



Research Article

Multi-Scale Habitat Selection of Elk in Response to Beetle-Killed Forest

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ABSTRACT Forests of the Rocky Mountains (USA and Canada) have experienced a large-scale bark-beetle (*Dendroctonus ponderosae*) epidemic that has led to widespread mortality of pine trees, followed by structural and compositional changes to the forest. The millions of dead trees resulting from this event likely have an effect on ecosystem processes, but currently those effects are mostly unclear. Changes to forest canopy and understory structure are likely to affect behavior and space use of large ungulates as forage abundance, thermal cover, and locomotive costs are presumably altered. We developed and tested hypotheses for how resource selection in summer of female elk (*Cervus canadensis*; $n = 47$; 2012–2016), the primary large mammal in our study area, was influenced by changes in canopy, understory vegetation, and downed logs in bark-beetle affected forest in south-central Wyoming, USA. We employed global positioning system (GPS) technology, an imagery-derived land cover classification specifically depicting beetle-affected forest, and on-the-ground forest measurements to develop resource and step selection functions. At the study area scale, elk avoided beetle-killed forest during nearly all parts of the day and selected for intact conifer forest during the day. At the micro-habitat scale, as canopy cover decreased in beetle-killed areas, there was a concomitant increase in grass biomass and downed logs. Nevertheless, while in the forest, elk did not alter resource selection relative to changes in understory vegetation or downed logs. The boost in forage abundance within beetle-killed areas was insufficient to overcome the presumed increases in energy expenditures associated with locomotion and thermoregulation in beetle-killed forests. The bark-beetle epidemic has altered how elk use the landscape and has resulted in a potential loss of forest habitat that elk use during the day. Our results indicate that habitat treatments (i.e., fire or harvest) that remove standing dead trees and downed logs in beetle-killed forest would further facilitate understory growth while reducing the locomotion costs associated with foraging in beetle-killed forest. © 2019 The Wildlife Society.

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

Natural and human-induced disturbances can affect wildlife habitat, resulting in altered movement of wildlife (Lytle 2001, Montgomery et al. 2013, McKelvey 2015). Disturbances can influence individuals by removing or altering preferred habitat and access to key resources such as food or nest sites (Gill et al.

1996, Cahall and Hayes 2009, Klenner and Sullivan 2009), ultimately altering fitness outcomes (Courtois et al. 2007). Following prescribed fire, for example, changes to the structure and characteristics of forests produce variable responses from avian species (Russell et al. 2009). Variability and uncertainty in how landscapes are affected by disturbances and how wildlife respond to the changes complicate the goals of wildlife and land managers to meet habitat requirements for wildlife, objectives of management plans, conservation of sensitive species, and population and harvest objectives.

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For nearly 2 decades, forests of the Rocky Mountains have experienced a bark-beetle epidemic of severity and duration that has not been observed in over a century (Raffa et al. 2008, Kayes and Tinker 2012, Black et al. 2013). For instance, between northern Colorado and southern Wyoming, USA, the mountain pine beetle (*Dendroctonus ponderosae*) alone has caused mortalities in >1.5 million ha of lodgepole pine (*Pinus contorta*; Kayes and Tinker 2012). The bark-beetle epidemic has changed the structure and composition of conifer forests by altering canopy cover and understory vegetation and increasing the number of downed logs (Klutsch et al. 2009, Collins et al. 2012, Pec et al. 2015). Wildlife species vary in their responses to these changes. For example, bark-drilling, cavity-nesting, and shrub-laying nesting birds responded favorably to habitat alterations created by the bark-beetle epidemic, whereas open-cup and ground nesting birds tended to decline (Saab et al. 2014). Moreover, red squirrels (*Tamiasciurus hudsonicus*) have responded negatively to the bark-beetle epidemic, whereas small mammals associated with forest understories have shown mixed effects depending upon the temporal scale (Saab et al. 2014). The structural changes that occur from the disturbance created by the bark beetle have the potential to influence foraging opportunities, thermal demands, locomotion, and refuge from predation for a variety of wildlife species.

Across western North America, large herbivores play a key role in ecosystem function (Frank and Evans 1997, Frank et al. 2000), contribute to local and regional economies (Duffield and Holliman 1988), and underpin a strong culture of hunting in many rural areas. Ungulates increase nitrogen cycling and positively affect primary productivity through the increase of plant nitrate assimilation (Frank and Evans 1997, Frank et al. 2000), serve as prey for a variety of predators, and provide food for a multitude of scavengers through natural and predator-induced mortalities (Wilmers et al. 2003). Because of their ecological and social significance, it is important to understand how ungulates respond to beetle-killed forest.

The North American elk (*Cervus canadensis*) is the primary (in terms of biomass) large mammal in beetle-killed forests in the northern Rocky Mountains of the United States. Elk distribution, like other ungulates, in particular during the growing season, is underscored by animals attempting to maximize net energy gain through the acquisition of highly palatable and nutritious forage at intermediate biomass (Fryxell 1991, Hebblewhite et al. 2008). Events such as prescribed fires, wild fires, and logging lead to transitions from climax communities of mature trees or shrubs to early-seral grass and forb species, typically resulting in increased use by elk (Lyon and Jensen 1980, Dyke and Darragh 2007, Biggs et al. 2010). Bark-beetle affected forests experience a somewhat similar transition as observed in other forest disturbances, changing from climax communities to a forest with increased heterogeneity, and in some instances increased understory vegetation (Kovacic et al. 1985, Stone and Wolfe 1996, Pec et al. 2015). Ungulates must attempt to maximize energy gain from forage intake and balance energy

expenditure (Long et al. 2016). To meet this balance, ungulates employ a number of behavioral tactics (Parker et al. 2009). For example, elk tend to avoid unnecessary explorations, avoid areas where search time for food is long, stay in patches where forage is abundant, and move in single file through deep snow (Geist 2002, Wolf et al. 2009). Energy costs for ungulates increase with activity level, surface slope (Fortin et al. 2005), snow depth, slash (tree debris) from clear cuts (Lyon and Jensen 1980), and gait changes (i.e., jumping or high-stepping, rather than walking; Parker et al. 1984). Landscape changes resulting from disturbance can influence energy balance if they create impediments to movement (Parker et al. 1984). Slash with height in excess of 0.5 m following forest clear-cuts, for example, deters use by ungulates (Lyon and Jensen 1980). Energetic balance is influenced not only by energy gain through forage and energy loss through locomotion but also by thermal regulation. The well-documented, disproportionate use of dense forest stands by ungulates (Irwin and Peek 1983, Leckenby 1984, Edge et al. 1987) functions in part to reduce the energetic costs of thermoregulation (Zahn 1985, Ockenfels and Brooks 1994). Elk possess the ability to sweat and pant to regulate body temperature, but mitigating heat load is an important behavioral strategy that has fitness implications (Skovlin et al. 2002; Long et al. 2014, 2016). A reduction in canopy and density of old conifer trees (Klutsch et al. 2009) in beetle-killed forests may reduce thermal refuge for elk.

