



Research Article

Bark Beetle-Affected Forests Provide Elk Only a Marginal Refuge from Hunters

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ABSTRACT For nearly 2 decades, the forests of the Rocky Mountains in the United States experienced a bark-beetle (*Dendroctonus ponderosae*) epidemic. The number of dead and falling trees from this epidemic likely will affect how elk (*Cervus canadensis*) and hunters use the forest and their interactions. Downed trees potentially create a component of refuge habitat that could affect the effectiveness of hunting to regulate abundance of growing elk populations. We evaluated how forests affected by bark beetles in south-central Wyoming, USA, influenced resource selection of 50 female elk and 374 hunters in 2012–2016, and interactions between elk and hunters. We employed global positioning system (GPS) technology on elk and hunters, and developed a satellite-derived land classification specifically depicting beetle-affected forests. We tested the predictions that elk would increase use of beetle-killed areas from summer to the hunting season, and that hunters would avoid beetle-killed areas regardless of elk use. Elk increased use of beetle-killed areas during hunting seasons as did hunters during the archery season; however, during the rifle season, hunters avoided beetle-killed areas. Nevertheless, during the rifle season, areas of beetle-kill with a high probability of elk occurrence dampened the aversion hunters had towards beetle-killed areas. Therefore, in contrast to our expectations, forests that have been altered by the bark-beetle epidemic may only function marginally as a refuge for elk. Our study area was at the beginning of the tree-fall phase (i.e., ~3–7 yr after peak infestation) of the bark-beetle epidemic; thus, future research efforts should focus on how a continued increase in downed trees will influence interactions between elk and hunters. At current levels of tree fall, however, beetle-kill should not limit the ability of managers to regulate elk herds through harvest. © 2020 The Wildlife Society.

KEY WORDS bark-beetle epidemic, *Cervus canadensis*, forest disturbance, land cover classification, resource selection function, Wyoming.

For decades, ecologists have examined how animals balance obtaining food with avoiding being killed by predators (Lima and Dill 1990, Blumstein and Daniel 2002, Creel and Christianson 2008). Moving into refuge areas is one of the main ways in which prey animals reduce risk of being killed by a predator (Cassini 1991, Holmes 1991, Cowlshaw 1997). Although refuge use reduces risk of predation, it can come at the expense of access to other important resources (Brown et al. 1999, Lima and Bednekoff 1999, Brown and Kotler 2004). For example, eastern grey kangaroos (*Macropus giganteus*) respond to high

risk of predation from red foxes (*Vulpes vulpes*) by using degraded habitats closer to refuge areas (Banks 2001) and bottlenose dolphin (*Tursiops aduncus*) retreat to refuge areas in deep water far from high-quality foraging areas when faced with high densities of tiger sharks (*Galeocerdo cuvier*; Heithaus and Dill 2002).

For ungulate prey, individuals retreat to refuge areas when faced with predation risk (Bergerud et al. 1984, Thaker et al. 2011). For instance, under the threat of predation from leopards (*Panthera pardus*) and African wild dogs (*Lycan pictus*), impala (*Aepyceros melampus*) select areas away from preferred foraging areas as they seek spatial separation in an East African savanna (Ford et al. 2014). In addition to non-human predators, many ungulate populations face the threat of hunting by humans (Little et al. 2014,

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Norum et al. 2015, Plante et al. 2016). Although ungulates use similar tactics to avoid risk of human hunters as they do animal predators (i.e., seeking refuge; Frid and Dill 2002), hunters often evoke a stronger and more prolonged fear response in elk (*Cervus canadensis*) than certain natural predators (Gude et al. 2006, Proffitt et al. 2009). Among a wide variety of human disturbances during different seasons and intensities, hunting provoked the highest level of vigilance in elk, leading to reduced foraging and potentially reduced fitness (Ciuti et al. 2012b).

During hunting seasons it is common for elk and other ungulates to seek refuge from hunters on private land (Conner et al. 2001; Vieira et al. 2003; Proffitt et al. 2010, 2013; Ranglack et al. 2017), in national parks (Martinka 1969), and within forested areas with few roads (Unsworth et al. 1998, Burcham et al. 1999, Millspaugh et al. 2000, Paton et al. 2017). Habitat management for elk historically has sought to provide adequate thermal and hiding cover away from roads to ensure adequate resources are available (i.e., Hillis paradigm; Hillis et al. 1991, Ranglack et al. 2017) and to decrease the risk of overharvest of male elk (Marcum 1975; Irwin and Peek 1979; Lyon 1979, 1983). Nevertheless, as elk populations across the West have grown (Johnson et al. 2000, O'Gara and Dundas 2002), wildlife agencies have struggled to obtain sufficient harvest of adult females to regulate elk herds that seek refuge on private lands with little hunter access (Burcham et al. 1999, Vieira et al. 2003, Brodie et al. 2013, Proffitt et al. 2013, Ranglack et al. 2017), which can have social and ecological ramifications. Other elk herds across the West forgo private land as a refuge and continue to rely on traditional forested areas on public land as refuge during the hunting season (Conner et al. 2001, Skovlin et al. 2002, Wolfe et al. 2002, Lamont et al. 2019); however, landscape-scale alterations to forested areas may well alter the effectiveness of hunting as a tool to regulate such elk populations.

For nearly 2 decades, forests of the Rocky Mountains in the United States have experienced a bark-beetle (*Dendroctonus ponderosae*) epidemic of severity and duration that has not been observed in more than a century (Raffa et al. 2008, Kayes and Tinker 2012, Black et al. 2013). The bark-beetle epidemic has changed the structure and characteristics of conifer forests by altering canopy cover and understory vegetation, and increasing the number of downed trees (Klutsch et al. 2009, Collins et al. 2012, Pec et al. 2015, Lamont et al. 2019). The changes to forests caused by the bark beetle have the potential to influence foraging opportunities (Pec et al. 2015), thermal demands (Long et al. 2014, 2016), locomotion (Parker et al. 1984), and refuge from predation for ungulate prey (Thurfjell et al. 2017). Many forests across the West affected by the bark-beetle epidemic also support abundant elk herds that are maintained through regulated hunting and active wildlife management (Ranglack et al. 2017). Currently elk avoid beetle-killed forested areas (i.e., beetle-kill are areas within conifer forests that have experienced mortality due to bark beetle infestation) during the summer months presumably in response to increased locomotive and thermoregulatory

costs (Lamont et al. 2019), but if elk use beetle-kill during the hunting season and hunters do not because of the increased number of downed trees, bark beetle-afflicted forests may serve as a novel refuge for elk.

