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Behavioral responses of male elk to hunting risk

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Abstract

Prey respond to predation risk with a range of behavioral tactics that can vary based on space use and hunting mode of the predator. Unlike other predators, human hunters are often more spatially and temporally restricted, which creates a period of short-duration, high-intensity predation risk for prey. Consequently, identifying the roles different hunting modes (i.e., archery and rifle), hunts for targeted and non-targeted species, and landscape features play in altering spatial and temporal responses of prey to predation risk by humans is important for effective management of harvested populations. From 2009 to 2016, we used a large-scale experiment including 50 animal-years of location data from 38 unique male elk (*Cervus canadensis*) to quantify changes in movement and resource selection in response to hunters during 3 separate 5-day controlled hunts for antlered males (elk archery, deer [*Odocoileus* spp.] rifle, and elk rifle) at the Starkey Experimental Forest and Range in northeast Oregon, USA. We evaluated competing hypotheses regarding elk responses to varying levels of prey risk posed by the different hunt types. We predicted that the strength of elk behavioral responses would increase with perceived hunter lethality (i.e., weak response to elk archery but similar response to elk and deer rifle hunts) and that prey response would be closely associated with hunter activity within the diel cycle (greater during diurnal than nocturnal hours) and across hunting seasons. Elk responses were

strongest during diurnal hours when hunters were active on the landscape and were generally more pronounced during both rifle hunts than during the archery hunt (supporting our perceived lethality hypothesis). Male elk avoided open roads across all periods except during nocturnal hours of the breeding season and alternated between avoidance of areas with high canopy cover during nocturnal hours and selection during diurnal hours. In combination these patterns led to distinct distributional changes of male elk from pre-hunt to hunt periods. Patterns of male elk selection highlight the importance of managing for heterogeneous landscapes to meet a variety of habitat, harvest, hunter satisfaction, and escapement objectives.

KEYWORDS

animal movements, anti-predator behavior, *Cervus canadensis*, elk, human-wildlife interactions, hunting risk, movement rates, predation risk, resource selection

Prey respond to the risk of predation with a range of behavioral tactics, including altered movement rates (Frair et al. 2005, Ciuti et al. 2012), adjusted activity patterns (Cleveland et al. 2012, Ordiz et al. 2012), and spatial and temporal changes to resource selection (Grignolio et al. 2011, Bonnot et al. 2013, Spitz et al. 2019). These tactics are not uniformly applied, however, and can vary based on the space use and hunting mode of the predator (Atwood et al. 2009, Thaker et al. 2011) and the structural complexity of the environment, which in turn can affect the probability of a predator encountering and killing prey (Hebblewhite et al. 2005). For example, Schmitz and Suttle (2001) proposed that the relatively persistent cues from sit-and-pursue and sit-and-wait predators provide prey with more spatial information about predation risk; by contrast, antipredator behavioral strategies should be less pronounced in response to cursorial predators whose presence is more variable and thus more weakly linked to cues. Conversely, others have suggested that these antipredator responses should be proportionate to predator lethality (Gal and Casas 2014). Studies separating lethality and risk effects are surprisingly rare in mammalian systems, despite some support at smaller scales (Schmitz and Suttle 2001, Preisser and Bolnick 2008).

Human hunting, unlike other forms of predation, is typically spatially and temporally predictable. For instance, hunter space use is often localized to areas allowing motorized vehicle access (Rowland et al. 2021) and restricted to limited seasons with legal hunting hours (Cromsigt et al. 2013). This creates a special form of short-duration high-intensity predation risk that can markedly influence prey behavior. Moose (*Alces alces*), for example, exhibit different movement and habitat selection strategies to avoid risk during hunting seasons based on the level of hunter access (Brown et al. 2018). Similarly, white-tailed deer (*Odocoileus virginianus*) decrease movement rates and area used to avoid detection by hunters (Little et al. 2014, Marantz et al. 2016), and western roe deer (*Capreolus capreolus*) use less risky habitats to avoid hunters (Padié et al. 2015).

These concepts have been most formalized with respect to elk (*Cervus canadensis*) across much of the western United States, where the majority of elk hunting takes place on public lands. The arrival of elk hunters often contributes to distributional shifts of elk from public to private lands (Conner et al. 2001, Proffitt et al. 2013). These shifts lead to reduced hunter opportunity on public lands, conflict with private landowners where elk seek refuge from hunters, and increased concern from wildlife managers to minimize damage on private lands. Consequently, contemporary habitat management for hunted populations of elk is now focused on providing a combination of adequate nutrition and areas of low human disturbance through road management during hunting and non-hunting

seasons, while further accounting for cover and topography to maintain desired elk distribution on public lands (Wisdom et al. 2018). This more comprehensive consideration of security has replaced past concepts of security cover (Hillis et al. 1991) that did not account for all habitat variables affecting distribution of hunted elk populations during hunting and non-hunting seasons.

While distributional shifts of elk from public to private lands can occur rapidly with the onset of hunting, most studies have evaluated effects of rifle seasons (Burcham et al. 1999; Proffitt et al. 2010, 2013). Substantially less is known about elk response to archery hunting (Ranglack et al. 2017, DeVoe et al. 2019, Lamont et al. 2020, Lowrey et al. 2020) or hunts for non-target species (e.g., deer [*Odocoileus* spp.]). Even less is known about how habitat conditions contribute to the direct risk of elk mortality and their spatio-temporal responses to hunting. Consequently, identifying the roles different hunting modes (i.e., archery and rifle), hunts targeting antlered deer versus elk, and landscape features play in altering spatial and temporal responses of prey to predation risk by humans is important to understanding risk-related behavioral responses to different types of hunting and effectively managing elk distributions on the landscape.

To test for competing hypotheses regarding the influence of predator characteristics on risk (Moll et al. 2017), we used a large-scale experiment to quantify changes in movement and resource selection of male elk before and during hunts for antlered male elk and deer. As rifle hunters are more analogous to coursing predators (Cleveland et al. 2012), they often exhibit a larger footprint (Rowland et al. 2021) than archery hunters, who are more akin to a stalking or ambush predator (Cleveland et al. 2012). In addition to different hunting modes (e.g., stalking vs. active searching; Schmitz 2008), rifle hunters also are often more successful than archery hunters (Rowland et al. 2021), with the latter requiring sufficient cover to approach within a relatively close range to harvest an animal. By comparison, rifle deer hunters provide similar predation cues (e.g., hunter presence and gunshots) as do rifle elk hunters but with no true risk of mortality for elk.