Our objective was to develop and test 3 hypotheses of how elk alter their selection of habitat in response to extensive tree mortality caused by bark beetles within conifer forests. We hypothesized that the bark-beetle infestation would enhance forage availability for elk (i.e., forage hypothesis) because loss of trees reduces canopy cover and opens the forest floor to an increase in moisture and sunlight, which promotes understory vegetation (Kovacic et al. 1985, Stone and Wolfe 1996, Pec et al. 2015). Accordingly, we expected beetle damage to promote understory growth and for elk to increase use of these areas during prime feeding times (i.e., crepuscular times) relative to traditional foraging areas. Second, we hypothesized that locomotion for elk would be affected negatively by increases in downed logs because dead trees fall following a bark-beetle epidemic (i.e., locomotion hypothesis; Schmid et al. 1985, Mitchell and Preisler 1998, Klutsch et al. 2009); we predicted that downed logs would increase in beetle-killed forest and that elk would avoid those areas consistently throughout the day given expectations for increased locomotive costs. Finally, we hypothesized that thermoregulatory constraints for elk would be modified following a bark-beetle infestation. Consistent with that hypothesis, we predicted that with the opening of the canopy, beetle-killed forests would be avoided by elk especially during the hot parts of the day when heat loads would be greatest.

STUDY AREA

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 south-central Wyoming delineated our 1,377-km² study area

(Fig. 1; Dillon et al. 2005). Our study period consisted of the summer months (Jun–Aug) of years 2012 through 2016, which was ~3–7 years after the peak of the bark beetle infestation in our region. The Sierra Madre is mountainous, and elevations ranged from around 1,900 m to 3,350 m. Temperatures ranged from -46°C during winter to 32°C in summer (Dillon et al. 2005), with daily peak temperatures occurring between 1000 and 1500. Precipitation in high elevations was primarily in the form of snow, with total precipitation ranging from 38 cm (low elevations) to 100 cm (high elevations; Dillon et al. 2005). The study area has a population of approximately 6,500–8,500 elk, and is devoid of a full suite of predators (i.e., no wolves [*Canis lupus*] or grizzly bears [*Ursus arctos*]) known to influence elk population dynamics. The dominant fauna included ungulates (elk, mule deer [*Odocoileus hemionus*], moose [*Alces alces shirasi*]), carnivores (black bear [*Ursus americanus*], mountain lion [*Puma concolor*], coyote [*Canis latrans*]), small mammals (red squirrel, porcupine [*Erethizon dorsatum*], American marten [*Martes americana*], Colorado chipmunk [*Tamias quadrivittatus*]), forest and upland birds (dusky [*Dendragapus obscurus*], sage [*Centrocercus urophasianus*], and sharp-tailed [*Tympanuchus phasianellus columbianus*] grouse), corvids (Canada jay [*Perisoreus canadensis*], Steller’s jay [*Cyanocitta stelleri*], raven [*Corvus corax*]), raptors (golden [*Aquila chrysaetos*] and bald [*Haliaeetus leucocephalus*] eagles, red-tailed [*Buteo jamaicensis*] and sharp-shinned [*Accipiter striatus*] hawk), and a wide variety of song birds.

Lower elevations typically consisted of grasslands and shrub lands that transitioned into lodgepole pine forests at higher elevations. About 78% of the study area was forested and 61% of those forests were primarily lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). The majority of the lodgepole pine forests

were affected by the bark-beetle epidemic. Aspen trees (*Populus tremuloides*) also were a significant feature across the study area and accounted for about 17% of the total land area (Dillon et al. 2005). Around 85% of the forests were ≤ 150 years old, indicating that either fire or timber harvest had affected most of the forested areas (Dillon et al. 2005). Land use included livestock grazing (e.g., cattle and sheep), timber harvest, and recreation (e.g., hunting, fishing, hiking, horseback and off-high vehicle riding, and camping).

METHODS

We assessed how the bark-beetle infestation influenced forest structure and composition, and tested predictions of 3 hypotheses as to how elk balance the competing, but not necessarily mutually exclusive, energetic demands of obtaining forage, mediating locomotion, and thermoregulation in response to a landscape-scale alteration. Although we did not explicitly measure forage acquisition, or locomotive and thermoregulatory costs, we formulated our expectations based on expectations associated with each one of the aforementioned potential forces on behavior of elk. We combined GPS collar data with a remotely sensed land-cover classification (study area scale) and forest-structure measurements (micro-habitat scale) to evaluate how elk respond to beetle-killed forest at different scales.

Elk 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 after capturing elk via helicopter net-gunning (Barrett et al. 1982). We captured and handled all animals according to protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol number 20140311MK00076). In

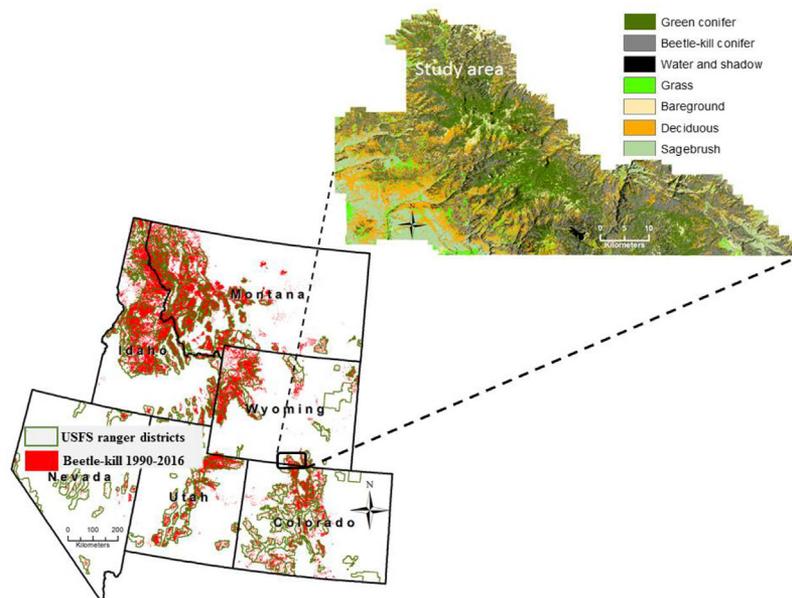


Figure 1. Distribution of bark-beetle affected forests (1990–2016) relative to United States Forest Service (USFS) lands in the Rocky Mountain West, USA (bottom left). Study area delineated by Medicine Bow-Routt National Forest boundary with land cover classes to distinguish beetle-killed from non-beetle-killed conifer in habitat selection models (top right), Sierra Madre Range, south-central Wyoming, USA.

February of 2012 and March of 2015, we deployed store-on-board radio-collars (Telonics, Mesa, AZ, USA [$n=26$], Advanced Telemetry Systems, Isanti, MN, USA [$n=15$]) with a remote-release mechanism and programmed to attempt a location fix every 90 minutes. We deployed an additional 15 Globalstar radio-collars (Advanced Telemetry Systems) programmed to attempt a location fix every hour in March and April 2016. We conducted analyses using a sample of 47 individual elk (GPS fix success ~ 0.95) following a combination of collar failure, elk movements outside of the study area, and mortality.

