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Research Article

Influence of Landscape Characteristics on Hunter Space Use and Success

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ABSTRACT Sport hunting of ungulates is a predominant recreational pursuit and the primary tool for managing their populations in North America and beyond, given its influence on ungulate distributions, social organization, and population performance. Similarly, land management, such as motorized vehicle access, influences ungulate distributions during and outside hunting seasons. Although research on ungulate responses to hunting and land use is widespread, knowledge gaps persist about space use of hunters and what landscape features discriminate among hunt types and between successful and unsuccessful hunters. We used telemetry location data from hunters ($n = 341$) to estimate space use from 2008–2013 during 3 types of controlled, 5-day hunts for antlered mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) in northeastern Oregon, USA: archery elk, rifle deer, and rifle elk. To evaluate space use, we developed utilization distributions for each hunter, created core areas (50% contours) for groups of hunters, and derived several metrics of space-use overlap between successful and unsuccessful hunters. We also modeled predictors of space use using resource utilization functions with beta regression and stepwise model building. Hunter space use was compressed, with even the largest core area (unsuccessful rifle elk hunters) encompassing <16% (1,178 ha) of the area. We found strong similarities in space use of rifle hunters compared to archers, and core areas of successful hunters were markedly smaller than those of unsuccessful hunters (e.g., $\bar{x} = 104$ ha vs. 681 ha, respectively, for archers). Percentage cover and distance from open roads were the most consistent covariates in the 6 final models (successful vs. unsuccessful for each of 3 hunts) but with different signs. For example, predicted use of archery and rifle elk hunters increased with cover but decreased for rifle deer hunters. Although the same covariates were in the final models for unsuccessful and successful rifle elk hunters, their negligible spatial overlap suggested they sought those features in different locales, a pattern also documented for rifle deer hunters. Our models performed well (Spearman's rank correlation coefficients = 0.99 for 5 of 6 models), reflecting their utility for managing hunters and landscapes. Our results suggest that strategic management of open roads and forest cover can benefit managers seeking to balance hunter opportunity and satisfaction with harvest objectives, especially for species of special concern such as mule deer, and that differences in space use among hunter groups should be accounted for in hunting season designs.

KEY WORDS archery hunt, *Cervus canadensis*, elk, hunter success, motorized access, mule deer, *Odocoileus hemionus*, rifle hunt, space use, utilization distribution.

Sport hunting of wild ungulates is a predominant recreational pursuit (Cordell 2012, White et al. 2016) and the primary tool for their management in North America and beyond (Stedman et al. 2004, Lebel et al. 2012, Diekert et al. 2016, Apollonio et al. 2017). Wildlife management agencies also regulate hunting to enhance hunter opportunity and experience on public lands by manipulating season lengths, opening dates, and hunter density to delay animal movement to private lands (Conner et al. 2001, Vieira et al. 2003). Hunting can directly alter movements and distribution (Proffitt et al. 2010, Cleveland et al. 2012,

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Neumann and Ericsson 2018), social organization (Singer and Zeigenfuss 2002), and genetics (Kardos et al. 2018) of ungulate populations, and indirectly affect disease spread (Davidson et al. 2012, Apollonio et al. 2017) and population performance (Davidson et al. 2012, Festa-Bianchet et al. 2017).

Land management, such as prescribed fire, also influences ungulate distributions during and outside hunting seasons (Wertz et al. 1996, Barker et al. 2019). Perhaps the most effective mechanism for influencing ungulate space use and hunter harvest, however, is managing road access. Effects of roads and motorized vehicle access on ungulate distributions (Rowland et al. 2005, Meisingset et al. 2013, Montgomery et al. 2013, Wattles et al. 2018) and vulnerability to harvest (Unsworth et al. 1993, Gratson and Whitman 2000*b*, Plante et al. 2017) are well-documented. Together these researchers illuminate the pronounced ecological effects of land management and hunting on target and non-target segments of ungulate populations. Despite this literature on road effects, coupled with the proliferation of all-terrain vehicles (ATV) and trail networks (Cordell 2012), management policies on public lands that limit motorized access remain highly contentious (Bengston and Fan 1999, Havlick 2002, Cerveny et al. 2011).