We tested 3 competing hypotheses regarding elk response to predation risk, specifically that elk response would be strongest during the first hunt but decline as subsequent hunts occurred (risk allocation hypothesis; Lima and Bednekoff 1999); closely linked to true, not perceived, risk of mortality posed to male elk (true lethality hypothesis; Gal and Casas 2014); or mostly influenced by predator hunting mode (i.e., archery vs. rifle; Schmitz and Suttle 2001), regardless of the species being hunted (perceived lethality hypothesis). Under the risk allocation hypothesis, as prey avoid risk, they expend energetic reserves and are consequently limited in their ability to respond to future encounters (Lima and Bednekoff 1999). Thus, response is strictly tied to duration of risk if all predators are equal. In accordance with this hypothesis, we predicted the strongest response by elk would occur during the first hunt of the season (archery elk) but decline as seasons progressed (rifle deer, then rifle elk) and energetic reserves were depleted. If prey respond strictly based on true, not perceived, lethality of the predator, we would predict the greatest response during the rifle elk hunt, followed by archery elk, and finally rifle deer (hunter lethality hypothesis). Alternatively, prey may assess risk based on hunting mode, in which prey response is more closely linked to predators that provide similar cues and perceived risk of mortality. Under this scenario, we would predict the weakest response of elk to archery hunters but with similar responses to rifle elk and rifle deer hunters (perceived lethality hypothesis). We predicted that the strength of elk behavioral responses would increase with perceived hunter lethality (i.e., support perceived lethality hypothesis), and, following the risk allocation hypothesis, prey response would be closely associated with presence of hunters on the landscape both within the diel cycle (greater during diurnal than nocturnal hours when hunters are not present) and by treatment (greater during hunting than non-hunting treatments).

STUDY AREA

We conducted our research on the United States Department of Agriculture (USDA) Forest Service, Starkey Experimental Forest and Range (i.e., Starkey) located in the Blue Mountains Ecoregion of northeast Oregon, USA (Figure 1). In 1987, Starkey was divided into multiple study areas encompassing approximately 10,125 ha of elk

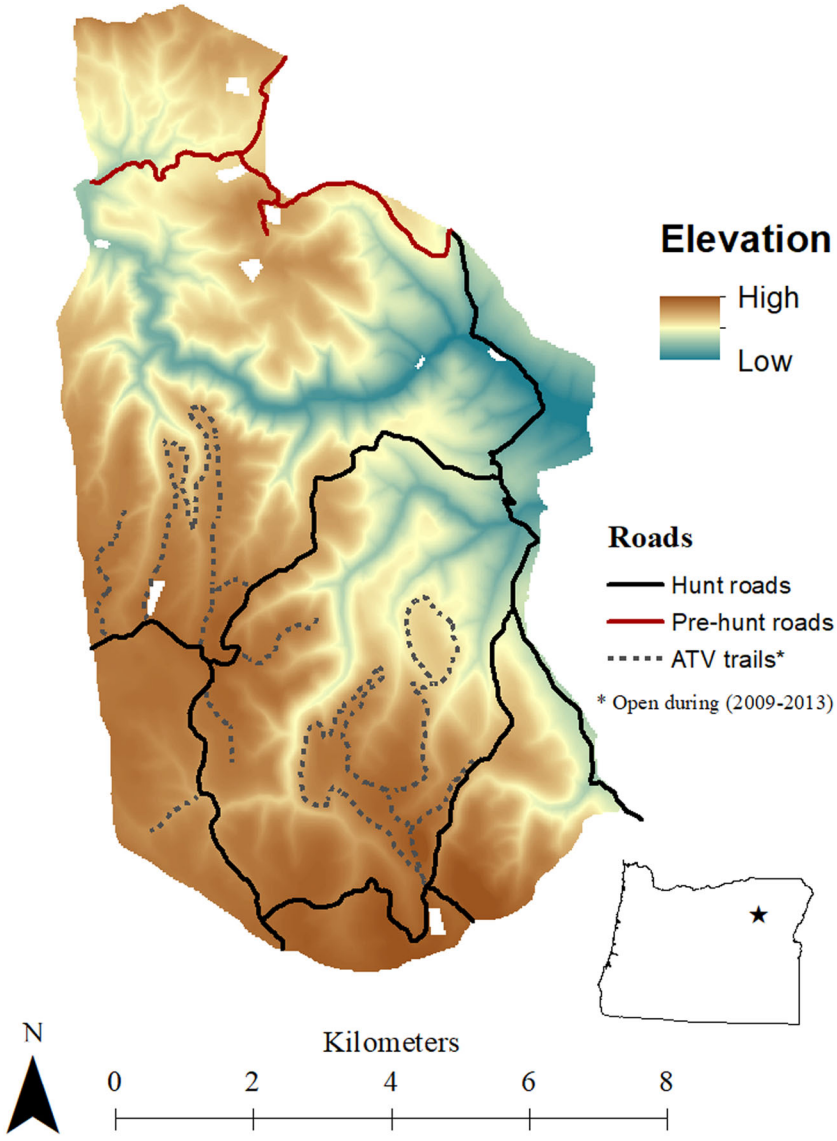

FIGURE 1 The 7,768-ha main study area of Starkey Experimental Forest and Range, Oregon, USA, 2009–2016. Lines denote the presence of main roads (black) and all-terrain vehicle (ATV) trails (broken) open during the hunts. Pre-hunt roads (red) were closed when hunters were present

summer range enclosed by a 2.4-m-high elk-proof fence for long-term ungulate research (Rowland et al. 1997, Wisdom 2005). The enclosure was designed to facilitate direct measures of behavioral, habitat use, animal performance, and population responses of elk to manipulative landscape experiments during spring-fall at second and third orders of selection (Johnson 1980) of direct relevance to management (Wisdom 2005). Our study was conducted in the main study area (7,768 ha), an enclosure exceedingly larger than seasonal home ranges of elk in the Blue Mountains Ecoregion, and thus allowed for evaluation of their responses to our manipulative study design with desired controls (e.g., using hunters as treatments under specified hunts and hunter densities, and under a defined, large area of resource availability to the elk population [Wisdom 2005, Spitz et al. 2019]).

Elevation ranged from 1,116 m to 1,502 m. Climate was continental with cold temperatures in winter (Dec to Feb) and warm temperatures in summer (Jun to Aug). Temperatures ranged from 18°C in July to −4°C in January and annual precipitation averaged 50.4 cm, with the majority falling as snow in winter (Skovlin 1991). Dominant vegetation consisted of a mosaic of bunchgrass meadows (*Pseudoroegneria* spp.) and mixed conifer, with the latter consisting primarily of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*). Topography consisted of moderately sloping uplands dissected by numerous drainages. Traffic levels, timber management, and recreational activities were similar to patterns on nearby public lands (Rowland et al. 1997, Preisler et al. 2006). Along with elk, mule deer (*O. hemionus*) and white-tailed deer were present year-round, whereas cattle were present from early summer (~15 Jun) to early fall (~15 Oct). Although the study area is surrounded by a 2.4-m-high fence, carnivores routinely enter and leave Starkey from surrounding public lands (Ruprecht et al. 2021*a*), with densities equivalent inside (Ruprecht et al. 2021*b*) and outside the enclosure (Oregon Department of Fish and Wildlife, unpublished data). Several carnivores occurred in the study area including mountain lions (*Puma concolor*), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and badgers (*Taxidea taxus*). Wolves (*Canis lupus*), while present in Oregon, did not use the study area until 2016.