Habitat Selection Analyses

Our analysis consisted of 3 parts. We conducted detailed analyses of forest habitat to assess the extent to which beetle-killed forest led to increased forage availability, canopy loss, and downed logs. Second, we assessed habitat selection of elk at the scale of the study area to test whether elk select beetle-killed areas during prime feeding times (Preisler et al. 2004), avoid beetle-killed areas during all times of days, or avoid beetle-killed areas during the hotter portions of the day. Finally, we assessed habitat selection at the micro-habitat scale (i.e., when elk were in the forest) to investigate whether elk select areas with increased understory vegetation, avoid areas with more downed logs, and avoid areas with less canopy cover. We conducted all statistical analyses in R version 3.3 (R Core Team 2016), unless otherwise noted.

Study area scale analysis.—We evaluated spatiotemporal variation in habitat selection of elk for bark-beetle affected forest at the study area scale using mixed-effects resource selection functions (RSF), 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 randomly selected 12 locations/day as used locations. We removed ($n=5$) any elk with <1 month of data during June–August from the analysis. We identified GPS locations ($n=78,469$) of 47 individual elk from June–August of years 2012 through 2016 as used locations and an equal number of available locations randomly chosen from within the study area boundary (Boyce et al. 2002).

We included variables that influence movement and space use of elk in our RSF: 1) elevation (National Elevation Dataset, U.S. Geological Survey; 10-m resolution), 2) slope (10-m resolution), 3) aspect (ranging from -1 as southerly to 1 as northerly aspects, 10-m resolution; Merkle et al. 2016), 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 (calculated as the difference between the elevation of a cell and the mean elevation of its nearest 80 surrounding cells, ranging from -50 as valley bottoms and 50 as ridgetops, 30-m resolution), 6) distance to roads (geographic information system [GIS] road layer from the Medicine Bow-Routt National Forests and Thunder Basin National Grassland's Brush Creek-Hayden Ranger District, calculated by rasterizing the vector layer and then using the distance function in ArcGIS, 10-m resolution), and 7) land cover type. We developed a land cover map using National Agricultural

Imagery Program (NAIP; 1-m resolution) imagery and a random forest model (Hayes et al. 2014) because we were interested in distinguishing between beetle-killed and non-beetle-killed conifer forest across our study area. Our land cover classification included green conifer (non-beetle-killed), beetle-killed conifer, grass meadows, sagebrush, deciduous trees and shrubs (aspen, willow, and cottonwood), and other (water, shadow, and bare ground; Appendix A; Fig. 1).

We fit 3 RSFs using mixed-effects logistic regression that we constructed to provide specific tests of our predictions. First, we developed a base model including all covariates, while combining land cover classes of green conifer and beetle-killed conifer into 1 class. We then evaluated whether elk responded to beetle-killed conifer by separating green conifer from beetle-killed conifer cover types while including all other covariates in our base model. Lastly, we separated every 24-hour period into 12 categorical blocks, each consisting of 2 hours and starting at midnight (i.e., 0000–0200 was the first 2-hour block of the 12 2-hour blocks). We then included the interaction of the 12 time periods with green conifer, beetle-killed conifer, and grass meadows to evaluate how selection changed throughout the day, which yielded a coefficient estimate for each 2-hour block for those 3 land cover types (Appendix A). In all models, we used the land cover class other as the reference category. Using simple selection ratios (Manly et al. 2002), the other category was used by elk in proportion to its availability and represented a meaningful proportion of the landscape (0.13). We included a random intercept for each individual-year in all models to account for a lack of independence within individual samples and inconsistencies in sample size among individuals (Gillies et al. 2006). Before fitting models, we scaled and centered all continuous variables (Schielezeth 2010). We used Pearson pairwise correlation to assess multicollinearity among the variables with a cutoff of 0.5. Elevation was correlated with green conifer ($r=0.6$); therefore, we removed elevation from consideration in the model set. We used Akaike's Information Criterion (AIC) scores to assess relative support of our 3 models (Burnham and Anderson 2002).

To assess the predictive power of our top model we used k -folds cross validation (Boyce et al. 2002). We randomly divided the data into 5 folds, using 80% of the data interactively to fit the model, and withholding the remaining 20% of data to validate the model. We assessed goodness-of-fit of a model by the correlation between ranked bins of predicted RSF values calculated from the withheld data and the frequency of occurrence of observed locations in those bins. A high positive Spearman rank correlation (r_s) suggests a model with excellent predictive power (Boyce et al. 2002). We replicated this process 100 times and calculated the mean and standard deviation of the resulting values.

Micro-habitat scale analysis.—We used a step selection function (SSF; Thurfjell et al. 2014) framework to evaluate the influence of imagery-derived and field-based forest measurements of habitat characteristics on movement steps by elk when they were in the forest based on 100 used points (paired with 3 available points for each used point, termed a strata). To create each strata, we randomly selected 100 elk locations (i.e., source; representing 18 individuals) on summer

range in 2014 when they were within conifer forest (Thurfjell et al. 2014). We identified elk locations within conifer forest by intersecting elk locations with conifer land cover types from our imagery-derived land cover classification. For each of the 100 elk locations, we generated 3 available steps (the second location of each step is referred to as the target) based on the distributions of turning angles and step lengths (Appendix B) from all observed steps simultaneously (Thurfjell et al. 2014). We then quantified key aspects of forest structure and composition at the used and available points. During June–August of 2016, we estimated percent cover of understory vegetation (grasses, forbs, and shrubs), percent cover and number of downed logs, percent canopy cover, and the proportion of live and dead trees for the case and 3 control plots, totaling 400 plots.

We developed an SSF by comparing the used and available points for the 100 strata mentioned above (Thurfjell et al. 2014). We built a base SSF where use was a function of elevation, slope, aspect, distance to roads, terrain position index, and distance to water at the target locations. As suggested by Forester et al. (2009), we included distance (in km) between the source and target locations as a covariate to better represent heterogeneity in the availability domain at each step. We evaluated the relative contributions of adding variables associated with forest structure to the SSF using AIC corrected for sample size (AIC_c) by individually adding those variables to the base model (uninformative variables [i.e., >0.05] were identified). Forest structure variables included percent canopy cover, percent cover and number of downed logs, percent cover and maximum height of grass, and percent beetle-killed forest (see Forest structure measurements section below for details on data collection). We parameterized the SSFs using conditional logistic regression (Thurfjell et al. 2014).