Researchers have adapted concepts of game theory and predator-prey ecology (Lima and Dill 1990) to model non-consumptive effects of hunters on prey species (Johnson et al. 2005, Visscher et al. 2017, Spitz et al. 2019, Brown et al. 2020). Other studies suggest that hunters who prioritize harvest over social aspects of hunting are more likely to adopt tenets of optimal foraging (i.e., maximizing energy gain at the lowest cost; Pyke et al. 1977, Smith and Yuan 1991). Although effects of human predators on prey are well-described, explicit behaviors and movements of hunters are less studied (Diefenbach et al. 2005, Papworth et al. 2012) and research tends to emphasize kill sites rather than broad-scale hunter distributions (Lebel et al. 2012, Plante et al. 2017). Instead, studies have often centered on socioeconomic effects of hunting and hunter attitudes and characteristics (Bolon 1994, Ward et al. 2008, Cordell 2012, Harper et al. 2012, Andersen et al. 2014).

Investigations of hunter movements began in the 1990s (Bryant et al. 1991, Stedman et al. 2004), and Lyon and Burcham (1998) published the first such study in the United States using global positioning system (GPS) telemetry to track elk (*Cervus canadensis*) hunters in Montana. More recent studies are increasingly sophisticated, describing elk and hunter space-use sharing (Millspaugh et al. 2000), habitat use of recreational hunters (Pauli et al. 2019), resource selection of caribou (*Rangifer tarandus*) hunters and their prey (Plante et al. 2017), habitat characteristics associated with white-tailed deer (*Odocoileus virginianus*) harvest (Lebel et al. 2012), and effects of beetle-killed forests on resource selection of elk and hunters (Lamont et al. 2020). No studies have related spatially explicit hunter movements to hunt outcome (i.e., successful vs. unsuccessful hunters), however, other than modeling success of white-tailed deer hunters with categorical spatial data from hunter surveys (Bhandari et al. 2006).

Knowledge gaps remain about hunter behavior, success, and space use in relation to their quarry, modes of hunting (e.g., archery vs. rifle), and the role of environmental features such as road networks or forest canopy cover. Understanding space-use patterns based on hunter success can help with wildlife management; successful hunters remove animals from the population, but unsuccessful hunters are typically far more numerous, and their movements can affect prey species despite not harvesting an animal (Spitz et al. 2019). Such research can help wildlife managers allocate tags to balance desired hunter opportunities with management objectives and benefit land managers making decisions about roads, trails, and timber harvest that may affect hunter harvest and distribution. "Understanding the behavior of hunters is as important in game management as knowing game and its habitat" (Thomas et al. 1976:500), a sentiment echoed by Lyon and Burcham (1998) and Yuan et al. (1991).

We implemented a 6-year study in northeastern Oregon, USA, to investigate a suite of hunt-related topics, including non-spatial factors influencing hunter success, effects of hunting on non-targeted (Spitz et al. 2019, Brown et al. 2020) and targeted animals, the role of ATVs in hunter success, and hunter distributions in relation to landscape characteristics. This paper addresses the last topic, space use of hunters during 3 types of hunts for antlered ungulates—archery elk, rifle deer, and rifle elk—with a spatial gradient of options for motorized road access. Our objectives were to compare successful and unsuccessful hunters within and among the 3 hunt types using data at multiple spatial and temporal scales by describing general patterns of space use, quantifying space-use sharing within hunt types, and modeling hunter space use. In developing our space-use models, we sought to elucidate the effects of landscape covariates that can be managed, such as forest cover and trails and roads open to motorized use, on hunter success and spatial distribution. We tested 3 broad hypotheses: space use will differ among the 3 hunt types, given different target species (mule deer [*Odocoileus hemionus*] vs. elk) and modes of hunting (rifle and archery); space use will differ by hunt outcome; and successful hunters will spend more time in habitats associated with their quarry. We predicted that probability of use near motorized routes would be greater for rifle hunters (Lyon and Burcham 1998, Stedman et al. 2004) than for archers (Ranglack et al. 2017). Being farther from roads would increase archers' ability to locate elk that were less disturbed by traffic and thus less vigilant, allowing a closer approach by archers. Second, we predicted archers would use areas with greater tree canopy cover compared to rifle hunters to better conceal their movements. Last, we predicted that successful mule deer hunters would concentrate use closer to roads than elk hunters because mule deer in our study area consistently select sites nearer to open roads than do elk (Johnson et al. 2000, Wisdom et al. 2005).