Areas open to motorized vehicle use varied across years and treatment periods (Figure 1). During legal hunting seasons, road access to the northernmost section of Starkey was closed to vehicle travel but was open prior to and after hunts. Additionally, all-terrain vehicle (ATV) trails were open to ATVs during legal hunting seasons from 2009 to 2013. These trails were closed to motorized vehicle travel from 2014 to 2016 and closed across all years outside of legal hunting seasons.

METHODS

Experimental design

From 2009 to 2016, 3 controlled hunts were held annually at Starkey for antlered male elk or deer, in chronological order: elk archery (late Aug), deer rifle (early Oct), and elk rifle (late Oct; Table A1). All hunts lasted 5 days with 25 tags issued (~0.32 hunters/km^2) per hunt. We defined a 20-day period around each hunt, consisting of 4 5-day treatments with varying levels of human disturbance: a control pre-hunt period (6–10 days prior to hunt), in which hunter activity was generally low or nonexistent; a scout period (1–5 days prior to hunt) during which hunters began to arrive and were active on the landscape but could not harvest animals; a hunt period when hunters were allowed to harvest animals; and a post-hunt period (1–5 days post-hunt) when hunters were absent or inactive. The temporal distribution of hunter activity varied by year and hunt treatment; however, nearly all hunters arrived ≥1 day before the start of the hunt and stayed through the majority of the hunt period, unless successful (M. M. Rowland, U.S. Forest Service, unpublished data). Consequently, we interpreted the scout and hunt treatments as representing a gradient in intensity and type of human activity (i.e., hunter activity was lower during the scout period compared to the hunt period), while the pre-hunt and post-hunt periods represented baseline levels of anthropogenic disturbance (i.e., low levels of human activity unrelated to hunting). While exact dates of each hunt varied by year (Table A1), timing between hunts was consistent. Archery elk hunts began the last full weekend in August, the elk archery post-hunt was 15 days prior to the rifle deer pre-hunt period, and the rifle deer post-hunt and elk rifle pre-hunt treatments were separated by 5 days across all years. Hunters could legally harvest antlered males from 30 minutes before sunrise to 30 minutes after sunset. Additionally, during both rifle hunts, harvest was prohibited within a 402-m buffer along the perimeter fence; during the archery hunt this was reduced to 46 m to increase probability of success given the traditionally low success rates of archery elk hunters at Starkey (Rowland et al. 2021).

Elk capture and handling

We collared male elk in March or April each year. Collars were equipped with both a very high frequency transmitter (Model 400; Telonics, Mesa, AZ, USA) and a global positioning system (GPS) unit (Quantum 400 Enhanced Ext Memory LSH20 SIRFIII; Telemetry Solutions, Concord, CA, USA) that acquired a fix every 15 minutes throughout the 20-day sampling periods surrounding each hunt. Specific collar details are provided by Dick et al. (2013). We retrieved collars from male elk in several ways: during the following winter when elk were recaptured, on the ground if the collar material broke, by hunters who harvested an elk, or at mortality sites. Prior to analysis, we visually inspected the data for errant locations (e.g., locations outside the perimeter fence), and checked for duplicates and outlier movements (i.e., max. movement speeds that were unlikely for elk to reach given the fix schedule; Bjørneraas et al. 2010). We then excluded data from collars with an acquisition rate lower than 0.85 to limit habitat-induced bias (Hebblewhite et al. 2007), resulting in 50 animal-years of location data from 38 unique individuals.

Treatment response

We characterized male elk response to hunt treatments by calculating mean movement rates (m/15 min) separately for nocturnal (1 hr after sunset to 1 hr before sunrise) and diurnal (all remaining) locations. We chose these divisions to allow diurnal movement rates to encompass a 30-minute buffer around legal hunting hours, a time we assumed hunters would be actively moving on the landscape and more likely to influence elk behavior. We expected increased hunter presence on the landscape would increase elk movement such that movement rates would be lowest during the pre-hunt period, increase during the scout period, and peak during the hunt, followed by a decline in the post-hunt period. Because of our frequent fix schedule, our sample size of step lengths to calculate movement rates was very large such that a statistically significant, but likely biologically insignificant (e.g., increase in movement of 2–3 m/15 min), difference would be probable with a formal statistical test. Therefore, we plotted results and looked for biologically meaningful values that might result in increased energetic expenditures (e.g., an increase of >10% in movement rates) of elk with subsequent fitness consequences.

To quantify hunters' effects on male elk behavior, we fit a series of population-level resource selection functions (RSFs). To account for strong diel temporal structure in elk behavior (Kohl et al. 2018; Spitz et al. 2018, 2019), we fit separate models with diurnal and nocturnal locations (noted above) to each of the 3 hunt periods (resulting in 6 models), using the same hours for each model as described above. As our primary interest was in quantifying differences in elk behavior during the hunt from a pre-hunt baseline, we excluded data from other treatments (i.e., scout and post-hunt) to limit model complexity. Because elk behavior may also change in relation to weather, plant phenology, and reproductive cycles (e.g., fall rut), we used the pre-hunt baseline as a comparison for each hunt period rather than an averaged single baseline across all models. This limited the temporal separation of baseline and treatment to ≤14 days, minimizing the possibility that environmental factors confounded interpretation of our results. The resulting model was structured as

$$w(x) = e^{(\beta_1 \times x_1 + \beta_{1h} \times x_1 \times \text{hunt} + \cdots + \beta_i \times x_i + \beta_{ih} \times x_i \times \text{hunt})},$$

where w was the relative probability of selection, $x_1 - x_i$ were covariates, $\beta_1 - \beta_i$ were coefficients associated with covariates, hunt was an indicator variable delineating the hunt period, and h indicated coefficients quantifying the magnitude of the hunt period on behavioral changes. We used a 1:1 ratio of used to available locations when defining availability (Spitz et al. 2019), and we defined the whole of Starkey's main area as available (second-order selection; Johnson 1980).