Forest structure measurements.—We established a 25-m² plot (Fig. 2) around the ending locations of each used and available step in the SSF analysis above. For each plot, we identified a north to south 25-m transect, with the center point of the plot at the 12.5-m point of the transect, and additional parallel transects 12.5 m to the east and west of the center transect. At the 0-m, 12.5-m, and 25-m points along each transect, we quantified percent cover of grasses, forbs, and shrubs using a 0.5-m² quadrat (Daubenmire 1959). Using a densiometer, we assessed percent canopy cover in all 4 cardinal directions at the 12.5-m point of each transect (Lemmon 1956, 1957). Every 5 m along each transect, we identified the closest standing tree as live or dead to estimate the proportion of live to dead trees per plot. Finally, we quantified the percent cover of downed logs by measuring the intersection length and height of all downed logs, and the height of any branches that crossed each transect. From the forest structure measurements, we calculated percent canopy cover for each 25-m² plot by averaging densiometer readings for the 4 cardinal directions for each transect, percent cover of downed logs for each 25-m² plot by summing all log intersection lengths per transect and then dividing by 25, the average number of downed logs per plot by adding the number of downed logs per transect, and the percent cover of

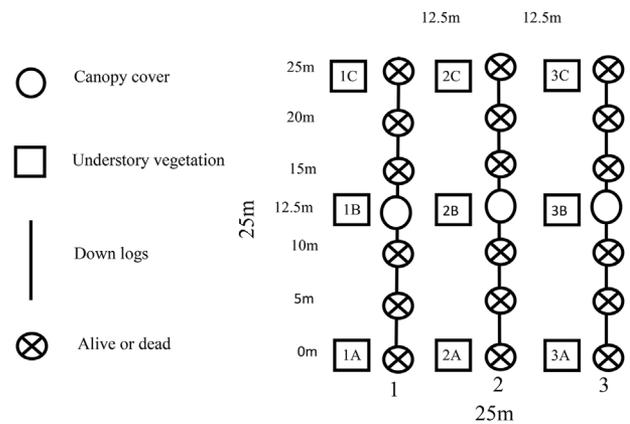


Figure 2. During June–August of 2016, we visited 400 used and available elk locations within our study area in the Sierra Madre Range, Wyoming, USA, to gather forest-structure measurements to be used in habitat selection analyses. At each location (origin), we established a 25-m² plot, which included 3 parallel 25-m north to south transects separated by 12.5 m. At each plot we measured percent canopy cover, percent cover of understory vegetation, percent cover of downed logs, and the proportion of alive and dead trees to quantify differences between beetle-killed and non-beetle-killed conifer forest.

understory vegetation by averaging the percent cover of each category (grass, forbs, and shrubs) for each quadrat (0 m, 12.5 m, 25 m) along a transect. For each of the above metrics, we averaged the 3 individual transect values to obtain a plot level statistic. Per visual inspection, we also assigned a qualitative description (i.e., green conifer, beetle-killed conifer, beetle-killed–green conifer mix) to each of the individual plots based on the composition and characteristics of species within each plot.

To assess the influence of changes in forest structure (i.e., canopy loss) on other attributes of the forest (i.e., understory vegetation and downed logs), we used linear regression and data from plots of available steps that were qualitatively described as green conifer, green conifer–beetle-killed conifer mix and beetle-killed conifer ($n = 230$). We eliminated all other qualitative classes (e.g., aspen, sagebrush) from these analyses.

RESULTS

Forest Structure

Forest characteristics varied across plots, including very few plots that were either completely green forest or completely beetle-killed forest. As canopy cover declined, percent cover ($P < 0.001$, $R^2 = 0.068$, $F_{1,230} = 16.84$; Fig. 3) and height of grass ($P < 0.001$, $R^2 = 0.11$, $F_{1,230} = 29.13$; Fig. 3) increased, but percent cover of forbs ($P = 0.9$) and shrubs ($P = 0.07$) did not. Based on qualitative descriptions (i.e., plots identified as being dominated by green conifer, beetle-killed conifer, beetle-kill–green conifer mix) of each of the plots visited, percent cover of downed logs was higher in beetle-killed plots ($P = 0.03$, $F_{1,230} = 4.79$; Fig. 3). Beetle-killed plots had 6.2 ± 2.17 (SE) more downed logs per plot ($P = 0.004$, $F_{1,230} = 8.11$; Fig. 3) than non-beetle-killed plots.

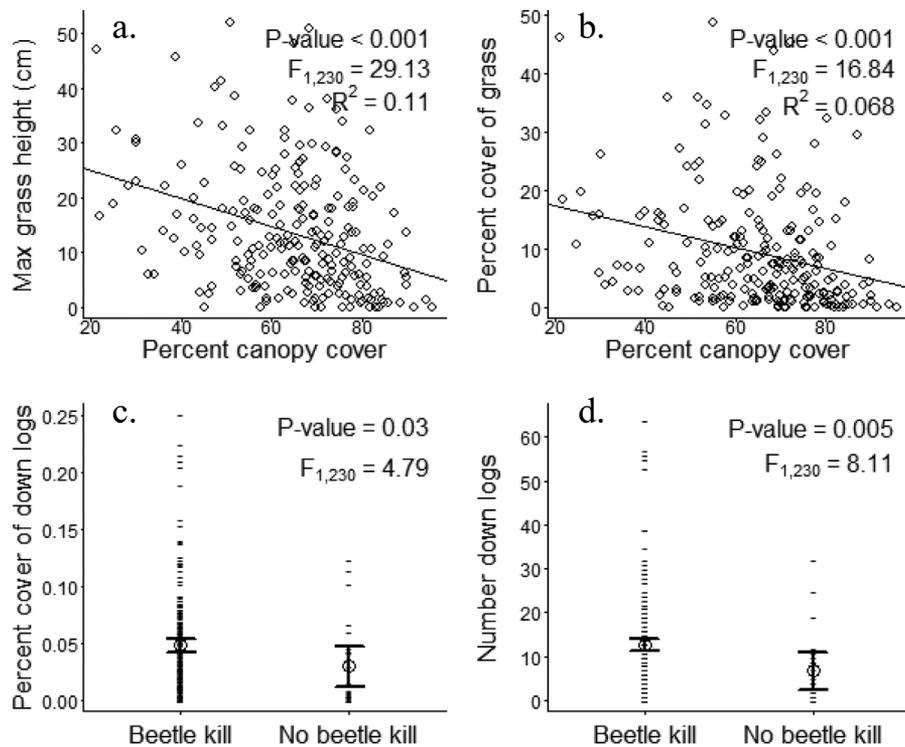


Figure 3. The influence of beetle-killed forest (i.e., canopy cover) on maximum grass height (a), percent cover of grass (b), percent cover of downed logs (c), and number of downed logs (d). We quantified forest structure measurements ($n = 230$) June–August 2016 in the Sierra Madre Range, Wyoming, USA. We defined beetle-kill versus no beetle-kill based on qualitative descriptions (i.e., plots dominated by only green conifer (no beetle-kill) or beetle-killed conifer and beetle-killed–green conifer mix (beetle-kill)).

Study Area Scale Selection

We included 78,469 used locations from 47 individual elk for June–August 2012–2016. Of the elk locations, 40% were located in conifer forest (i.e., 15% beetle-killed and 25% green-conifer). Used locations for elk occurred on average 0.16 km from roads and 1.65 km from water, in areas that were 2,407 m in elevation with 2 degrees of slope on slightly southerly aspect (-0.09) and on ridges (2.02 terrain position index). In summer, elk avoided steep slopes, and selected south-facing slopes, areas farther from roads and closer to water sources, and valley bottoms over ridges (Appendix C).

