study combined canopy cover characterizations with wildlife habitat modeling after a pine beetle infestation to assess the effect of pine beetle on elk security through reductions in canopy cover. We observed an 8.5% reduction in canopy cover within pine beetle-infested lodgepole pine forests compared to historical levels before the pine beetle outbreak. Nonetheless, canopy cover in pine beetle-infested forests remained relatively high ($\bar{x} = 69 \pm 15\%$) and had higher cover values than uninfested 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 an important predictor of male and female elk distributions in the archery and rifle hunting seasons. However, given the relatively high degree of cover offered by lodgepole pine forests, including those affected by pine beetles, the changes in cover associated with defoliation after the pine beetle 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 hunting 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 pine beetle-infested forests, the level of reductions that we observed in our study did not appear to negatively affect elk security after the pine beetle infestation.

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., contiguous 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 elk security on public lands is varied across the western United States. In areas with expansive forest cover, elk security can be influenced by 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 (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 public lands and private lands with restricted hunter access 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 the covariate value that corresponded to half of the change in the relative probability of use over the observed covariate range (Ranglack et al. 2017). Although these methods may be well suited for relationships between use and cover characterized by pseudothreshold curves with a sharp rollover, they are arbitrary in the selection of 0.5 and less appropriate for curves with a broad rollover where half of the total gain across the *x*- and *y*-axes may not result in meaningful management recommendations. Rather than provide a single minimum value, our approach provided a range for canopy cover and distance to motorized routes based on the cumulative elk 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 motorized routes between 1,846 m and 3,679 m characterize most elk use within our Elkhorn Mountain study area 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 better accommodates the varied shapes of our predictive curves and meaningfully translates to elk resource 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 regarding canopy cover and security from this study compared to Ranglack et al. (2017) and Hillis et al. (1991). First, Ranglack et al. (2017) included female elk on public and private lands when defining elk security. In contrast, our recommendations were developed for male and female elk that predominately occupied 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 because hunting pressure is relatively lower. Second, although we were unable to estimate hunter densities specifically for lands open to unrestricted public hunting within our study area or across Montana, the Elkhorn Mountains hunting district (HD 380) is subject to relatively high hunting pressure with record highs of 3,936 hunters and 31,786 hunter days in 2015. Moreover, on average the Elkhorn Mountains received 5.4 times (range = 1.4–35) more hunters and 5.7 times (range = 1.4–28) more hunter days than the populations from Ranglack et al. (2017). Lastly, in contrast to Hillis et al. (1991), which was conducted in densely forested systems in western Montana, 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 elk to have stronger selection for forest cover and security areas than when pooling elk across areas with restricted and unrestricted hunting access (Ranglack et al. 2017) or when working in systems that are largely forested (Hillis et al. 1991).

Although our results indicated elk continued to use areas affected by pine beetles post-infestation during the hunting season, regionally there have been mixed results regarding elk use of pine beetle-infested forests. In south-central Wyoming, USA, Lamont et al. (2019) reported that during summer female elk avoided pine beetle-infested forests during nearly all parts of the day and selected for intact coniferous forests during daytime. The selection for intact forests during daytime in summer highlights the need for thermal refuge, which may be compromised in pine beetle-infested forests (Lamont et al. 2019). In contrast, Ivan et al. (2018) documented an increase in the use of pine beetle-infested forests by elk, mule deer, and moose during summer months across Colorado, USA, presumably influenced 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 pine beetle 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 pine beetle 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 pine beetle-infested forests in our study area. An increase in fallen trees is presumed to influence wildlife mobility in pine beetle-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 pine beetle 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 before tree blowdown. Although Lamont et al. (2019) did document an increase in downed trees in pine beetle-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 pine beetle-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 pine beetle-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 pine beetle-infested forest across 3 different severities (10%, 50%, and 90% mortality) spanning 0–11 years after initial outbreak.

As pine beetle-infested forests transition from standing dead to blowdown, understanding the effect 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 affected throughout the western United States, relatively minor avoidance of these areas could result in a notable net loss of habitat that provides demographic benefits through increased security and thermal cover. As pine beetle-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 effect 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.

## MANAGEMENT IMPLICATIONS

We recommend that managers include measures of canopy cover and distance to motorized routes in definitions of elk security and encourage managers to implement seasonal or permanent road closures in areas with forest canopy cover to provide elk security during hunting seasons. In the Elkhorn Mountains and other landscapes with similar forest characteristics and hunting pressures, we recommend managing for security with canopy cover values of 23–60% and distance from motorized routes of 1,846–3,679 m based on our definitions of security and preferred security areas, respectively. Where possible, the implementation of more stringent objectives at the upper end of the canopy cover and distance to road thresholds will more strongly reflect preferred security areas. In addition, locating security areas in relatively rugged terrain and moderate slope angles (i.e., 18°) can further enhance elk security. Given the relatively small difference in selection patterns between males and females and the archery and rifle hunting seasons, these recommendations are appropriate for both sexes and both the archery and rifle hunting seasons. Managing for these habitat security attributes on public lands may help to reduce the redistribution of elk to private lands that restrict hunting during the archery and rifle seasons. In the presence of pine beetle infestations, we also recommend prioritizing intact forests with high canopy cover to help retain security areas as infestations mature and blowdown, potentially further affecting habitat conditions within infested forests. Because of the relatively narrow temporal window of our study, approximately 7–10 years after the beetle infestation, we recommend future work that investigates the relationships with pine beetle-infested areas post-blowdown as changes in ground structure may provide the biggest effect to habitat and security for elk and other ungulates.

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# APPENDIX A. TOP-RANKED HABITAT SECURITY MODEL COEFFICIENT ESTIMATES

**Table A1.** 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[a] | Beta | SE |
|---|---|---|---|
| Female-archery | Intercept | −2.629 | 0.047 |
| | Canopy cover | 0.294 | 0.040 |
| | DMOT | 0.196 | 0.039 |
| | Slope | 0.222 | 0.048 |
| | $\text{Slope}^2$ | −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 |
| | $\text{Slope}^2$ | −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 |
| | $\text{Slope}^2$ | −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 |
| | $\text{Slope}^2$ | −0.533 | 0.087 |
| | Ruggedness | 0.189 | 0.059 |

[a] DMOT= distance to motorized route.