We included covariates that can be directly managed to influence sources of human disturbance (e.g., road access), cover, and other landscape characteristics (defined as process covariates or their surrogates by Wisdom et al. 2020) and covariates that may account for elk behavior but cannot be actively managed (contextual covariates; Wisdom et al. 2020). We used the following covariates in all models: 1) distance (m) to roads open to motorized use during the hunt (includes open ATV trails from 2009–2013; Figure 1), 2) canopy cover (1–100%), 3) slope (°), 4) greenness (amplitude of the normalized difference vegetation index (NDVI; i.e., peak photosynthetic activity relative to baseline 1–100; Meier and Brown 2014), 5) topographic positioning index (TPI; representing concavity, values <0 denote valleys, values >0 denote ridges; Spitz et al. 2019), and 6) elevation (m). We included distance to motorized roads, NDVI, and canopy cover as time-varying covariates with values that differed among years. We restricted our analysis to these variables because they influence elk behavior during hunting seasons (Spitz et al. 2019). Covariates that can be influenced by land managers and influence elk responses to hunting included distance to road or trail open to motorized vehicle use, which influences hunter access (Proffitt et al. 2013), and forest canopy cover, an assumed index of hiding cover. Based on prior estimates of elk response to motorized roads in this system (Rowland et al. 2000, Preisler et al. 2006, Spitz et al. 2019), we truncated the effect of this variable to 1.5 km. We chose canopy cover over a stand density index for ease of interpretation and its broad-scale use as a surrogate for elk hiding cover (Ranglack et al. 2017, Spitz et al. 2019, Lowrey et al. 2020). Additionally, canopy cover and stand density were highly correlated ($R^2 > 0.90$) across our study area. We interpreted greenness as an index to available forage (Ranglack et al. 2017, Spitz et al. 2019). Slope and TPI were included as potential hiding cover for elk and their influence on hunter access (McCorquodale et al. 2003, Lowrey et al. 2020). We included elevation because it likely captures information on local vegetative communities.

We found no highly correlated variables (i.e., $|r| \geq 0.6$) and included all variables in the same model. We centered and standardized all continuous covariates by subtracting the mean and dividing by one standard deviation. We estimated model parameters using generalized linear mixed effects modeling (glmer) in the lme4 package (Bates et al. 2015) for program R (R Core Team 2018) to perform statistical analysis. We included independent individual-specific slopes for all covariates to account for individual response to habitat availability. We used our final model results to create a predictive map of elk space use over the study area to visualize changes in elk distribution across hunts and treatments. For each set of predictions, we binned values into 10 equal-area categories with hotter colors indicating relative selection and cooler areas relative avoidance. We evaluated model performance across the 3 hunt types using a 5-fold cross-validation based on individual blocking (Roberts et al. 2017). We partitioned data into 20% testing and 80% training datasets by individual and validated models for each treatment period separately. We did this 5 times, withholding a different 20% for testing each iteration and calculated mean Spearman rank correlations between fitted and predicted values (r_s). To evaluate individual covariate importance, we used Wald statistics (i.e., z = estimate/SE; Hosmer et al. 2013), whereby the sign indicates the direction of the relationship (>0, relative selection; <0, relative avoidance) and the magnitude represents relative explanatory power. Thus, values farther from zero (either positive or negative) indicate greater explanatory importance in the model (i.e., where the signal is large relative to noise), while values closer to zero indicate weaker relationships.

RESULTS

Number of male elk monitored across hunt periods ranged from 0 to 15, including 2012 when no male elk were collared (Table A1). Mean number of males monitored across each hunt was 6.5 ± 1.7 (SE) for elk archery, 4.4 ± 1.7 for deer rifle, and 6.5 ± 1.5 for elk rifle. Known ages of elk ranged from 2 to 11 years of age consisting of 18 2-year-olds, 10 3-year-olds, and 14 elk >3 years old. Of the 4 males that were harvested, 2 were 2 years old and 2 were 6 years old.

Movement rates

Except for the archery hunt and post-hunt treatments, mean movement rate of male elk during diurnal hours was higher (non-overlapping error bars) than the nocturnal hours across all treatments (pre-hunt, scout, hunt, and post-hunt) in all hunt types (archery, deer rifle, and elk rifle; Figure 2). We found movement rates during the 2 elk hunts followed a similar pattern of increasing from pre-hunt to hunt periods, in both diurnal and nocturnal hours, before declining during both post-hunt periods (Figure 2). During these hunts, increases in movement rates from pre-hunt to hunt treatment were >10% (likely biologically significant) and ranged from 11% during the diurnal elk rifle hunt to 22% during the nocturnal elk rifle hunt. Male elk did, however, exhibit the highest movement rates during the rifle deer season (which also coincided with the elk breeding period), with the fastest movements occurring during the pre-hunt period and declining throughout all subsequent treatments (Figure 2). During this hunt, movement rates decreased from the pre-hunt to hunt period by 12% and 13% over diurnal and nocturnal hours, respectively.

Population-level resource selection

Male elk resource selection behavior and the explanatory importance of covariates varied by hunt (elk archery, deer rifle, and elk rifle), treatment (pre-hunt vs. hunt), and by time of day (diurnal vs. nocturnal; Table 1; Figure 3). Canopy cover and distance to motorized roads were both important predictors of elk behavior, and elk displayed distinct patterns of selection for each covariate. During the day, elk selected areas with higher canopy cover across all periods, but only during the elk rifle season was selection higher than during the pre-hunt period (Figure 3). In contrast, elk selected against areas of higher canopy cover during nocturnal hours, with strength of selection

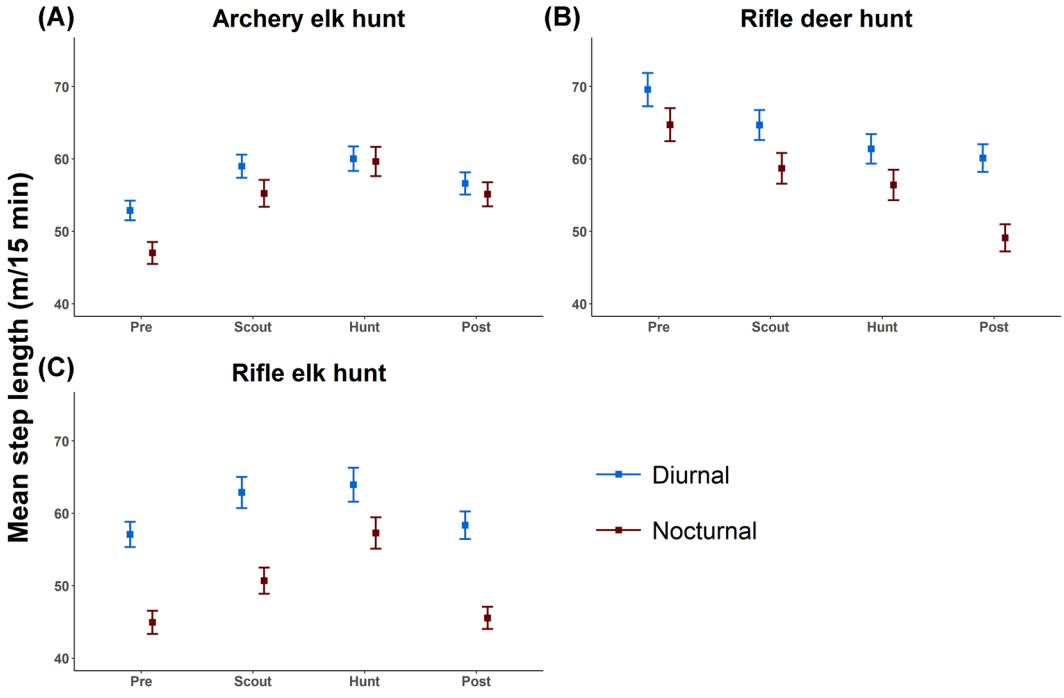

FIGURE 2 Mean step length (m/15 min) of male elk in Starkey Experimental Forest and Range, Oregon, USA, 2009–2016. Each period (*x* axes) represents a 5-day treatment period during both diurnal and nocturnal hours. The rifle deer hunt overlapped the elk breeding period, which likely also influenced male elk movement rate