STUDY AREA

We conducted our study at the Starkey Experimental Forest and Range (Starkey), established as a research site in 1940 by the United States Forest Service (Fig. 1; Rowland et al. 1997). An ungulate-proof fence was erected in 1987, enclosing several study areas totaling approximately 10,125 ha, to allow for manipulative, landscape-scale experiments to address a variety of land uses and human activities, such as timber harvest, livestock grazing, and road access, and potential effects on ungulates (Wisdom 2005). The main study area (7,768 ha), where we conducted our research, contained a mosaic of forest and grassland vegetation types common in the Blue Mountains ecoregion (Franklin and Dyrness 1988, Rowland et al. 1997), dominated by ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis*), Douglas fir (*Pseudotsuga menziesii*), and bunchgrass communities (e.g., bluebunch wheatgrass [*Pseudoroegneria spicata*]). Topography was rolling with mostly gentle slopes ($\bar{x} = 15\%$). Climate was typical of the ecoregion, with warm, dry summers and cold, moist winters (Heyerdahl et al. 2002), and elevations ranged from 1,116 m to 1,502 m. Mean annual precipitation was 50.4 cm, with mean temperatures of 18°C in July and −4°C in January. Mule deer, white-tailed deer and elk were present, and cattle were grazed from June–October each year under a standard Forest Service permit system (Rowland et al. 1997, Wisdom 2005).

A variety of tags, season lengths, start dates, and hunt and weapon types have been offered during >30 years of Starkey hunting research (Rowland et al. 1997, Johnson et al. 2005, Davidson et al. 2012). Estimated densities of the closed but free-ranging populations of mule deer and elk during our study period (2008–2013) were approximately 1.3 deer/km^2 and 4.5 elk/km^2. Mean densities on summer range in the surrounding Wildlife Management Units (WMUs) were higher for mule deer (4.7 deer/km^2) and lower for elk (1.6 elk/km^2). Oregon Department of Fish and Wildlife (ODFW) manages for post-harvest male:female ratios of 15–25:100 for deer and 10–20:100 for elk; Starkey populations were managed to maintain these ratios at a minimum.

Access at Starkey was administered using a travel management system whereby roads designated with a sign with a green dot were open to motorized use by the public; prior to the study, 45 km of roads were open for any vehicle type (e.g., ATVs, passenger cars, recreational vehicles). During our study, however, road access was altered to provide a range of open road and trail access options for hunters. In the northern part of Starkey, closure of a 9.7-km open road segment resulted in about 35% of the study area being >1.5 km from the nearest motorized access (Fig. 1). By contrast, motorized access was increased in another 35% of