Our objective was to examine how the bark-beetle epidemic influences resource selection by elk, hunters, and their subsequent interactions during the autumn hunting seasons. We tested the hypothesis that beetle-kill would serve as a refuge for elk from hunting pressure given that increased density of downed trees associated with the bark-beetle infestation may alter patterns of movement of elk and hunters (i.e., refuge hypothesis). To evaluate the refuge hypothesis, we tested 3 predictions. Prediction 1 was that elk use of beetle-killed areas will increase from summer to the hunting season as elk respond to the new risk from hunting by humans by seeking refuge in beetle-killed areas. Prediction 2 was that hunters will avoid beetle-killed areas during the archery (Sep) and rifle (Oct) seasons because of the challenges associated with traversing areas with downed beetle-killed trees. Prediction 3 was that if predictions 1 and 2 are supported, then we expect that hunters will avoid beetle-killed areas even if those areas have high elk use. In association with this prediction, we developed predicted maps to identify areas of high elk use but low use by hunters as a potential management tool.

STUDY AREA

Our study area, the Sierra Madre Range of south-central Wyoming, USA, was dominated by a lodgepole pine (*Pinus contorta*) forest affected by the bark-beetle epidemic (our study occurred from 2012–2016, which was ~3–7 yr after peak infestation) and was home to a large elk herd (~7,000–10,000 animals). The boundaries of the Sierra Madre portion (107°1'12.296"W, 41°9'42.818"N) of the Medicine Bow-Routt National Forest in Wyoming delineated the study area (Fig. 1). The study area included hunt areas 21, 13, and 15, which received considerable hunting pressure (~5,000 hunters/season) and harvest (~2,000 elk) for female and male elk. The area was approximately 137,651 ha (Dillon et al. 2005). The Sierra Madre is mountainous, and elevations range from 1,900–3,350 m. Temperatures ranged from –46°C during winter (Dec–Mar) to 32°C in summer (Jul–Aug; Dillon et al. 2005). Precipitation in high elevations was primarily in the form of snow, with precipitation ranging from 38 cm (low elevations) to 100 cm (high elevations; Dillon et al. 2005).

Low elevations typically consisted of grasslands and shrub lands that transitioned into lodgepole pine forests. About 78% of the study area was forested and 61% of forests were primarily lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Dominant fauna included elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), black bears (*Ursus americanus*), mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and a variety of small mammals, song and upland birds, fish and amphibians. Land use primarily consisted of timber harvest, live-stock grazing, and recreation. Aspen (*Populus tremuloides*)

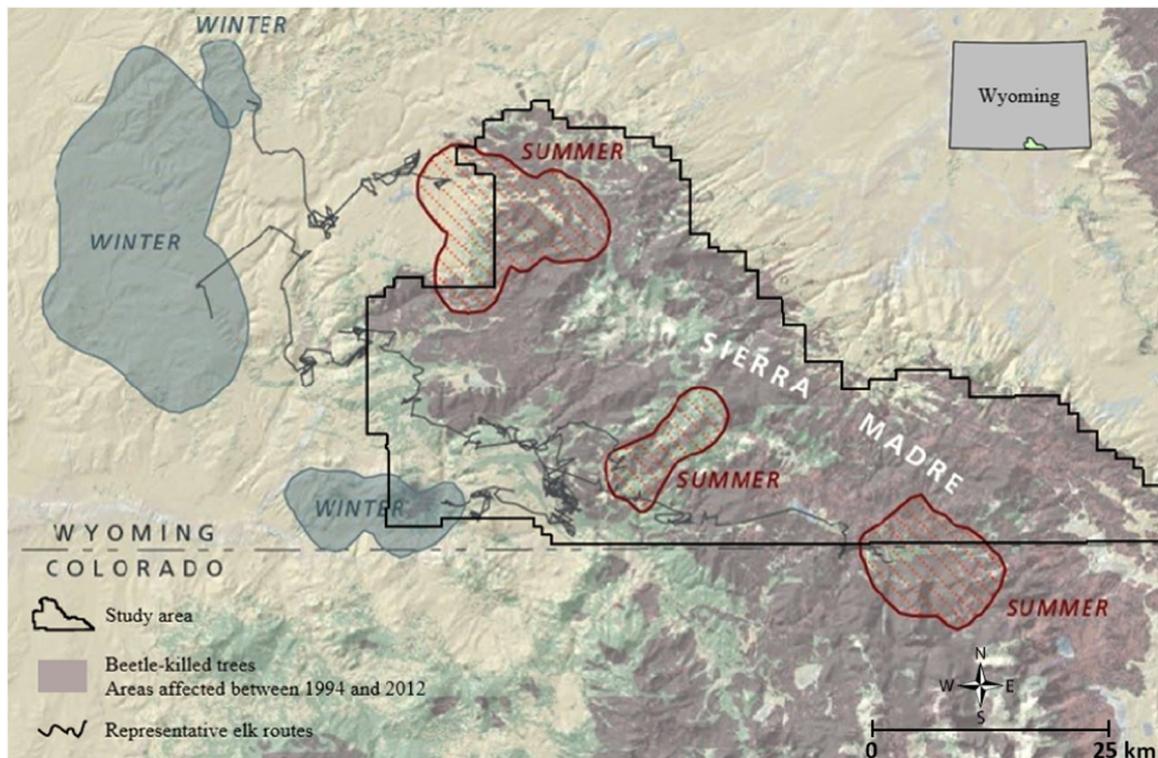


Figure 1. Project study area, delineated by the Medicine Bow-Routt National Forest boundary, including the distribution of beetle-killed areas that occurred from 1994 to 2012, and a representative sample of migratory routes and seasonal ranges for elk in the Sierra Madre Range, Wyoming, USA.

forests were a prominent feature across the study areas accounting for about 17% of the land area. Around 85% of the forests were ≤ 150 years old, indicating that historically either fire or timber harvest had affected most of the forested areas (Dillon et al. 2005). More recently, starting in the late 1990s, an unprecedented bark-beetle epidemic occurred that killed 60–80% of the lodgepole pine, and to a lesser extent, Engelmann spruce (Raffa et al. 2008, Kayes and Tinker 2012, Black et al. 2013). This event dramatically changed the structure and characteristics of conifer forests within the study area (Klutsch et al. 2009, Collins et al. 2012, Pec et al. 2015, Lamont et al. 2019).