TABLE 1 Wald statistics for covariate effects on population-level resource selection by male elk in Starkey Experimental Forest and Range, Oregon, USA, 2009–2016. Effects are divided by diurnal and nocturnal hours, hunt period (elk archery, deer rifle, elk rifle), and treatment (pre-hunt vs. hunt). Elk behavior and the explanatory importance of covariates varied by diel period, hunt period, and treatment. Units are omitted because all covariates were standardized

	Elk archery		Deer rifle		Elk rifle	
	Pre-hunt	Hunt	Pre-hunt	Hunt	Pre-hunt	Hunt
Diurnal						
Canopy cover	32.80	−1.86	21.86	0.38	11.49	9.25
Distance to motorized	20.85	7.00	8.07	12.42	14.69	9.33
Slope	33.08	−2.83	7.86	3.00	4.64	5.57
TPI[a]	−16.40	1.29	−2.86	−0.19	−2.61	0.55
Elevation	24.31	−0.62	−0.75	5.68	8.03	4.78
Greenness	4.02	−4.35	4.10	6.23	1.81	7.51
Nocturnal						
Canopy cover	−0.18	−1.49	−11.51	−5.92	−23.83	0.96
Distance to motorized	17.59	1.89	−5.39	14.17	6.66	8.58
Slope	14.75	0.25	2.33	4.79	−7.61	11.52
TPI	−2.06	−0.38	5.23	−1.11	0.94	2.66
Elevation	17.89	1.58	−0.67	3.69	−0.45	5.72
Greenness	1.99	−0.82	6.57	4.30	5.19	6.62

[a]Topographic position index (TPI) representing concavity, values <0 denote valleys, values >0 denote ridges.

against high canopy cover increasing during the rifle hunts. With the exception of the nocturnal hours during the rifle deer hunt, male elk exhibited strong selection for areas farther from roads across treatments and hunt periods. Elk avoidance of roads was stronger during the day than night, and during the hunt in comparison to the pre-hunt treatment, with the exception of the archery hunt during nocturnal hours (Table 1; Figure 3). During both rifle hunts, elk also consistently selected areas with higher greenness values during diurnal and nocturnal hours, with stronger selection during the hunt compared to both pre-hunt treatments (Figure B1). Additionally, elk tended to avoid areas with lower slope during all diurnal time periods, with the strongest avoidance exhibited during the rifle elk hunt in comparison to the pre-hunt period (Table 1; Figure B1). Elk also showed the strongest selection for higher elevations during the elk archery season regardless of treatment but shifted to indifference or weaker selection for these same areas during both rifle hunts (nocturnal and diurnal; Figure B1). There was no clear pattern of elk resource selection during pre-hunt versus hunt treatments for any hunt treatment relative to TPI (Figure B1). Cross validation of our population-level resource selection models indicated they generally performed with high precision during both hunts targeting elk (archery diurnal $r_s = 0.99$, archery nocturnal $r_s = 0.96$, rifle diurnal $r_s = 0.93$, rifle nocturnal $r_s = 0.85$), while performing modestly during the deer rifle period (diurnal $r_s = 0.78$, nocturnal $r_s = 0.61$). Diurnal models also performed better during than nocturnal models across all 3 hunt periods.

These results collectively demonstrated the variability in predicted patterns of space use both within and between hunts (Figure 4). In general, male elk were most widely distributed across the study area during nocturnal pre-hunt treatments and tended to be more dispersed as seasons progressed from archery through rifle hunts. In contrast, elk were more concentrated during diurnal hours, shifting space use to areas farther from roads. These patterns were most noticeable during the rifle hunts (Figure 4). With the exception of the diurnal pre-hunt deer

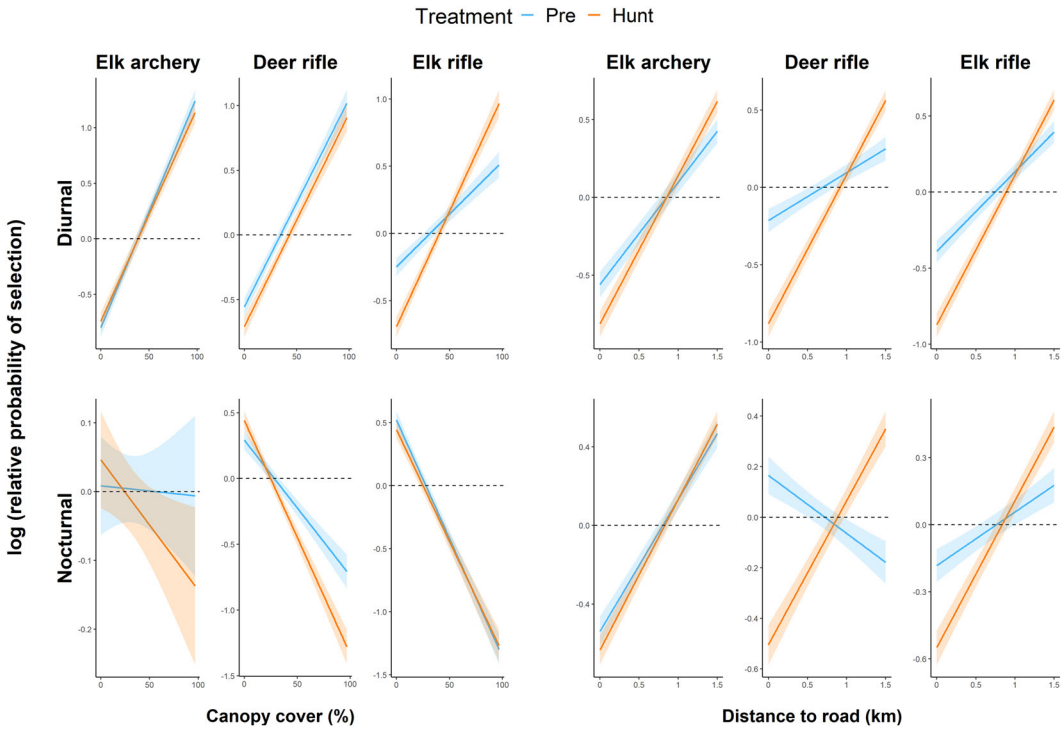

FIGURE 3 Predicted changes in male elk resource selection behavior between pre-hunt (blue) and hunt (orange) treatments in Starkey Experimental Forest and Range, Oregon, USA, 2009–2016, considering covariates that can be actively managed. Plotted relationships are from population-level resource selection functions by diel (vertical) and hunt (horizontal) treatments. Predictions are shown with 95% confidence intervals and were generated across the observed range of each focal covariate while all other covariates were held constant at mean values. The dashed lines at $y = 0$ demarcate non-significant (i.e., neither positive nor negative) effects

season, male elk avoided motorized areas across all time periods, while use of canopy cover alternated between selection for higher cover during diurnal time periods and avoidance of those areas during nocturnal hours.