Elk responded to beetle-killed forest; the delineation of beetle-killed areas within conifer forest resulted in a marked improvement in model fit (Table 1). Elk avoided beetle-killed forest ($\beta = -0.25 \pm 0.05$), compared with our reference land cover class (other), which included water, shadow, and bare ground. Nevertheless, habitat selection for land cover varied throughout the day as indicated by support for the inclusion of an interaction with hour of day (Table 1). Elk avoided beetle-killed conifer during most parts of the day (Appendix C; Fig. 4). Selection for green conifer was highest during daytime hours but diminished during crepuscular times of the day (Appendix C; Fig. 4). Selection for grass meadows was highest during crepuscular times and lowest during early to mid-day hours (Appendix C; Fig. 4). Elk selected green conifer over beetle-killed conifer during the hotter part of the day (1000–1500; Fig. 4), and selected grass meadows over beetle-killed and green conifer during prime

feeding times (crepuscular and night; Appendix C; Fig. 4). The top RSF model (Table 1) was robust to k-folds cross validation, with excellent predictive ability ($r_s = 1 \pm 0$ for observed locations; and $r_s = -0.006 \pm 0.380$ for available locations).

Micro-Habitat Scale Selection

Based on our random sample of 100 steps, elk did not appear to discriminate among available forested habitat. The inclusion of elevation, slope, aspect, distance to road, terrain

Table 1. Models and Akaike's Information Criterion (AIC) values from resource selection functions to assess habitat selection of elk at the study area scale from 2012–2014 in the Sierra Madre Range, Wyoming, USA.

Model	K^a	logLik ^b	ΔAIC	AIC
Beetle-kill with hour model ^c	13	-101,402.1	0.0	202,894.1
Beetle-kill model ^d	10	-102,011.3	1,152.5	204,046.6
Base model ^e	9	-102,351.7	1,831.4	204,725.5

^a Number of parameters in model.

^b Log of the likelihood function of the model.

^c Slope + aspect + distance to roads + terrain position index + distance to water + green conifer + green conifer:hour + beetle-killed conifer + beetle-killed conifer:hour + sagebrush + deciduous + grass meadows + grass meadows:hour.

^d Slope + aspect + distance to roads + terrain position index + distance to water + green conifer + beetle-killed conifer + sagebrush + deciduous + grass meadows.

^e Slope + aspect + distance to roads + terrain position index + distance to water + conifer + sagebrush + deciduous + grass meadows.

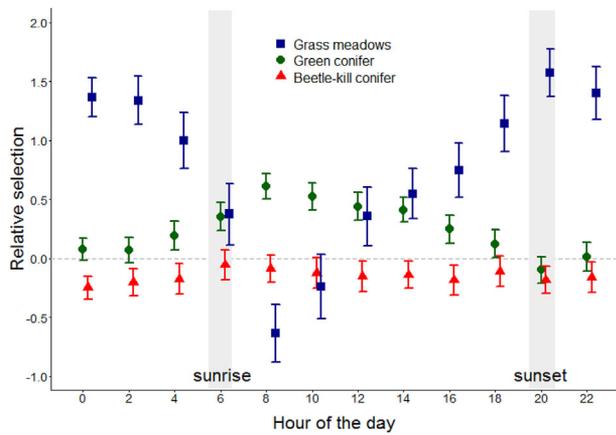


Figure 4. Beta coefficients (95% CI) from our top resource selection function model comparing relative selection for grass meadows, green conifer, and beetle-killed conifer across hours of the day for elk ($n = 47$) during June–August of 2012–2016 in the Sierra Madre Range, Wyoming, USA. We derived coefficients from interaction terms between each land cover type and hour of the day, defined as a factor representing 2-hour increments. The other category (i.e., water, shadow, and bare ground) was the reference category.

position index, and distance to water did not result in an improvement of model fit (based on ΔAIC_c). Further, we did not detect any improvement in model fit with the addition of percent canopy cover, percent cover and maximum height of grass, percent beetle-killed conifer, or percent cover and number of downed logs (model fit improved with inclusion of number of downed logs but the variable was not significant at 0.05; Table 2).

DISCUSSION

Millions of hectares of forest across the Rocky Mountains (USA and Canada) have and continue to experience changes to their structure and composition because of the bark-beetle epidemic (Raffa et al. 2008, Kayes and Tinker 2012, Black et al. 2013). With many wildlife species relying on these forests, it is important to understand how such changes may influence habitat selection of animals as they seek to adapt to landscape-level changes. At the time of our study elk consistently avoided beetle-killed forests at the study area scale during the summer, whereas we did not detect a strong

influence on elk selection at the micro-habitat scale. We suspect that once elk are in beetle-killed forest, which is avoided at a broader scale, the characteristics of beetle-killed forests do not strongly affect movement behavior. Although there was more forage available in the beetle-killed portions of the forest, elk avoided these areas, contesting the notion that increased forage biomass associated with opening of the canopy invariably promotes increased use by elk. Elk avoided beetle-killed forest during almost all parts of the day (Fig. 4) during the summer, in contrast to green conifer being selected by elk during daylight hours, thereby supporting the thermal cover hypothesis. Consistent avoidance of beetle-killed areas within conifer forest, even during key feeding periods, lends correlative support to avoiding unnecessary costs of locomotion associated with navigating downed logs within beetle-kill forest. Because green conifer forests are important for elk (Irwin and Peek 1983, Leckenby 1984, Edge et al. 1987), especially during the hotter parts of the day (Fig. 4), the conversion of green to beetle-killed forest may be acting as a net loss of habitat for elk because the boost in forage availability from opening of the canopy does not appear to translate to habitat use by elk.

In contrast to our forage hypothesis, elk consistently avoided beetle-killed areas within conifer forest during summer, a result counter to other studies reporting that elk often seek areas following a disturbance (i.e., forest fires or clear cuts) to capitalize on the newly available forage (Lyon and Jensen 1980, Forester et al. 2007, Biggs et al. 2010). Although grass cover and height increased with loss of canopy in beetle-killed forest (Fig. 3), elk continued to use more reliable feeding areas in grass meadows that provide easy access to large quantities of highly palatable and nutritious food. We suspect the continued presence of standing dead trees in beetle-killed areas is not yielding comparable reductions in canopy cover and corresponding response in understory vegetation as is often observed in other forest disturbance including fire or clear cuts (Pearson et al. 1972, Oswald and Covington 1983, Bataineh et al. 2006). As time passes, more dead trees will fall, which may further open the canopy and stimulate understory growth, unless subsequent conifer replacement advances rapidly enough to reduce the degree of canopy opening (Forester et al. 2007). In addition to the limited increases in understory vegetation, the avoidance of beetle-killed areas also may be a result of the increase in costs of locomotion caused by downed logs (Parker et al. 1984), and added costs to thermoregulation with the opening of the canopy (Long et al. 2016). Benefits of the meager new foraging opportunities from beetle-associated reductions in canopy cover currently appear to be outweighed by other costs.

If thermal cover is one of several important determinants of elk fitness (Long et al. 2014, 2016), then the loss of green conifer (~54 % in our study area), which is ultimately a loss to the overall amount of thermal cover available to elk, may lead to fitness consequences associated with increased thermoregulation. Indeed, elk avoided beetle-killed conifer during all parts of the day, in contrast to intact conifer, which was selected strongly during daylight hours and presumably, supports an explanation associated with seeking thermal cover. The peak in

Table 2. Mean beta coefficients and difference in corrected Akaike's Information Criterion (ΔAIC_c) values from step selection function models when variables were added to base model one at a time to assess elk selection at micro-habitat scale in 2014 in the Sierra Madre Range, WY (USA).