METHODS

Elk and Hunter Movement Data

To evaluate the influence of the bark-beetle epidemic on elk, we deployed global positioning system (GPS) radio-collars on 71 female elk between 2012 and 2016 via helicopter net-gunning. All animals were captured and handled according to University of Wyoming Institutional Animal Care and Use Committee protocols (protocol numbers 20140311MK00076-01, 02, and 03). In February 2012 and March 2015, we deployed 41 store-on-board radio-collars (Telonics, Mesa, AZ, USA; Advanced Telemetry Systems, Isanti, MN, USA) with a remote-release mechanism, and programmed collars to attempt a location fix every hour. We deployed an additional 15 globalstar radio-collars (Advanced Telemetry Systems) in March and April of 2016 and programmed collars to attempt a location fix every hour. After censoring animals because of a combination of

collar failure, elk movements outside the study area, and mortality, we conducted our analyses using a sample of 50 individual elk.

To evaluate the influence of the bark-beetle epidemic on hunters, we acquired GPS data from a sample of hunters across our study area. During the hunting season, we drove the majority of roads within our study area (i.e., hunt areas 21, 13, and 15) looking for hunters. When we found hunters, we asked them to carry hand held GPS units (Etrex 10, Garmin, Olathe, KS, USA) in their hunting packs for 1 day of their hunt (we sampled each hunter only once during our study). We set the GPS to record a location every time the hunter changed direction, elevation, or speed. At the end of the day after the hunter carried the unit, we retrieved the GPS. During the 2012–2016 hunting seasons, we sampled approximately 500 hunters, and used 374 of the hunter tracks in our analyses following censoring a combination of GPS unit failure, hunter movements outside of the study area, and operator error.

Habitat Selection Analyses

Our habitat selection analyses consisted of 4 steps. We first assessed differences across seasons (i.e., summer, archery [Sep], rifle [Oct]; model 1; prediction 1) in habitat selection of elk with respect to beetle-kill, green conifer, and grass meadows. Second, we assessed habitat selection by hunters during the archery and rifle seasons to test whether hunters avoided beetle-kill (model 2; prediction 2). Third, we tested how variation in predicted use by elk influences selection of beetle-kill by hunters (model 5; prediction 3). Lastly, we developed predictive maps for managers to aid in

consideration of areas for beetle-killed tree removal. These maps are based on the predicted resource selection function (RSF) values of elk and hunters to specifically identify overlap areas that are in beetle-kill (models 3 and 4; Appendix A).

Model covariates.—We included 7 variables that influence movement and space use by elk and hunters in our RSFs: 1) elevation (National Elevation Dataset, U.S. Geological Survey, 10-m resolution), 2) slope (10-m resolution), 3) aspect (where positive values represent northerly aspects, and negative values represent southerly aspects, 10-m resolution), 4) distance from water (based on water bodies, streams, and rivers of the Topologically Integrated Geographic Encoding and Referencing data set, U.S. Census Bureau, 0.5-m resolution), 5) terrain position index (TPI; calculated as the difference between the elevation of a cell and the mean elevation of its nearest 80 surrounding cells, ranging from -50 in valley bottoms and 50 on ridgetops, 30-m resolution), 6) distance to roads (geographic information system road layer from the Medicine Bow-Routt National Forests and Thunder Basin National Grassland's Brush Creek and Hayden Ranger District, 10-m resolution), and 7) land cover type (1-m resolution).

We developed a land cover map using National Agricultural Imagery Program (NAIP) imagery and a random forest model (Hayes et al. 2014) because we were interested in distinguishing between beetle-killed conifer and non-beetle-killed conifer across our study area. Our land cover classification included green conifer, beetle-killed conifer, grass meadows, sagebrush, deciduous (aspen, willow, and cottonwood), bare ground, and other (water and shadow). Lamont et al. (2019) provide additional information on the land cover map.

Elk and hunter habitat selection (steps 1–2).—We evaluated spatiotemporal variation in habitat selection of elk and hunters at the spatial scale of the study area (Johnson 1980) using separate mixed effects RSFs for elk (model 1) and hunters (model 2), following a use versus availability design (Manly et al. 2002, Thomas and Taylor 2006). To account for variation in fix intervals of elk collars, we built a reduced database (full database included 248,158 locations) of used points by randomly sampling 12 locations/day from all the locations collected each day an individual was alive. We censored any elk with <1 month of data. To account for variation in fix intervals of GPS units carried by hunters, we subsampled the data to 1 used location every 5 minutes. In addition, we retained elk and hunter data only during periods of the day when most hunters were actively hunting, operationally defined as 30 minutes before sunrise to 1000, and from 1500 to 30 minutes after sunset. Doing so ensured that our RSFs were comparable between elk and hunters. We randomly chose an equal number of available locations to the used locations for elk and hunters from within the study area boundary (Boyce et al. 2002), which we defined as the Sierra Madre portion of the Medicine Bow-Routt National Forest boundary.

We fit the elk (model 1) and hunter (model 2) RSFs using mixed effects logistic regression. Elk and hunter models

included all habitat and land cover variables listed above, and an interaction between season (summer [elk only], archery [Sep], and rifle [Oct]) and beetle-killed conifer, green conifer, and grass meadows to assess differences in selection for covariates across seasons. In our models, we used the land cover class other, which included water and shadow, as the reference category. Using simple selection ratios (Manly et al. 2002), this category (other) was generally used in proportion to its availability for both elk and hunters, and represented about 8% of the landscape. We included a random intercept for individual and year (used only individual for hunters because we monitored individual hunters for 1 day) in our models to account for a lack of independence within individual samples and inconsistencies in sample size among individuals (Gillies et al. 2006).

To assess the internal predictive power of our models, we used k-folds cross validation following the methods of Boyce et al. (2002). In brief, we divided our data into 5 folds, where we used 80% of the data to fit the models, and withheld the remaining 20% of data to validate the models. We assessed the predictive power of a model by the correlation between 10 ranked, equal area bins of predicted RSF values calculated from the fitted data and the frequency of occurrence of observed locations from the withheld data in those bins. A high (i.e., >0.9) positive Spearman rank correlation (r_s) suggests a model with excellent internal predictive power (Boyce et al. 2002). We replicated this process 100 times and calculated the mean and standard deviation of the resulting (r_s) values. To verify there was no bias in selection of our available points, we assessed the expected r_s using the above methods, but instead of calculating r_s values using the used points in the withheld data, we used the available points. In this case, r_s values near zero represent unbiased available points (Boyce et al. 2002).