DISCUSSION

Behavioral responses of male elk to the hunts demonstrated their perception of predation risk from humans based on strong, short-duration temporal behavioral changes in direct response to hunters. As per the risk allocation hypothesis, elk responses were strongest during diurnal hours when hunters were active on the landscape and were more pronounced during the hunt treatment in comparison to pre-hunt treatments. Elk responses to the hunts did not follow a chronological pattern of increasingly stronger response with successive hunts (risk allocation hypothesis) or showing the weakest response to rifle deer hunters (lethality hypothesis). Instead, elk exhibited a greater response to rifle hunters, both deer and elk, than to archery elk hunters (perceived lethality hypothesis), with elk rifle hunters eliciting the strongest response. This suggests that while male elk can perceive predation risk from humans, they lack perfect information to distinguish between true risk (elk hunters) and perceived risk (deer hunters). Success rates of archery hunters are typically much lower than those of rifle hunters, whereas the start of rifle seasons, regardless of targeted species, is associated with rifle shots, which likely provide elk with both temporal and spatial information of the risk of human predation. Ultimately, male elk responding strongly to the

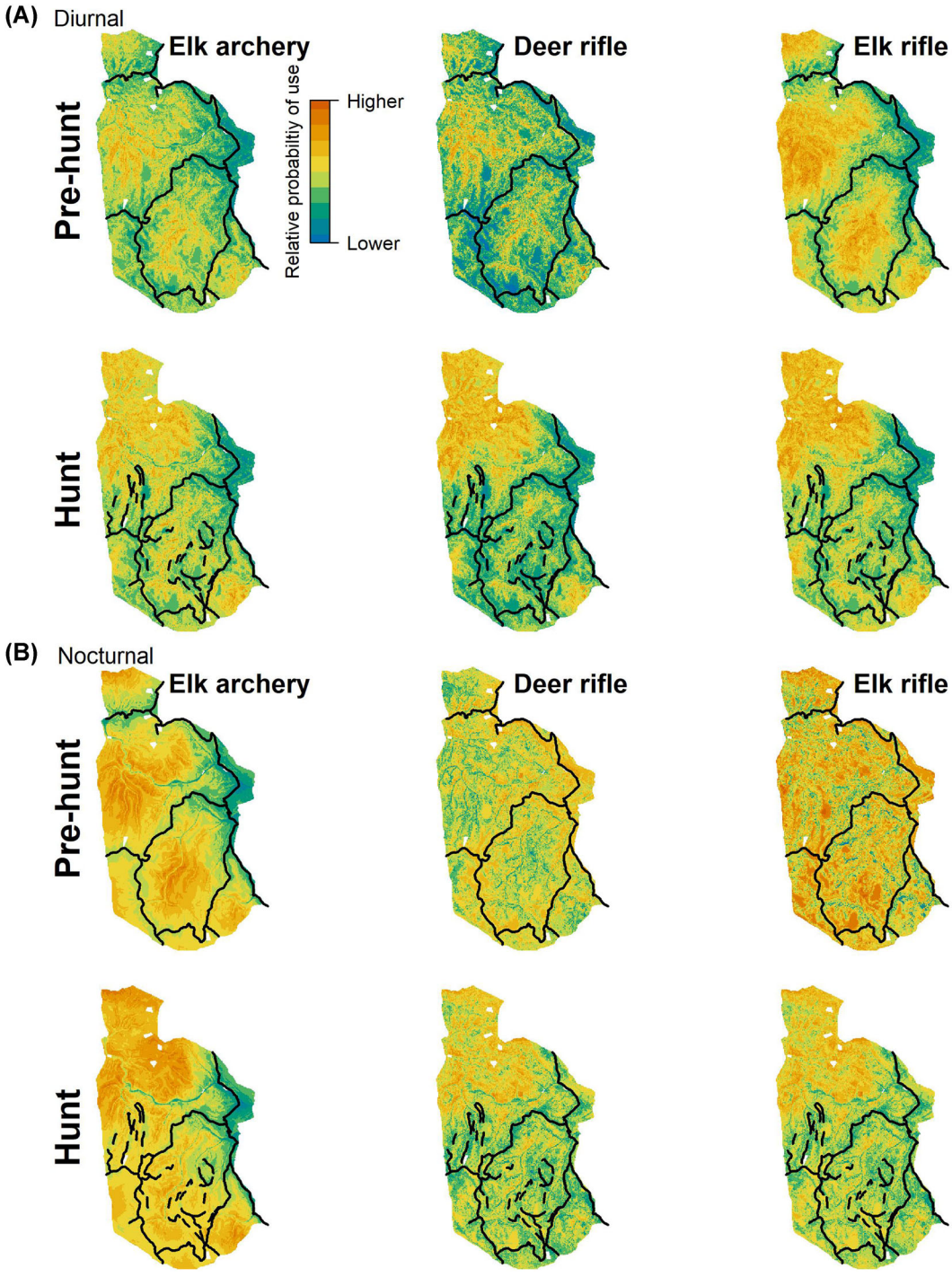

FIGURE 4 Population-level model predictions of diurnal (A) and nocturnal (B) relative resource selection by male elk in Starkey Experimental Forest and Range, Oregon, USA, 2009–2016. For each set of predictions, values were binned into 10 equal-area categories with hotter colors indicating relative selection and cooler areas relative avoidance. Predictions are presented by hunt (horizontal: elk archery, deer rifle, elk rifle) comparing the pre-hunt reference to the hunting treatment (vertical). Solid lines represent roads open to all motorized vehicles, dashed lines represent roads open to all-terrain vehicles only

start of any rifle season is likely an adaptive strategy because the consequences of incorrectly assessing that risk from a rifle elk hunter may be fatal, whereas the cost of inaccurately assessing risk from deer hunters is a relatively small and non-lethal effect on fitness from decreased foraging opportunities or increased movement rates during the short hunt window (Smith et al. 2021).