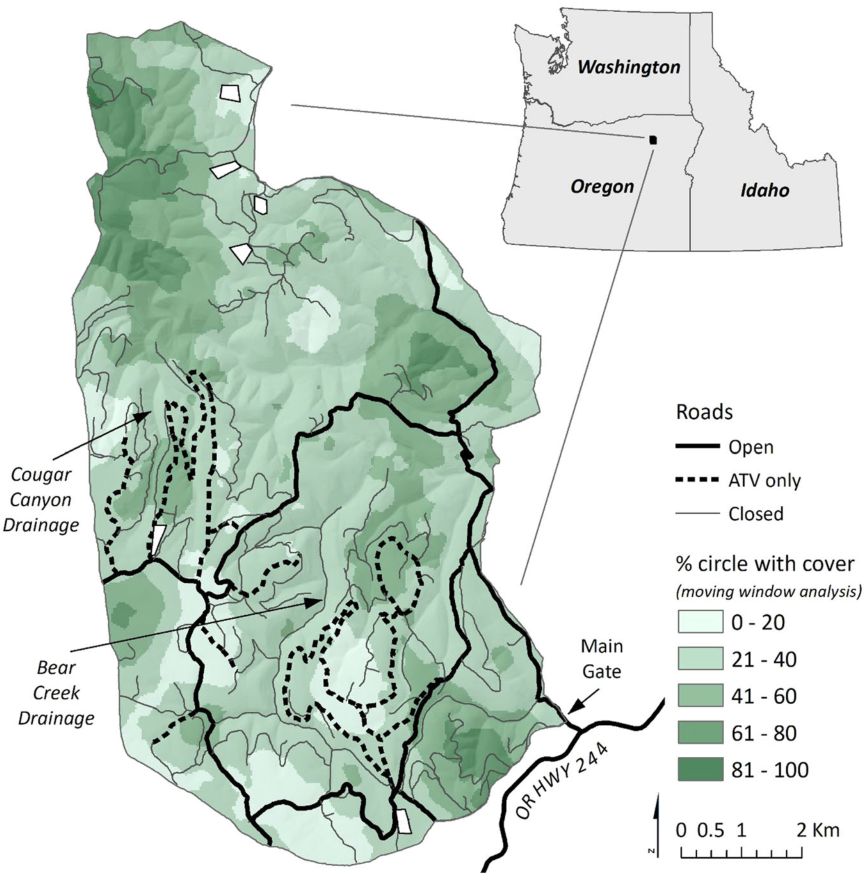

Figure 1. The main enclosure of Starkey Experimental Forest and Range, northeastern Oregon, USA, and the road and all-terrain vehicle (ATV) trail system operating during controlled, 5-day hunts for antlered mule deer and elk, 2008–2013. All hunter entry was through a gate where the check station was located. Canopy cover is displayed as the percentage of pixels in a 600-m radius with tree canopy cover >20%.

the area by opening 33.9 km of administrative roads to ATV-only use, encompassing the Bear Creek drainage and areas just south of Cougar Canyon (Fig. 1). This change resulted in the highest open road and trail density (>3 km/km^2), with most of this area <0.5 km from the nearest motorized access. Closed roads (112.8 km) were available to Starkey hunters throughout the study area for access on horseback, foot, or mountain bike (Fig. 1). This road configuration was maintained during hunts for all years of study.

METHODS

Hunt Designs

The controlled hunts were implemented by ODFW as part of the study design, and all were for antlered males. Each hunt period was 5 days, preceded by a 5-day scouting period. Archery hunts occurred in late summer, concurrent with the start of statewide archery seasons (i.e., the Saturday of the last full weekend in Aug; Table 1). Rifle deer hunts began 5 weekends after archery season started, generally late September or early October, and rifle elk hunts began the last week of October, also coincident with hunts outside Starkey (Table 1). Twenty-five permits were assigned to hunters for each hunt through the ODFW application process. Hunters drawing permits could enter Starkey at any time it was open to the public (1 May–15 Nov) but were required to check in upon their first visit to Starkey, whether scouting or hunting.

Only 1 access point into Starkey (State Highway 244) was available for hunter entry and exit (Fig. 1; Rowland et al. 1997, Johnson et al. 2005). A check station was established there at the start of each scouting period and staffed throughout the hunts to provide hunters with details about the hunt, the road and trail system, and data collection protocols. Hunting was prohibited within a 400-m buffer inside the Starkey perimeter fence. All hunters were required to complete a questionnaire before departure to inform structuring of future hunts, providing details such as their prior hunting experience, hours and mode of hunting each day, and their satisfaction with the Starkey hunt.