Elk and hunter interactions (step 3).—To further assess the ability of beetle-kill to act as a refuge for elk from hunting pressure, we assessed how variation in predicted use by elk (model 3) influenced selection of beetle-kill by hunters (i.e., prediction 3). We conducted this analysis only for the rifle season because prediction 2 (i.e., hunters avoid beetle-kill) was not supported for archery hunters. We first fit an elk RSF for the rifle season (model 3) using mixed effects logistic regression using the same land cover, topographic covariates, and random effects of individual and year as described above (model 1). In contrast to the RSF in step 1 (model 1), we did not scale covariates before fitting the RSF, to facilitate the ease at which we could calculate RSF predictions across the study area. We predicted the fitted RSF on a 30-m grid and normalized predicted values between 0 and 1. We then developed a model for hunters during the rifle season (model 5) that included only an interaction between predicted RSF values for elk (model 3) and beetle-kill, with a random effect of individual, to evaluate if hunters were willing to venture into beetle-kill if it was an area of high elk use (i.e., as evidenced by a positive interaction term).

Management maps (step 4).—To aid in identification of areas where beetle-kill may be providing refuge for elk, thus

reducing the probability of hunter success and management of elk, we built maps that identified areas where elk use was high, but hunter use was low. We developed a map that represented the subtraction between the binned (based on 10 equal area bins) predicted values of a fitted elk RSF (model 3), and the binned predicted values of a fitted hunter RSF (model 4). Thus, high values represent high elk and low hunter use, and low values represent low elk and high hunter use. We based the elk model on model 3, explained above. We constructed the hunter model (model 4) in the same way as the elk predictive model outlined above (i.e., model 3; rifle season only), with the addition of an interaction term between predicted values of the elk RSF (model 3) and beetle-kill (Appendix B).

To evaluate the predictive ability of our elk and hunter models (models 3 and 4), we summed the binned predicted values of the elk and hunter RSFs (i.e., high values represent locations where there is a high probability of use for elk and hunters), and binned those values into 10 equal area bins. We then extracted those binned values to locations where elk and hunters co-occurred within a distance of 1 km from each other, within a 70-minute time frame ($n = 43$; identified from our elk and hunter GPS data). We then plotted a histogram of the bins, and calculated a Spearman rank correlation (r_s) between the bin number and the number of elk-hunter co-occurrences. If elk-hunter co-occurrences were in areas with high predicted RSF values for both elk and hunters, this provided support that our RSFs were robust and predictive. In all RSFs, we used Pearson pairwise correlation to verify if any variables were correlated above 0.5; no correlation at or above this threshold occurred. We conducted all analyses in R version 3.3 (R Core Team 2016).

RESULTS

Habitat Selection Analyses

Elk habitat selection.—We included 55,437 used locations collected from 50 individual elk for June–October in 2012–2016. Of the used locations, 37,699 occurred during summer (Jun–Aug), 9,493 during archery (Sep), and 8,245 during rifle season (Oct). Of the elk locations located in conifer forests only (i.e., beetle-kill and green-conifer), 36% were in beetle-kill and 64% were in green conifer during summer, 40% were in beetle-kill and 60% in green conifer during archery season, and 56% were in beetle-kill and 44% were in green conifer during rifle season (Appendix C). On average, elk used locations 0.97 km from roads (Fig. 2), 0.54 km from water, 2,630 m in elevation, with 13 degrees of slope, with an aspect of 0.041 (slightly northerly), and with a TPI of 0.64 (i.e., areas characterized by ridges).

Elk avoided beetle-killed conifer (BK) during summer ($\beta_{BK_summer} = -0.35 \pm 0.03$ [SE]) but used it in proportion to its availability during archery season ($\beta_{BK_summer} + \beta_{BK_summer \times BK_archery} = -0.03 \pm 0.04$), and selected it during rifle season ($\beta_{BK_summer} + \beta_{BK_summer \times BK_rifle} = 0.12 \pm 0.04$). Elk selected green conifer (GC) during summer ($\beta_{GC_summer} = 0.24 \pm 0.03$) and archery seasons

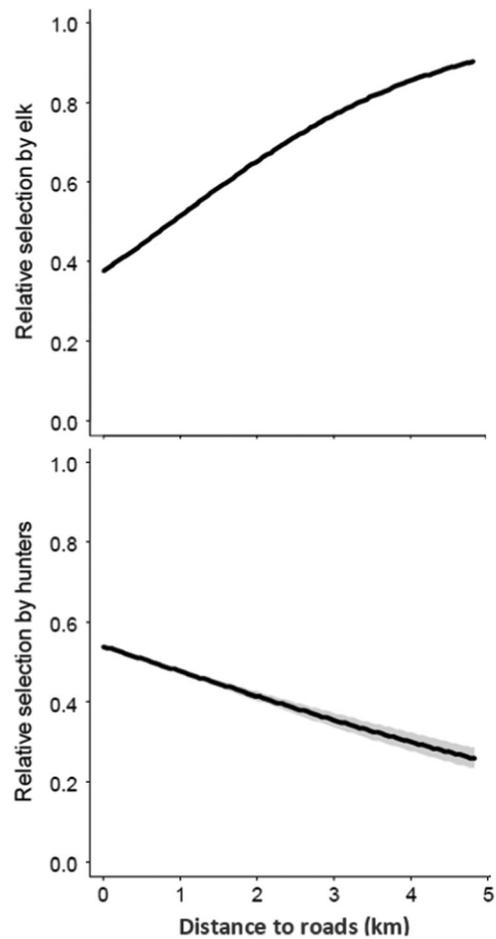


Figure 2. A comparison of relative selection by 374 hunters and 50 elk for distance to roads during the archery and rifle seasons of 2012–2016 in the Sierra Madre Range, Wyoming, USA. We derived coefficients using a mixed effects resource selection model that included land cover and other habitat variables of importance to elk and hunter use. The reference category for land cover in both the hunter and elk RSFs included water and shadow (models 3 and 4).

($\beta_{GC_summer} + \beta_{GC_summer \times GC_archery} = 0.38 \pm 0.03$), and used it in proportion to its availability during rifle season ($\beta_{GC_summer} + \beta_{GC_summer \times GC_rifle} = 0.01 \pm 0.04$). Although elk selected grass meadows (GM) during summer ($\beta_{GM_summer} = 0.48 \pm 0.04$) and rifle seasons ($\beta_{GM_summer} + \beta_{GM_summer \times GM_rifle} = 0.21 \pm 0.08$), they avoided them during archery season ($\beta_{GM_summer} + \beta_{GM_summer \times GM_archery} = -0.53 \pm 0.10$; Fig. 3; Appendix D). Our model (model 1) was robust to k-folds cross validation, with excellent internal predictability (Appendix E).