While elk avoided roads across all diurnal time frames, strength of avoidance increased during hunt treatments in comparison to their respective pre-hunt treatments. In contrast, elk showed little to no difference in selection for canopy cover during diurnal hours across the elk archery and deer rifle hunts in comparison to pre-hunt periods yet did exhibit significantly stronger selection for high canopy cover areas during the rifle elk hunt. This pattern would suggest that male elk are responding to predation risk by relying on finer-scale cues (e.g., hunter movement characteristics and hunt type). Research on hunter space use patterns in Starkey indicates that deer rifle hunters spend more time closer to open roads than elk rifle hunters (Rowland et al. 2021). Consequently, it would appear male elk are attempting to minimize risk of predation by first avoiding open roads, the primary conduit for human activities, and then seeking areas with greater canopy cover. Given the strong differences in hunter space use between deer and elk rifle hunters (Rowland et al. 2021), this strategy is likely the most efficient anti-predator response while also minimizing non-consumptive costs (e.g., reduced foraging opportunities, increased vigilance). The only time period where elk demonstrated selection for areas closer to motorized roads was during the rifle deer pre-hunt treatment during nocturnal hours. Rather than a response to hunter space use, we interpret this result as likely related to a change in elk behavior associated with the breeding period. Previous research in this system has indicated approximately 60% to 80% of conceptions occur from 15–30 September (Noyes et al. 1996), which roughly corresponds to the pre-hunt and scout periods during the rifle deer season. Additionally, female elk in this same system select for areas closer to motorized roads during nocturnal hours across similar time periods (Spitz et al. 2019).

Elk use of canopy cover varied across hunts and with the diel cycle, with male elk demonstrating strong avoidance of lower canopy cover areas during the day but equally strong selection for low canopy cover during nocturnal hours, especially during the rifle hunts. These results may suggest a tradeoff between predation risk and foraging opportunity (Hernández and Laundré 2005). Using areas of lower cover at night to forage will allow male elk to forage while risk of predation from humans is lowest. In contrast, during daylight hours, male elk reduced predation risk by moving to areas with increased forest cover, likely resulting in reduced foraging opportunities.

While we did not explicitly measure and model elk use of security cover based on previously published definitions (e.g., min. of 1 km^2 of continuous forest >0.8 km from open roads, Hillis et al. 1991; ≥13% canopy cover and ≥2.76 km from open roads, Ranglack et al. 2017), our results affirm the importance of vertical structure and routes open to motorized vehicle use in defining relatively secure areas perceived by elk. Notably, recent work examining elk use of defoliated lodgepole pine (*Pinus contorta*) forest in Montana, USA, revealed that, despite some reduction in canopy cover in mountain pine beetle (*Dendroctonus ponderosae*)-infested forests, these areas remained important for elk use and for maintaining elk distributions during the archery and rifle hunting seasons (Lowrey et al. 2020). Thus, while canopy cover can be correlated with vertical interception and concealment, accounting for stand density and stand type may provide additional insights into areas elk perceive as secure during hunting seasons. Nevertheless, given the spatiotemporal pattern of elk avoidance of hunting activity, we observed 2 patterns of selection related to hunting risk. First, avoidance of open roads is integral to male elk resource selection response to human hunters. Second, elk exhibited strong temporal shifts in their use of canopy cover regardless of hunter presence. The contrasting use of canopy cover highlights the need to account for the strong diel temporal structure in elk behavior when assessing resource selection (Kohl et al. 2018; Spitz et al. 2018, 2019). For example, during both diurnal rifle hunt treatments, elk started selecting forested areas at about 40% canopy cover, while during the nocturnal hours the inflection point for selection was at about 25% canopy cover. If this selection was averaged across a 24-hour period, this inflection point between selection and avoidance would have been much lower because of the strong avoidance of these same areas during nocturnal hours. Thus, future studies assessing

security cover should account for temporal structure by evaluating daytime versus nighttime use of patches mapped as secure habitat, both before and during hunts, to more accurately identify habitats ungulates perceive as low risk.

During both elk hunts, movement rates increased with increasing hunter presence and were highest during the hunt period (both diurnal and nocturnal) when elk were actively being pursued before declining during the 5-day post-hunt period. We interpret this as elk having increased encounters with humans when hunters were most active on the landscape and were directly pursuing elk, which caused elk to have flight responses (i.e., large movements) that increased mean movement rates. Non-targeted female elk in the same system showed a similar pattern where movement at the highest quantiles (i.e., large movements that likely indicate flight responses) increased during the hunt periods (Spitz et al. 2019). In addition, female elk at Starkey increase their flight responses, movement rates, and distributional shifts away from motorized recreation on summer range during non-hunting periods (Wisdom et al. 2004, Preisler et al. 2006, Preisler 2013) and substantially reduce their foraging time (Naylor et al. 2009), in support of over 30 studies documenting consistent elk avoidance of motorized routes on public lands during both hunting and non-hunting periods (Rowland et al. 2005, Wisdom et al. 2018).

We observed the highest movement rates across all hunts and seasons during the pre-hunt rifle deer treatments, with rates declining throughout each successive 5-day period during the deer rifle season. We contend this response was related to breeding behavior peaking during the pre-hunt rifle period and declining thereafter (see above). Collectively, these results indicate male elk are adept at perceiving risk and altering movement behavior associated with hunting (increased movements during target hunts), yet the non-consumptive effects they incur are likely within the range of effects they incur from other activities (e.g., breeding). If elk respond to hunting pressure in a similar manner regardless of the duration of the hunt, longer hunts could potentially have negative fitness consequences on male elk. Increases in movement may ultimately affect energy reserves (Heglund et al. 1982), which may accumulate to substantial effects during prolonged hunting seasons. These effects could be additive to the substantial energetic costs male ungulates incur from engaging in breeding (Forsyth et al. 2005) leading to reduced body condition, which could lower survival. Nevertheless, adult survival is the last demographic parameter affected by reduced nutritional condition in ungulates (Gaillard et al. 1998, 2000; Eberhardt 2002), so males could likely incur reduced body fat with minimal fitness results (in contrast to females that might exhibit reduced pregnancy). Regardless, when setting season dates, managers should recognize there are likely energetic consequences for non-target individuals (Brown et al. 2020) or non-target components of elk populations (Spitz et al. 2019).

While our study design allowed us to compare behavioral responses of elk across a gradient of low (pre-hunt) to high predation risk (hunts periods) from human hunters, several factors may limit extrapolation to broader scales. First, duration of each of our 3 controlled hunts was 5 days, whereas in many jurisdictions elk hunts can extend for several weeks and include multiple species (e.g., elk, deer). Based on the risk allocation hypothesis (Lima and Bednekoff 1999), animals should exhibit greater anti-predator behavior during short duration bouts of predation risk. Consequently, longer hunts may produce less pronounced effects than those we observed over a 5-day season. Second, hunter densities were relatively constant over the course of our study (range = 0.23–0.36 hunters/km^2), yet responses of elk are likely to vary as a function of hunter density. For example, Johnson et al. (2004) observed the magnitude of ungulate movement responses increased with hunter density, and Davidson et al. (2012) reported pregnancy rates of elk declined with increasing densities of elk archery hunters in Starkey. Lastly, because of the limited sample size of harvested elk ($n = 4$), we were unable to determine how male age may influence resource selection, movements, and ultimately how these correspond to risk of harvest. Among 2-year-old male elk in Alberta, Canada, those that were harvested showed higher movement rates and increased use of more open areas than unharvested 2-year-olds (Ciuti et al. 2012). Similar results were documented for female elk aged 2–9 years; however, within this group movement rates decreased with increasing age and no female elk >9 years was harvested (Ciuti et al. 2012). Equivalent adaptability to local environments would likely apply to male ungulates.