Hunter Telemetry Data

At check-in we provided each hunter with a store-on-board GPS unit (GPSLogger™, TenXsys, Eagle, ID, USA) and instructions about its use. The units were enclosed in a hard case and inserted in a pouch worn on a belt. Each unit was programmed to obtain a location every 5 minutes from the time a hunter first checked in and the unit deployed. We asked hunters to wear units continuously during legal shooting hours each day, regardless of activity (e.g., scouting, hunting, in camp). Hunters returned GPS units to Starkey staff after harvesting an animal, at the conclusion of the hunt if unsuccessful, or whenever leaving the study area during the hunt.

Given our objective to quantify space use during active hunting (Gerrits et al. 2020), we censored locations as follows. We excluded camp locations by mapping hunter locations in ArcGIS (Esri, Redlands, CA, USA) and visually inspecting them to identify the centroid of clusters of each hunter's locations during night-time hours (defined as any locations outside legal shooting hours ±1 hr). We determined that most stationary locations (i.e., consecutive locations in camp) were contained within a 200-m radius of the cluster centroid; thus, we excluded from analysis any telemetry locations within a 200-m radius of hunter camps. We further censored locations to exclude those obtained during the scouting period, outside legal shooting hours plus a 1-hour buffer before and after (Lamont et al. 2020), within 300 m of the check station (Gerrits et al. 2020), and after the day of harvest (successful hunters only; Plante et al. 2017).

Creating and mapping utilization distributions.—We used the locations to estimate a utilization distribution (UD; Marzluff et al. 2004, Millspaugh et al. 2006) for each hunter across Starkey, given the variability in number of locations for some hunters (Table S1, available online in Supporting Information). We estimated UDs using a Brownian bridge movement model (BBMM; Horne et al. 2007, Sawyer et al. 2009) with the BBMM package (Nielson et al. 2013) in the R statistical environment, which we used for all statistical analyses (version 3.6; R Core Team 2019). Missing observations, or fix-rate bias (Nielson et al. 2009), were a concern in our analysis because fix success of the hunter GPS units varied from 11–87%. Fix failure due to

Table 1. Start dates, numbers of hunters by hunt type and harvest outcome (1 = successful, 0 = unsuccessful), and overall success rates for 5-day controlled hunts for antlered male mule deer and elk in Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013.

	Archery elk			Rifle deer			Rifle elk		
Year	Date	1	0	Date	1	0	Date	1	0
2008	30 Aug	0[a]	20	4 Oct	8	13	29 Oct	9	7
2009	29 Aug	3	17	3 Oct	3	14	28 Oct	3	16
2010	28 Aug	1	15	2 Oct	0	22	27 Oct	7	16
2011	27 Aug	1	16	1 Oct	5	15	26 Oct	5	18
2012	25 Aug	0	21	29 Sep	7	9	24 Oct	9	11
2013	24 Aug	0	16	28 Sep	10	4	23 Oct	8	12
All years		5	105 (0.045)[b]		33	77 (0.30)		41	80 (0.340)

[a] Numbers include only those hunters with sufficient data to use in analyses. Twenty-five tags were authorized for each hunt; in addition, a small number (1–3) of tribal hunters and outfitter-guided hunters were present during some years and hunts.
[b] Values in parentheses are success rates for each hunt averaged across the 6 years of study.

habitat characteristics can lead to biased estimates of space use (Hebblewhite et al. 2007, Nielson et al. 2009).

The BBMM may improve inference when locations are missing (Millspaugh et al. 2006, Hooten et al. 2013, Eckrich et al. 2020), but multiple consecutive missing locations can artificially inflate Brownian motion variance (Horne et al. 2007) or result in convergence problems during model estimation. To avoid these issues, we restricted BBMM estimation to locations ≤15 minutes apart (or 3 consecutive missing locations). If a movement sequence had >3 consecutive missing locations, we estimated 2 UDs—1 before the missing locations and 1 after—and then combined and rescaled the UD values.