Hunter habitat selection.—We included 28,379 used locations from 374 individual hunters from September to October during 2012–2016. Of the used locations, 13,501 were archery (Sep) and 14,878 were rifle (Oct). Of the hunter locations in conifer forest (i.e., beetle-kill and green-conifer), 63% were in beetle-kill and 37% in green conifer during the archery season, whereas 74% were in beetle-kill and 26% in green conifer during the rifle season (Appendix F). On average, hunters used locations 0.48 km from roads (Fig. 2), 0.55 km from water, 2,570 m in elevation, with 8 degrees of slope, with an aspect of -0.02

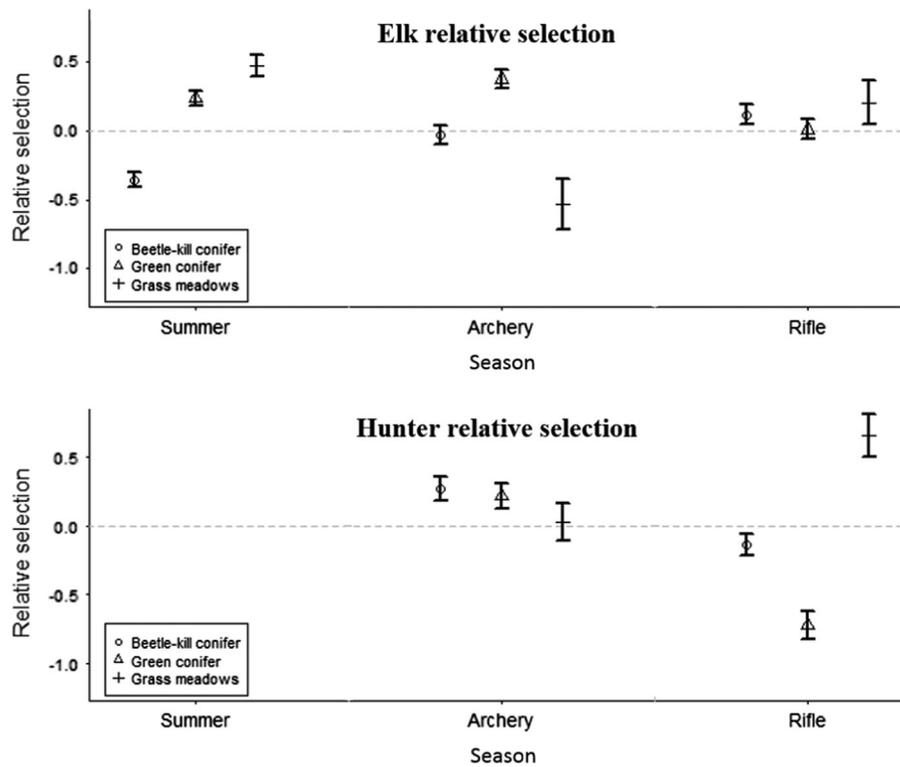


Figure 3. Predicted probability of use from resource selection functions comparing relative selection for grass meadows, green conifer, and beetle-killed conifer across seasons (summer, archery, rifle) for elk ($n = 50$) and hunters ($n = 374$) during June–October 2012–2016 in the Sierra Madre Range, Wyoming, USA. We derived coefficients from interaction terms between each land cover type and season. The reference category for land cover in the hunter and elk RSFs included water and shadow (models 1 and 2).

(i.e., slightly southerly), and with a TPI of 0.80 (i.e., areas characterized by ridges).

Hunters used beetle-kill ($\beta_{\text{BK_archery}} = 0.27 \pm 0.04$) and green conifer ($\beta_{\text{GC_archery}} = 0.21 \pm 0.05$) during archery season but avoided both during rifle season ($\beta_{\text{BK_archery}} + \beta_{\text{BK_archery} \times \text{BK_rifle}} = -0.14 \pm 0.04$; $\beta_{\text{GC_archery}} + \beta_{\text{GC_archery} \times \text{GC_rifle}} = -0.73 \pm 0.05$, respectively). Hunters selected grass meadows in proportion to their availability during archery season ($\beta_{\text{GM_archery}} = 0.02 \pm 0.07$), and selected them during rifle season ($\beta_{\text{GM_archery}} + \beta_{\text{GM_archery} \times \text{GM_rifle}} = 0.66 \pm 0.08$; Fig. 3; Appendix G). Our model (model 2) was robust to k-folds cross validation, with excellent internal predictability (Appendix E).

Elk and hunter interactions.—Because elk selected beetle-kill and hunters avoided beetle-kill during rifle season (but not in archery season), we tested prediction 3 for the rifle season only (model 5). In general, hunters avoided beetle-kill

during rifle season ($\beta = -0.18 \pm 0.03$; Table 1), but if the probability of elk use in beetle-kill was high, then the negative effect of beetle-kill on habitat selection of hunters was dampened ($\beta_{\text{BK} \times \text{ElkRSF}} = 0.16 \pm 0.03$; Fig. 4; Table 1).

Predictive models and management maps.—Our elk and hunter RSFs (models 3 and 4) were robust in their predictive ability; 77% of our elk-hunter co-occurrences were in the highest 2 bins of high elk and high hunter

Table 1. Coefficient values, standard errors, and 95% confidence intervals from a mixed effects resource selection function (RSF) representing the effects of predicted elk use, beetle-kill, and an interaction between the 2 on resource selection of hunters ($n = 374$) during the rifle seasons of 2012–2016 in the Sierra Madre Range, Wyoming, USA (model 5).