MANAGEMENT IMPLICATIONS

Our results illustrate that male elk exhibit strong changes in resource selection and movement rates based on the diel cycle and hunter presence on the landscape. Such anti-predator responses are likely to be hunt-type specific, and we urge caution when interpreting our results during the elk breeding season as elk may perceive risk differently or tolerate more risk to allow for breeding opportunities. The patterns of selection we observed highlight the need to manage for heterogeneous landscapes that provide adequate foraging opportunities while having access to cover (i.e., canopy cover or stand density) in areas with low motorized vehicle access. Wildlife and land managers should collaborate on strategic vegetation management (e.g., thinning or controlled burns) designed to create a mosaic of forest conditions to meet the needs of elk and other public land use objectives. These vegetation mosaics should be coupled with strategic closures of motorized vehicle routes to help maintain high elk use of public landscapes during hunting seasons. In addition to potential land-management actions, wildlife managers may consider altering tag numbers in areas of high hunter pressure (i.e., high road density) to reduce human disturbance and ensure escapement of sufficient quantity of older males within the population to support efficient and timely breeding of females.

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CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

ETHICS STATEMENT

All animals were handled in accordance with Institutional Animal Care and Use Committee 92-F-0004 (Wisdom et al. 1993).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX A: HUNT DATES

TABLE A1 Dates describing 5-day hunt periods with varying levels of human disturbance in the Starkey Experimental Forest and Range, Oregon, USA, 2009–2016, including number of hunters and number of targeted animals (i.e., deer vs. elk) harvested

Year	Hunt	Collared elk	Start	End	Number of hunters	Number harvested
2009	Male elk archery	2	29 Aug 2009	2 Sep 2009	22	3
2009	Male deer rifle	0	3 Oct 2009	7 Oct 2009	19	4
2009	Male elk rifle	0	28 Oct 2009	1 Nov 2009	28	5
2010	Male elk archery	7	28 Aug 2010	1 Sep 2010	22	1
2010	Male deer rifle	0	2 Oct 2010	6 Oct 2010	24	1
2010	Male elk rifle	6	27 Oct 2010	31 Oct 2010	28	8
2011	Male elk archery	11	27 Aug 2011	31 Aug 2011	23	1
2011	Male deer rifle	10	1 Oct 2011	5 Oct 2011	26	7
2011	Male elk rifle	9	26 Oct 2011	30 Oct 2011	27	6
2012	Male elk archery	0	25 Aug 2012	29 Aug 2012	22	0
2012	Male deer rifle	0	29 Sep 2012	3 Oct 2012	21	8
2012	Male elk rifle	0	24 Oct 2012	28 Oct 2012	24	11
2013	Male elk archery	4	24 Aug 2013	28 Aug 2013	18	0
2013	Male deer rifle	3	28 Sep 2013	2 Oct 2013	22	16
2013	Male elk rifle	4	23 Oct 2013	27 Oct 2013	27	12
2014	Male elk archery	7	30 Aug 2014	3 Sep 2014	20	1
2014	Male deer rifle	4	4 Oct 2014	8 Oct 2014	19	3
2014	Male elk rifle	4	29 Oct 2014	2 Nov 2014	24	13
2015	Male elk archery	6	29 Aug 2015	2 Sep 2015	21	0
2015	Male deer rifle	5	3 Oct 2015	7 Oct 2015	23	6
2015	Male elk rifle	4	28 Oct 2015	1 Nov 2015	23	11
2016	Male elk archery	15	27 Aug 2016	31 Aug 2016	22	0
2016	Male deer rifle	13	1 Oct 2016	5 Oct 2016	22	10
2016	Male elk rifle	13	26 Oct 2016	30 Oct 2016	25	13

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APPENDIX B: PREDICTED CHANGES IN ELK RESOURCE SELECTION

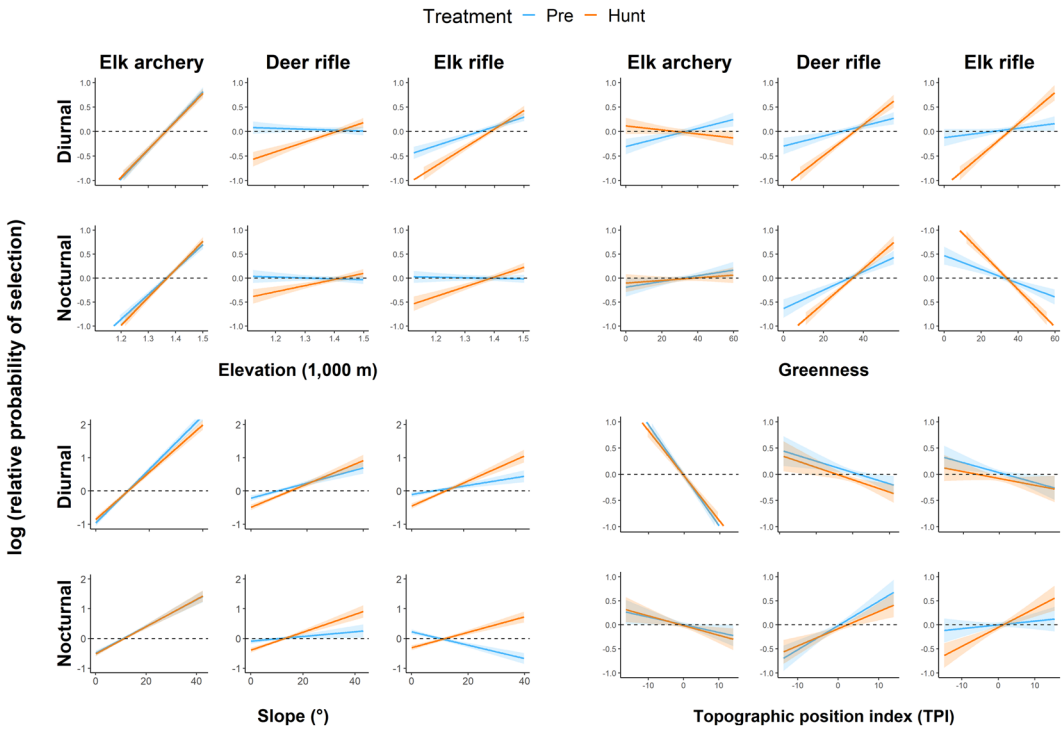

FIGURE B1 Predicted changes in male elk resource selection behavior between pre-hunt (blue) and hunt (yellow) treatments in the Starkey Experimental Forest and Range, Oregon, USA, 2009–2016, considering covariates that cannot be actively managed but can be accounted for in management. Plotted relationships are from population-level resource selection functions divided by diel (rows) and hunt (columns) periods. Predictions are shown with 95% confidence intervals and were generated across the observed range of each focal variable while all other covariates were held constant at mean values. The dashed lines at $y = 0$ demarcate non-significant (i.e., neither positive nor negative) effects