We limited our analyses to hunters with ≥20 locations during a hunt to ensure sample sizes were sufficient for BBMM calculations. We also eliminated hunters whose UDs were based on GPS locations collected over an extremely short period of time, resulting in UDs that were highly suspect. Based on stationary field tests, we used a conservative value of 37 m for the standard deviation of location errors (Horne et al. 2007). Values of predicted use from the BBMM for each hunter were assigned to every 30-m pixel ($n = 85,726$) within the study area.

We identified centers of activity in the UDs where use was more intense (Kernohan et al. 2001, Wilson et al. 2010) by using the 50% contour (i.e., the 50% isopleth representing the top half of predicted use) to represent core areas (Fieberg and Kochanny 2005, Robert et al. 2012, Yen et al. 2019).

To understand broad patterns of space use and potential overlap among groups of interest, we created yearly mean UDs and 50% core areas for each of the 3 hunt types and 2 hunt outcomes. Some year-outcome-hunt type combinations had no data (e.g., successful archers, 2008) and thus we were unable to create a UD. We also created 6 composite UDs by averaging yearly mean UDs across all years for the primary groups of interest (successful and unsuccessful hunters × 3 hunt types). We calculated yearly mean and composite UDs by summing predicted probabilities across individual hunter UDs and yearly mean UDs, respectively, and then scaling so the sum equaled 1. We used the UDs developed at these differing spatial and temporal scales in complementary analyses as described below.

Model Covariates

To model hunter space use, we developed a suite of *a priori* model covariates from available spatial data sources (Table S2, available online in Supporting Information), based on our hypotheses and predictions and review of literature describing environmental characteristics influencing hunter movements and success (Thomas et al. 1976, Stedman et al. 2004, Pauli et al. 2019). Covariates included those that can be managed, such as trails and roads and vegetation structure (e.g., distance from cover-forage edge), and abiotic characteristics that may also account for space use like slope and distance from physical features. We developed spatial layers at 30-m resolution for all covariates in ArcGIS. We derived some covariates, hypothesized to affect hunter behavior, at multiple scales to accommodate potential scale-dependent differences in hunters' responses to habitat characteristics. For example, we generated percentage of a 100-m-radius and 600-m-radius circle with canopy cover >20% because archery hunters may use forest cover differently than do rifle hunters (Table S2). We also included quadratic terms for covariates when we predicted that hunter use might peak or plateau at some intermediate value, including distance from open roads and ATV trails, canopy cover, and slope. If 2 covariates were highly correlated based on Pearson's correlation coefficient (i.e., $|r| > 0.6$), we either dropped one, retaining the one with greater management relevance, or did not use them together in the same model (Table S2).

Data Analysis

Space-use overlap.—To characterize spatial patterns of use and overlap among hunt types, hunt outcome, and years, we derived several metrics using the yearly mean UDs. First, for each year we calculated the core area (i.e., 50% contour) of each UD, 2-dimensional overlap of core areas between successful and unsuccessful hunters within a hunt type, and joint area (union) of cores for successful and unsuccessful hunters by hunt type. This last metric described the combined core footprint of hunters afield during any one hunt. We also mapped and quantified the 2-dimensional area overlap of the 6-year composite UD cores to reveal patterns of space-use sharing among hunters on a larger spatial and temporal scale.