Covariate	β			
	\bar{x}	SE	Lower CI	Upper CI
Intercept	0.05	0.01	0.02	0.07
Elk RSF rifle	0.07	0.01	0.05	0.10
Beetle-kill	-0.18	0.03	-0.24	-0.13
Elk RSF rifle \times beetle-kill	0.16	0.03	0.10	0.22

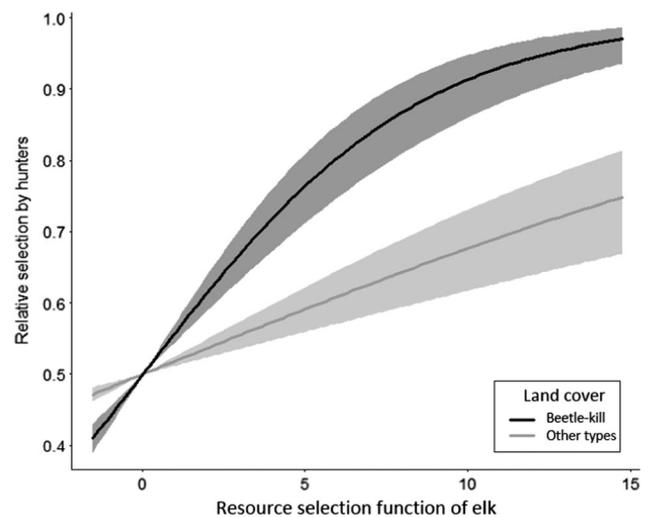


Figure 4. Relative selection by hunters ($n = 374$) as a function of predicted elk use in beetle-killed conifer versus other land cover variables during the rifle seasons (Oct), Sierra Madre Range, Wyoming, USA, 2012–2016 (model 5).

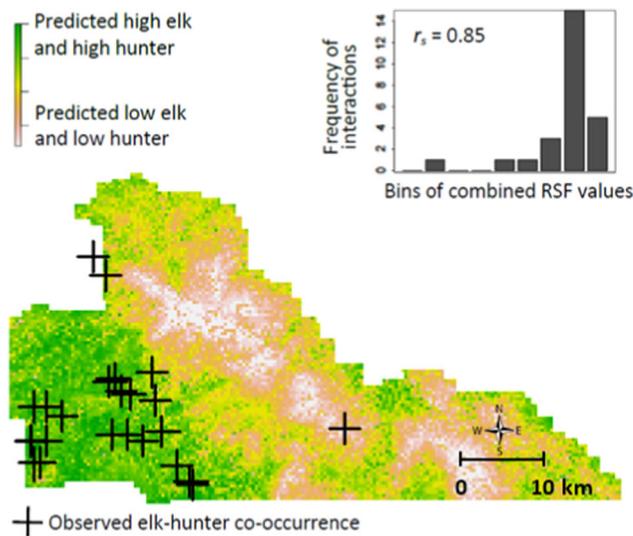


Figure 5. Predicted overlap and validation test of elk and hunter resource selection functions (RSFs). High values in the map represent high elk and high hunter use, whereas low values represent low elk and hunter use. We identified elk-hunter co-occurrences ($n = 43$) by matching global positioning system locations for individual elk and hunters that fell within 1 km of each other within a time frame of 70 minutes during the 2012–2016 hunting season (Oct), Sierra Madre Range, Wyoming, USA. Bins represent equal area quantiles of the predicted values of the overlap between predicted elk and hunter RSFs.

combined predicted RSF values ($r_s = 0.85$; Fig. 5). We identified areas of high elk and low hunter use areas across the study area. Eighteen percent of all high elk and low hunter use areas occurred in beetle-kill exclusively; 82% occurred in other land cover types.

DISCUSSION

At the time of our study (~3–7 yr after the peak of the bark-beetle epidemic in our region), beetle-killed portions of conifer forests in southeast Wyoming provided limited or no additional refuge for adult female elk from hunting pressure. Although elk transitioned from using open areas during summer to increased use of beetle-kill during hunting season (prediction 1), this behavioral shift did not result in avoidance of hunters. Our expectation that hunters would avoid beetle-killed forest (prediction 2) received mixed support. Hunters avoided beetle-kill during the rifle season but selected beetle-kill and other conifer forest during the archery season. Further, in contrast to our final prediction that use of beetle-kill would be independent of elk use (prediction 3), hunters were more likely to use beetle-killed forests in search of elk if those areas had a relatively high probability of elk occurrence.

Forests across the West have experienced structural and compositional changes as a result of the bark-beetle epidemic (Collins et al. 2012). The rate at which these changes occur is influenced by a suite of factors, most notably, time since and severity of infestation, stand condition before epidemic, and other environmental factors (i.e., soil type, moisture, slope, aspect, density of trees, size of tree, wind events; Mitchell and Preisler 1998, Lewis and Hartley

2006). In our study area, at approximately 3–7 years after peak infestation, an earlier study observed 6.2 more downed trees/plot in beetle-kill than non-beetle-kill plots and estimated that approximately 10–15% of beetle-killed trees had fallen (Lamont et al. 2019). Further, when Klutsch et al. (2009) modeled changes in downed woody debris after infestation, the difference from 10% tree fall at year 6, to 80% at year 12, projected a 4-fold increase in downed trees. Although we found little, if any, support for the refuge hypothesis, as dead trees continue to fall, it is still possible that beetle-killed areas may end up providing refuge for elk from hunters.

Relative to summer (recreation use in our study area was minimal during the summer relative to during the hunting season), elk gradually shifted their patterns of habitat selection to include more cover (i.e., beetle-infected and non-infected forested areas) and less grass meadows during the hunting seasons, which is consistent with studies demonstrating that some ungulates use cover disproportionately to its availability (Irwin and Peek 1983, Leckenby 1984, Paton et al. 2017) and seek cover during the hunting season to increase survival (Ciuti et al. 2012a, Lone et al. 2015, Thurfjell et al. 2017). Somewhat counter to our findings, however, Proffitt et al. (2010) did not report a strong relationship between elk use of forested areas while elk were under the threat of hunting. The difference may be attributed to study area differences in habitat characteristics, natural predation, land ownership, and hunting pressure. Our study area received heavy hunting pressure (i.e., ~5,000–6,000 hunters) and harvest (i.e., ~2,000) in a very short time frame (i.e., 30-day archery season, and 20–30-day rifle season), which prompted strong anti-predatory behavior and required elk to seek refuge in nearly impenetrable locations that could buffer them from hunting pressure (Picton 1991, Geist 2002).

During the rifle hunting season, elk selected beetle-kill more strongly than green conifer. Although it may be subtle, these results suggest there may be a benefit to elk by using beetle-kill over intact green conifer when hunting pressure is high (i.e., reduced predation risk or access to other resources; Hernández and Laundré 2005, Bonnot et al. 2013). We suspect elk use of beetle-kill may offer a perceived refuge (Mysterud and Østbye 1999, Thurfjell et al. 2017) while simultaneously increase foraging opportunities (Pec et al. 2015), which may thus reduce the tradeoff associated with seeking refuge at the cost of access to forage. Although recent researchers in the same study area did not report that increases in understory in beetle-kill resulted in increased use of these areas by elk (Lamont et al. 2019), this work was explicitly focused on summer (Jun–Aug), and it may be that when elk are faced with hunting pressure they use this novel forage resource while attempting to reduce exposure to hunters (Lone et al. 2015).