Variable	β	<i>P</i>	ΔAIC_c
Base model ^a			0.0000 ^b
Number of downed logs	0.022	0.094	-0.6925
% cover of downed logs	4.152	0.188	0.3813
% canopy cover	-0.006	0.379	1.3146
% cover of grass	-0.005	0.695	1.9290
Beetle-killed land cover	-0.088	0.737	1.9727

^a Distance between source and target + elevation + slope + aspect + distance to roads + terrain position index + distance to water + strata.

^b $AIC_c = 277.2767$.

selection of green conifer occurred mid-morning rather than during the hottest part of the day (mid-afternoon; Fig. 4). Nevertheless, the avoidance of beetle-killed conifer during the warm parts of the day, when intact conifer was strongly selected, points toward some role of a thermoregulatory mechanism of habitat use. With shifting climate regimes favoring warm and dry summers in combination with a dramatic reduction in thermal cover, beetle-killed conifer is liable to continue to negatively affect habitat use by elk, and likely other heat-sensitive mammals (Monteith et al. 2015).

Given the prediction that there will be a 4-fold increase in downed logs when 80% of beetle-killed trees fall following the bark-beetle epidemic (Klutsch et al. 2009), increased downed logs may affect fitness negatively via increased energetic expenditures for elk moving through beetle-affected forest. In our study, there were on average 6 more downed trees per 25-m transect in beetle-killed areas compared with areas of intact conifer. With the Sierra Madre being in the early stages of tree fall, our current estimates of downed logs in beetle-killed areas are conservative and will surely increase as standing dead trees begin to fall. Assuming elk will continue to mediate the costs of unnecessary locomotion by avoiding these areas (Geist 2002), as more trees fall, we suspect avoidance by elk to strengthen, further limiting the amount of available habitat to elk.

The bark-beetle epidemic in our study area began in 2000 and peaked near 2009, with most trees entering the gray stage by 2012 (S. S. Loose, U.S. Forest Service, personal communication). Our study occurred from 2012 to 2016, when trees were just beginning to fall. As the bark-beetle epidemic unfolds, a subsequent increase in downed trees and understory vegetation could further alter elk movements. Additionally, although our land classification model was generally predictive, error in prediction associated with beetle-killed conifer likely affected our results to some degree (Appendix A; Table 3). We doubt however that any classification errors were sufficient to bias our habitat selection analyses in ways that would have affected interpretation. Moreover, we were not able to provide insight to how elk would respond to beetle-killed conifer during the winter or how predation may interact with the patterns observed. Most of the elk in our study system spend the winter off the forest in sagebrush grasslands, precluding an assessment for winter. Finally, predation can play a role in habitat selection of ungulate prey in ways similar to what we observed (Lima and Bednekoff 1999, Kohl et al. 2018); however, major large carnivores (i.e., wolves and grizzly bears) were absent in our system, so presumably the effect of predation on habitat selection was negligible.

Events such as prescribed fires, wild fires, and logging lead to a forest that transitions from a climax community of mature trees to early-seral grass and forb species, resulting in increased use by elk (Lyon and Jensen 1980, Dyke and Darragh 2007, Biggs et al. 2010). Bark-beetle affected forests experience a somewhat similar transition as observed in other forest disturbances, from climax communities to a forest with increased understory vegetation (Kovacic et al. 1985, Stone and Wolfe 1996, Pec et al. 2015). Nonetheless, we demonstrate an avoidance of these areas by elk during summer. The difference

in elk response to differing types of forest disturbances may be a result of subtle but important differences (i.e., nutrient cycling, structural changes, and vegetation responses) in the way forests change following these events.

MANAGEMENT IMPLICATIONS

Wildlife and land managers across western North America are facing challenges from the bark-beetle epidemic that have not been encountered in modern wildlife management. Our findings at the time of our study indicated strong avoidance of beetle-killed areas during the summer by elk. Treating beetle-killed areas with excessive standing dead and downed trees through prescribed fire or other removal techniques may be effective at reducing the negative costs to elk from beetle-killed forests, provide elk with the adequate mixture of foraging areas and hiding and thermal cover, and potentially decrease conflicts caused by redistribution.

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APPENDIX A. METHODS FOR CREATING REMOTELY SENSED LAND COVER CLASSIFICATION

Beetle-killed forests are not identified in typically used land cover databases (e.g., National Land Cover Database). Thus, we created a high-resolution land cover classification that included beetle-killed and non-beetle-killed forest using the Random Forest modeling approach (Hayes et al. 2014). We acquired National Agricultural Imagery Program (NAIP) imagery, collected in August 2012, for the Sierra Madre Range area from the Wyoming Geographic Information Science Center (WyGISC; wygisc.uwyo.edu, accessed 1 Dec 2014). The NAIP imagery contains 4 bands (red, green, blue [RGB] visible spectrum and near-infrared [NIR]) at 1-m spatial resolution imagery. We established training data for 10 distinct land cover classes most critical for elk ecology and management (i.e., green conifer, beetle-killed conifer, water, lush grass [meadows], bare ground, aspen, sagebrush, shadow, willow, and cottonwood). Using ArcGIS, we digitized in excess of 200 polygons per class from the NAIP imagery.

To execute the Random Forest classification, we combined the digitized polygons from the NAIP imagery with a 16-band stacked image including the 4-band NAIP and 12 supporting bands. Supporting data included Digital Elevation Model (DEM), 10-m re-sampled to 1-m resolution, (Gesch et al. 2002); slope and aspect, derived from DEM, re-sampled to 1-m resolution; band 3 texture and band 4 texture, derived from 1-m NAIP using a standard deviation moving window calculation (Wulder et al. 1998); normalized difference vegetation index (NDVI), derived from 1-m NAIP red and NIR bands (Jordan 1969); curvature, relative change in slope, derived from DEM, re-sampled to 1-m resolution (Bolstad and Lillesand 1992); compound topographic index (CTI), a steady state wetness index, derived from DEM and re-sampled to 1-m resolution (Moore et al. 1993, Gessler et al. 1995); amplitude (AMP), difference between maximum NDVI and

start of season NDVI, derived from western United States 250-m eMODIS remote sensing phenology data, re-sampled to 1-m resolution (Swets et al. 1999); time of maximum NDVI (MAXT), day of year corresponding to the maximum NDVI in an annual time series derived from western United States 250-m eMODIS remote sensing phenology data, re-sampled to 1-m resolution (Swets et al. 1999); start of season-time (SOST), day of year identified as having a consistent upward trend in time series NDVI, derived from western United States 250-m eMODIS remote sensing phenology data, re-sampled to 1-m resolution (Reed et al. 1994); and TRASP, solar-radiation aspect index, derived from DEM and re-sampled to 1-m resolution (Roberts and Cooper 1989).

We completed several iterations of the modeling process to refine accuracy and increase predictive power. To assess accuracy, we used 33% of the data to validate the classification constructed from the remaining 66% of data to calculate an out-of-bag error rate (Table A1; Breiman 1996); we visually inspected the predicted land cover classification by comparing it to the NAIP, allowing us to identify deviations from actual imagery; and we conducted a *post hoc* validation by randomly selecting 75 locations per class from the predicted land cover layer and compared these locations to the NAIP imagery (Table A2). Because of some confusion between classes within our land cover classification, water, shadow, willow, cottonwood, and aspen were combined into single classes during a *post hoc* analysis (Table A3).