During the archery season hunters used conifer forest, whereas hunters during the rifle season used more open areas (Weber 1998, Thurfjell et al. 2017). Hunters likely occupy thicker cover during the archery seasons because of the necessity of getting close to elk, whereas lethal shots

with rifles may be made at much farther distances and thus are possible within more open terrain (Thomas et al. 1976, Lyon and Burcham 1998, Ciuti et al. 2012a). Although rifle hunters avoided beetle-killed areas in general, they used beetle-killed areas if they coincided with areas selected by elk (Millsbaugh et al. 2000), which weakens the potential refuge benefits of beetle-killed areas. By assessing hunter use with the inclusion of the interaction between elk use and beetle-kill, we detected a response by hunters that was not otherwise observed by simply looking at beetle-kill use alone. It was apparently possible for some hunters to overcome challenges presented by beetle-kill when the opportunity to encounter elk was high. However, although we observed that space use of some elk and hunters overlapped in beetle-kill, our design did not allow us to detect whether that equated to successful harvests. Moreover, it may be that elk continue to buffer themselves from hunters in beetle-kill to some degree because hunting conditions (i.e., difficult to traverse quietly, hard to find shooting lanes) in beetle-kill continue to allow an anti-predatory advantage to elk.

The bark-beetle epidemic in our study area began around 2000 and the peak occurred near 2009, with most trees entering the gray stage by 2012 (S. Loose, U.S. Forest Service, personal communication). Our study occurred from 2012 to 2016, when some trees were just beginning to fall. As the beetle-kill epidemic unfolds, a subsequent increase in downed trees and understory vegetation could influence hunter and elk movements differently than what we observed. Additionally, although our land classification model was generally predictive, error in prediction associated with beetle-kill likely affected our results to some degree (Lamont et al. 2019). We doubt, however, that any classification errors were sufficient to bias our habitat selection analyses. Although not tested explicitly, to our knowledge the different radio-collars had similar GPS error. Further, the mean GPS error of all these collars is generally lower than the resolution of our habitat data (10-m). Finally, although we encouraged hunters to hunt with our GPS units as they would on any normal day of hunting, it is possible they may have tried harder or hunted differently, knowing they were being tracked. We are, nevertheless, unable to quantify or account for any bias in the hunter data.

Although refuge for elk from hunting pressure can buffer animals from mortality (Ciuti et al. 2012a), these interactions are often nuanced (Lone et al. 2015) because of potential changes in habitat characteristics, predators, road networks, or management strategies. In our study system, the bark-beetle epidemic provided an opportunity to assess how a landscape-level transformation of forests may influence interactions between elk and hunters. Our results demonstrated that elk indeed seek refuge in forested areas (beetle-kill or green conifer) during the hunting season, but they also demonstrate that the novel barriers to hunters (i.e., downed trees) do not provide elk with a higher level of refuge than would be normally expected from a typical forest that provides hiding cover from hunters. This net zero gain by hunters and elk is supported further with Wyoming Game and Fish harvest results during the period of our

study. Despite the changes to the forest associated with dead and dying trees, and downed logs (Lamont et al. 2019), harvest rates and effort remained similar from before the bark-beetle epidemic restructured the forest (Wyoming Game and Fish Department, unpublished data), excluding decreased harvest related to management actions (i.e., decrease in available licenses and length of the general female elk season).

MANAGEMENT IMPLICATIONS

Our results suggest that although conifer forests are important for elk security during the hunting season, beetle-killed forests did not result in a marked reduction in the propensity for hunters to access elk in these areas. Therefore, during the approximate 3–7 years following the beetle infestation, it does not appear as if beetle-killed forests necessitate any new innovative management approaches to harvest management. Nevertheless, as beetle-killed trees continue to fall, there is a possibility for more robust refuge habitat to develop (i.e., some of the predictions of the refuge hypothesis were supported). If this occurs, managers could replicate our methods, and identify areas for management actions using our management map framework. With our framework, beetle-killed areas with low hunter use and high elk use could be targeted for habitat treatments such that hunters can better access areas with high probability of elk use.

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APPENDIX A. FULL MODELS

Table A1. We assessed spatiotemporal variation in resource selection of elk and hunters in the Sierra Madre Range, Wyoming, USA, 2012–2016, by fitting 5 resource selection function (RSF) models using mixed effects logistic regression. Covariates evaluated included slope, aspect, elevation (elev), distance to road (road), topographic position index (tpi), distance to water (water), land cover (land cov: bare ground, beetle-kill [BK], deciduous, green conifer [GC], grass meadows [GM], sagebrush), and season (seas; summer, archery, rifle). A random intercept (1|) for individual (id) was included for each model and some included random intercepts for year (yr).

Model	Covariates	Prediction
Model 1	Slope + aspect + elev + road + tpi + water + land cov + BK × seas + GC × seas + GM × seas + (1 id_yr)	Elk selection for BK increases from summer to rifle season. Scaled model.
Model 2	Slope + aspect + elev + road + tpi + water + land cov + BK × seas + GC × seas + GM × seas + (1 id)	Hunter's selection for BK shows avoidance for archery and rifle seasons. Scaled model.
Model 3	Slope + aspect + elev + road + tpi + water + land cov + (1 id_yr)	Elk model for management map and predictions for prediction 3 test, rifle only (Oct), non-scaled model.
Model 4	Slope + aspect + elev + road + tpi + water + land cov + elk RSF × BK + (1 id)	Rifle hunter model for management map predictions, non-scaled model.
Model 5	Elk RSF × BK + (1 id)	Rifle hunter, prediction 3 test, scaled model.