Using the final version of the land cover classification, we assessed the necessity of using land cover buffers around elk global positioning system (GPS) locations. We ran models to assess differences between using no buffer; models using a 5-m, 10-m, and 15-m buffer, taking the land cover class with the highest proportion within each buffer; and models using a 5-m, 10-m, and 15-m buffer with the individual proportions of all land cover classes within each buffer (Appendix D). Based on coefficient values, we detected marginal differences between buffer options so we elected to use the no buffer model.

Table A1. Confusion matrix providing out-of-bag-error for the Random Forest model, which we used to generate land cover classification in the elk study area from 2012–2014 in the Sierra Madre Range, Wyoming, USA.

	Green conifer	Beetle-killed conifer	Water	Grass meadows	Bare ground	Aspen	Sagebrush	Shadow	Willow	Cottonwood	Class error
Green conifer	3,137	16	0	3	5	9	0	18	4	0	0.02
Beetle-killed conifer	14	3,240	1	0	1	0	2	8	0	0	0.01
Water	1	11	3,130	1	1	5	4	22	1	0	0.01
Grass meadows	7	7	0	3,030	3	20	9	0	41	0	0.03
Bare ground	5	26	2	0	3,076	3	5	5	0	0	0.01
Aspen	11	9	0	4	4	3,139	2	1	29	0	0.02
Sagebrush	0	45	0	18	13	9	3,100	1	1	0	0.03
Shadow	15	7	0	0	0	0	0	3,153	0	0	0.01
Willow	16	4	0	15	0	16	1	1	3,053	2	0.02
Cottonwood	0	0	0	0	0	0	0	0	0	3,012	0.00

Table A2. Original land cover classification validation for the elk study area from 2012–2014 in the Sierra Madre Range, Wyoming, USA. We randomly selected 75 points per land cover class and compared them to National Agricultural Imagery Program (NAIP) imagery to assess accuracy of random forest model predictions.

	Green conifer	Beetle-killed conifer	Water	Grass meadows	Bare ground	Aspen	Sagebrush	Shadow	Willow	Cottonwood	Total	% user accuracy
Green conifer	51	1	0	1	0	0	0	22	0	0	75	0.68
Beetle-killed conifer	5	50	0	1	8	1	4	6	0	0	75	0.67
Water	0	7	38	0	0	1	3	26	0	0	75	0.51
Grass meadows	0	0	0	53	0	1	20	0	1	0	75	0.71
Bare ground	2	0	0	9	51	0	13	0	0	0	75	0.68
Aspen	11	0	0	6	1	49	0	7	1	0	75	0.65
Sagebrush	0	0	0	8	9	3	54	1	0	0	75	0.72
Shadow	2	4	0	0	5	0	0	64	0	0	75	0.85
Willow	3	0	0	6	0	31	1	1	33	0	75	0.44
Cottonwood	0	0	0	6	0	30	7	0	17	15	75	0.20
Total	74	62	38	90	74	116	102	127	52	15		
% producer accuracy	0.69	0.81	1.00	0.59	0.69	0.42	0.53	0.50	0.63	1.00		

Table A3. Land cover classification validation for the elk study area from 2012–2014 in the Sierra Madre Range, Wyoming, USA, following the *post hoc* re-class combining water and shadow, as well as aspen, willow, and cottonwood. We randomly selected 75 points per land cover class and compared them to National Agricultural Imagery Program (NAIP) imagery to assess accuracy of random forest model predictions.

	Green conifer	Beetle-killed conifer	Water and shadow	Grass meadows	Bare ground	Aspen, willow, cottonwood	Sagebrush	Total	% user accuracy
Green conifer	51	1	22	1	0	0	0	75	0.68
Beetle-killed conifer	5	50	6	1	8	1	4	75	0.67
Water and shadow	0	5	70	0	0	0	0	75	0.93
Grass meadows	0	0	0	53	0	2	20	75	0.71
Bare ground	2	0	0	9	51	0	13	75	0.68
Aspen, willow, cottonwood	10	1	4	4	3	51	2	75	0.68
Sagebrush	0	0	1	8	9	3	54	75	0.72
Total	68	57	103	76	71	57	93		
% producer accuracy	0.75	0.88	0.68	0.70	0.72	0.89	0.58		

APPENDIX B. HISTOGRAM OF STEP LENGTH DISTRIBUTION USED IN STEP SELECTION FUNCTIONS

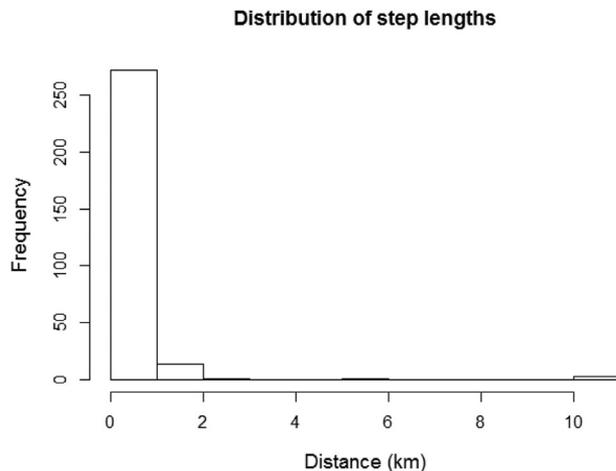


Figure B1. Histogram of step length distribution used in step selection functions from 2014 elk movements in the Sierra Madre Range, Wyoming, USA.

APPENDIX C. COEFFICIENTS OF VARIABLES PREDICTED TO AFFECT ELK RESOURCE SELECTION

Table C1. Comparison of coefficient values and 95% confidence intervals from a mixed-effects resource selection function representing the effects of habitat, distance to roads, distance to water, terrain position index (selection for position, valley bottom to ridge), and hour (time of day, 2-hour intervals) on elk ($n = 47$) resource use for 2012–2016 during the summer (Jun–Aug) in the Sierra Madre Range, Wyoming, USA.