APPENDIX B. MANAGEMENT MAP INPUTS

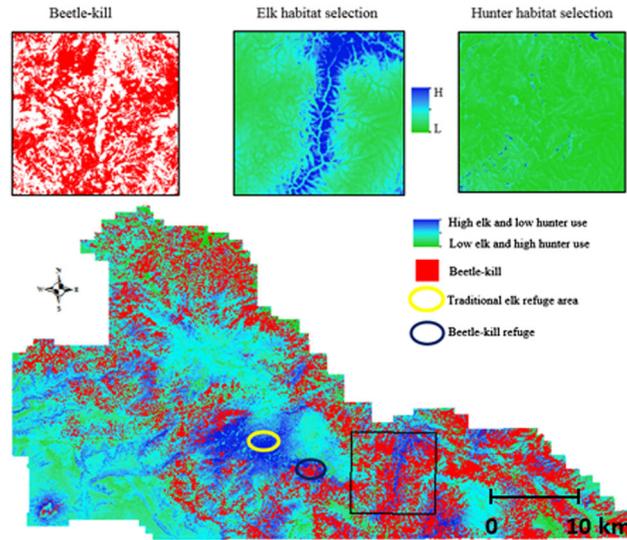


Figure B1. Predicted values from resource selection functions (RSF) for elk and hunters in beetle-kill during the rifle (Oct) seasons of 2012–2016 in the Sierra Madre Range, Wyoming, USA. High elk and low hunter use areas in beetle-kill may provide land managers locations to institute habitat treatments if the aim is to increase access for hunters into high use elk areas. This includes hunter model with the interaction elk RSF \times beetle-kill.

APPENDIX C. ELK USE AND AVAILABILITY

Table C1. Percentage of used and available elk locations by land cover types across seasons, Sierra Madre Range, Wyoming, USA, 2012–2016.

Land cover type	Summer		Archery		Rifle	
	Available	Used	Available	Used	Available	Used
Bare ground	0.05	0.03	0.06	0.03	0.05	0.03
Beetle-kill	0.27	0.15	0.26	0.20	0.26	0.24
Deciduous	0.20	0.29	0.20	0.28	0.21	0.29
Green conifer	0.24	0.27	0.24	0.30	0.24	0.19
Grass meadows	0.04	0.06	0.04	0.02	0.04	0.05
Other (shadow and water)	0.07	0.06	0.08	0.08	0.08	0.08
Sagebrush	0.12	0.14	0.12	0.09	0.12	0.12

APPENDIX D. ELK RESOURCE SELECTION

Table D1. Comparison of standardized coefficient values and 95% confidence intervals from a mixed effects resource selection function representing the effects of habitat characteristics, distance to roads, distance to water, terrain position index (selection for position, valley bottom to ridge), and season (summer, archery, and rifle) on elk ($n = 50$) resource use, Sierra Madre Range, Wyoming, USA, 2012–2016.

Covariate	β			
	\bar{x}	SE	Lower CI	Upper CI
Intercept	-0.16*	0.03	-0.22	-0.11
Slope	-0.08*	0.01	-0.09	-0.06
Aspect	-0.06*	0.01	-0.07	-0.04
Elevation	-0.22*	0.01	-0.24	-0.20
Distance to road	0.53*	0.01	0.52	0.55
Topographic position index	0.03*	0.01	0.02	0.04
Distance to water	-0.03*	0.01	-0.04	-0.02
Bare ground	-0.34*	0.04	-0.42	-0.26
Beetle-killed conifer	-0.35*	0.03	-0.41	-0.30
Deciduous	0.58*	0.03	0.52	0.63
Green conifer	0.24*	0.03	0.18	0.29
Grass meadows	0.48*	0.04	0.39	0.56
Sagebrush	0.18*	0.03	0.12	0.24
Beetle-killed conifer \times archery	0.33*	0.04	0.26	0.40

(Continued)

Table D1. (Continued)

Covariate	β			
	\bar{x}	SE	Lower CI	Upper CI
Beetle-killed conifer \times rifle	0.47*	0.04	0.40	0.54
Green conifer \times archery	0.14*	0.03	0.08	0.20
Green conifer \times rifle	-0.23*	0.04	-0.30	-0.15
Grass meadows \times archery	-1.01*	0.10	-1.19	-0.82
Grass meadows \times rifle	-0.27*	0.08	-0.43	-0.11

* Statistically significant.

APPENDIX E. VALIDATION

The k-folds validation analysis for elk and hunter resource selection function (RSF) models for observed and available locations, Sierra Madre Range, Wyoming, USA, 2012–2016.

RSF model	Observed		Available	
	\bar{x}	SD	\bar{x}	SD
Elk	0.9987879	0.003654683	0.0079537	0.3042582
Hunter	0.9998788	0.001212121	0.0510721	0.3306618

APPENDIX F. HUNTER USE AND AVAILABILITY

Table F1. Percentage of used and available hunter locations by land cover types across seasons, Sierra Madre Range, Wyoming, USA, 2012–2016.

Land cover type	Archery		Rifle	
	Available	Used	Available	Used
Bare ground	0.05	0.13	0.05	0.15
Beetle-kill	0.26	0.29	0.27	0.23
Deciduous	0.20	0.20	0.20	0.20
Green conifer	0.24	0.17	0.25	0.08
Grass meadows	0.04	0.06	0.04	0.12
Other (shadow and water)	0.08	0.07	0.07	0.06
Sagebrush	0.12	0.09	0.12	0.17

APPENDIX G. HUNTER RESOURCE SELECTION

Table G1. Comparison of standardized coefficient values and 95% confidence intervals from a mixed effects resource selection function representing the effects of habitat characteristics, distance to roads, distance to water, terrain position index (selection for position, valley bottom to ridge), and season (archery and rifle) on hunter ($n = 374$) resource use, Sierra Madre Range, Wyoming, USA, 2012–2016.

Covariate	β			
	\bar{x}	SE	Lower CI	Upper CI
Intercept	-0.06	0.04	-0.13	0.02
Slope	-0.49*	0.01	-0.52	-0.47
Aspect	-0.07*	0.01	-0.08	-0.05
Elevation	-0.50*	0.01	-0.53	-0.48
Distance to roads	-0.17*	0.01	-0.19	-0.15
Topographic position index	0.16*	0.01	0.14	0.18
Distance to water	0.08*	0.01	0.06	0.10
Bare ground	1.18*	0.05	1.09	1.28
Beetle-killed conifer	0.27*	0.04	0.18	0.36
Deciduous	-0.15*	0.04	-0.23	-0.07
Green conifer	0.21*	0.05	0.12	0.31
Grass meadows	0.02	0.07	-0.11	0.16
Sagebrush	-0.37*	0.05	-0.46	-0.28
Beetle-killed conifer \times rifle	-0.41*	0.04	-0.49	-0.33
Green conifer \times rifle	-0.94*	0.05	-1.04	-0.84
Grass meadows \times rifle	0.63*	0.08	0.48	0.79

* Statistically significant.