Covariate	Mean β	SE β	Lower CI	Upper CI
Intercept	-0.37	0.03	-0.42	-0.32
Slope	-0.20	0.01	-0.21	-0.19
Aspect	-0.12	0.01	-0.14	-0.11
Distance to road	0.49	0.01	0.48	0.51
Terrain position index	-0.02	0.01	-0.03	-0.01
Distance to water	-0.07	0.01	-0.08	-0.06
Beetle-killed conifer	-0.25	0.05	-0.35	-0.15
Green conifer	0.08	0.05	-0.02	0.17
Sagebrush	0.67	0.02	0.62	0.71
Deciduous	0.85	0.02	0.81	0.71
Grass	1.36	0.08	1.20	1.53
Beetle-killed conifer×hour 2	0.05	0.06	-0.07	0.16
Beetle-killed conifer×hour 3	0.07	0.07	-0.06	0.20
Beetle-killed conifer×hour 4	0.19	0.07	0.06	0.32
Beetle-killed conifer×hour 5	0.16	0.06	0.05	0.27
Beetle-killed conifer×hour 6	0.13	0.07	-0.002	0.25
Beetle-killed conifer×hour 7	0.09	0.07	-0.03	0.22
Beetle-killed conifer×hour 8	0.11	0.06	-0.01	0.22
Beetle-killed conifer×hour 9	0.06	0.07	-0.06	0.19
Beetle-killed conifer×hour 10	0.14	0.07	0.01	0.27
Beetle-killed conifer×hour 11	0.06	0.06	-0.05	0.18
Beetle-killed conifer×hour 12	0.09	0.07	-0.04	0.22
Green conifer×hour 2	-0.001	0.06	-0.12	0.10
Green conifer×hour 3	0.12	0.06	-0.002	0.24
Green conifer×hour 4	0.28	0.06	0.16	0.40
Green conifer×hour 5	0.53	0.05	0.43	0.64
Green conifer×hour 6	0.45	0.06	0.33	0.56
Green conifer×hour 7	0.36	0.06	0.25	0.48
Green conifer×hour 8	0.33	0.05	0.23	0.44
Green conifer×hour 9	0.17	0.06	0.05	0.29
Green conifer×hour 10	0.05	0.06	-0.07	0.17
Green conifer×hour 11	-0.17	0.06	-0.28	-0.06
Green conifer×hour 12	-0.06	0.06	-0.19	0.06
Grass×hour 2	-0.02	0.10	-0.23	0.18
Grass×hour 3	-0.36	0.12	-0.60	-0.13
Grass×hour 4	-0.99	0.13	-1.24	-0.73
Grass × hour 5	-1.99	0.13	-2.24	-1.75
Grass×hour 6	-1.60	0.14	-1.87	-1.33
Grass×hour 7	-1.00	0.13	-1.25	-0.76
Grass×hour 8	-0.81	0.11	-1.03	-0.60
Grass×hour 9	-0.62	0.12	-0.85	-0.39
Grass×hour 10	-0.22	0.12	-0.46	0.01
Grass×hour 11	0.21	0.10	0.01	0.41
Grass×hour 12	0.04	0.12	-0.19	0.27

APPENDIX D. LAND COVER EXTRACTION METHODS COMPARISON

Table D1. Comparison of land cover extraction methods for elk global positioning system (GPS) locations. We compared resource selection functions (RSFs) based on extracting land cover type without a buffer around each GPS location and with a 5-m, 10-m, and 15-m circular buffer taking the land cover class with the highest proportion (MainLC), and with a 5-m, 10-m, and 15-m buffer using individual proportions of all land cover classes. For all models, we used the land cover category other (included bare ground, water, and shadow) as the reference and removed elevation because of correlation with green conifer.

Covariate	Mean β	SE β	Lower CI	Upper CI
No buffer model				
Slope	-0.20	0.01	-0.21	-0.19
Aspect	-0.12	0.01	-0.13	-0.11
Distance to road	0.49	0.01	0.48	0.51
TPI ^a	-0.02	0.01	-0.03	-0.01
Distance to water	-0.07	0.01	-0.08	-0.06
Beetle-killed conifer	-0.15	0.02	-0.19	-0.11
Green conifer	0.27	0.02	0.24	0.31
Sagebrush	0.67	0.02	0.62	0.71
Deciduous	0.85	0.02	0.81	0.88
Lush grass ^b	0.92	0.03	0.87	0.98
5-m main land cover buffer model				
Slope	-0.20	0.01	-0.21	-0.19
Aspect	-0.12	0.01	-0.13	-0.11
Distance to road	0.49	0.01	0.48	0.50
TPI ^a	-0.01	0.01	-0.02	-0.00
Distance to water	-0.07	0.01	-0.08	-0.06
Beetle-killed conifer	-0.22	0.02	-0.26	-0.18
Green conifer	0.28	0.02	0.24	0.32
Sagebrush	0.67	0.02	0.63	0.72
Deciduous	0.87	0.02	0.83	0.91
Lush grass ^b	0.91	0.03	0.86	0.97
10-m main land cover buffer model				
Slope	-0.20	0.01	-0.21	-0.19
Aspect	-0.12	0.01	-0.13	-0.11
Distance to road	0.49	0.01	0.47	0.50
TPI ^a	-0.01	0.01	-0.02	0.00
Distance to water	-0.07	0.01	0.08	-0.06
Beetle-killed conifer	-0.23	0.02	-0.27	-0.18
Green conifer	0.31	0.02	0.26	0.35
Sagebrush	0.67	0.02	0.62	0.72
Deciduous	0.88	0.02	0.83	0.92
Lush grass ^b	0.93	0.03	0.87	0.99
15-m main land cover buffer model				
Slope	-0.20	0.01	-0.21	-0.19
Aspect	-0.12	0.01	-0.13	-0.11
Distance to road	0.49	0.01	0.47	0.50
TPI ^a	-0.01	0.01	-0.02	0.00
Distance to water	-0.07	0.01	-0.08	-0.06
Beetle-killed conifer	-0.23	0.02	-0.27	-0.18
Green conifer	0.32	0.02	0.28	0.37
Sagebrush	0.67	0.02	0.62	0.72
Deciduous	0.88	0.02	0.84	0.93
Lush grass ^b	0.92	0.03	0.86	0.98
5-m proportion buffer model				
Slope	-0.19	0.01	-0.20	-0.18
Aspect	-0.10	0.01	-0.11	-0.09
Distance to road	0.50	0.01	0.48	0.51
TPI ^a	0.00	0.01	-0.01	0.01
Distance to water	-0.08	0.01	-0.09	-0.07
Beetle-killed conifer	-0.45	0.03	-0.51	-0.38
Green conifer	0.60	0.03	0.55	0.66
Sagebrush	0.91	0.03	0.86	0.97
Deciduous	1.43	0.03	1.38	1.49
Lush grass ^b	1.26	0.04	1.19	1.33
10-m proportion buffer model				
Slope	-0.18	0.01	-0.19	-0.17
Aspect	-0.10	0.01	-0.11	-0.08
Distance to road	0.49	0.01	0.48	0.51
TPI ^a	0.01	0.01	-0.00	0.02
Distance to water	-0.08	0.01	-0.09	-0.07
Beetle-killed conifer	-0.49	0.03	-0.56	-0.42

(Continued)

Table 7. (Continued)

Covariate	Mean β	SE β	Lower CI	Upper CI
Green conifer	0.81	0.03	0.75	0.87
Sagebrush	1.06	0.03	1.00	1.12
Deciduous	1.71	0.03	1.65	1.77
Lush grass ^b	1.46	0.04	1.38	1.54
15-m proportion buffer model				
Slope	-0.18	0.01	-0.19	-0.17
Aspect	-0.09	0.01	-0.11	-0.08
Distance to road	0.49	0.01	0.48	0.51
TPI ^a	0.01	0.01	0.00	0.02
Distance to water	-0.08	0.01	-0.09	-0.07
Beetle-killed conifer	-0.49	0.04	-0.56	-0.42
Green conifer	0.95	0.03	0.88	1.02
Sagebrush	1.16	0.03	1.09	1.23
Deciduous	1.89	0.03	1.82	1.95
Lush grass ^b	1.59	0.04	1.50	1.67

^a Terrain Position Index.

^b Meadows.