To further illuminate patterns of static space-use sharing across hunt types and leverage the probabilistic data in the UDs (Millspaugh et al. 2004, Fieberg and Kochanny 2005), we calculated 2 additional metrics with the yearly mean UD cores. The first, the probability of home range overlap (PHR; Fieberg and Kochanny 2005: equation 4), is the summed probability of use of UD_j (e.g., unsuccessful hunters) in the overlap area with UD_i, (e.g., successful hunters). Thus, the PHR reveals the probability of hunters in one group being in the core area of the other, given that they are already in their own core area (Fieberg and Kochanny 2005, Benson and Patterson 2015). Second, we calculated the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005). Values typically range from 0 (no overlap) to 1 (100% overlap and UDs are uniformly distributed) but can exceed 1 if the 2 UDs have high overlap and are non-uniformly distributed (see Auxiliary Methods, available online in Supporting Information).

Modeling resource utilization of hunter groups.—We used the composite UD for each hunt type and outcome as the response variable in resource utilization functions (RUFs) to identify relationships between hunter space use and landscape characteristics (Marzluff et al. 2004, Papworth et al. 2012, Hooten et al. 2013). The RUF models a continuous probability, or relative probability in this case, of use and relates values from a UD to a spatially defined set of resources (Marzluff et al. 2004). The spatial scale for RUF modeling was the main enclosure of Starkey (Fig. 1), for which we had values for relative probability of use for each

30-m pixel from the composite UDs. We drew a systematic sample of approximately 25% of the cells in our study area for modeling (training) and held out the remainder for model evaluation (Wisdom et al. 2020). This process resulted in reducing the spatial correlation in the response variable to <0.41 for nearest neighbors and <0.1 out to 500 m. Autocorrelation in the response will itself not bias regression estimates but may result in biased estimates of precision for the estimated coefficients. To obtain the 90% confidence intervals for model coefficients, we bootstrapped by year (block bootstrapping; Roberts et al. 2017), matching the primary sampling unit of this study and using 500 replicates.

We used beta regression (Ferrari and Cribari-Neto 2004) to model the relation between relative probability of use and environmental characteristics. We chose the logit link for the response in the beta regression model and the log link for estimating the dispersion parameter (*phi*; Ferrari and Cribari-Neto 2004). We conducted modeling using library betareg in the R statistical environment.

We are not aware of any published study relating hunter probability of success to space use in a multivariate framework, so we approached the model selection process with open minds and few pre-conceptions, other than the list of covariates believed to have potential value in predicting hunter distributions (Table S2). We did not create a list of *a priori* models but instead used a stepwise model-building approach, guided by Akaike's Information Criterion, corrected for small sample size (AIC_c; Burnham and Anderson 2004), to develop final models. Starting with a null model, we added or removed variables from the model until we reached a final model where the AIC_c value did not decrease or the number of covariates reached a maximum of 5. We considered quadratic terms for some covariates along with their linear version during model development, and we inspected marginal plots to determine if the contribution of the quadratic term improved interpretation. If not, we dropped the quadratic term to reduce model complexity (see Auxiliary Methods for details).

We used AIC_c only as a guide during model building because "to compute by reflex is a sure recipe for disaster" (Good and Hardin 2009:134) and can lead to models that are difficult to interpret, unknowingly affected by multicollinearity, or of little utility. We calculated the variance inflation factor (VIF; Stine 1995) during the model development process to identify potential multicollinearity issues; however, the VIF was not developed to identify multicollinearity when both linear and quadratic forms of a covariate are in a model, and there are no clear rules-of-thumb for VIF thresholds (O'Brien 2007). We also carefully monitored estimates of model coefficients and standard errors, providing more obvious evidence of multicollinearity (see Auxiliary Methods for details).

We evaluated the 6 final RUF models by visually inspecting model residual plots (McCulloch et al. 2008, Pereira 2019), and in 2 other ways using the approximate 75% of the pixels within the study area withheld from model training. First, we calculated a Pearson's correlation coefficient between the predicted values from beta regression made to 75% of the study area and the estimated values from the original UD (response). Before this calculation we applied a logit transformation to both sets of values to address the highly skewed data. Second, we classified predictions of relative probability of use into 20 equal-area bins (i.e., 5% quantiles) and summed the observed (UD) and response (i.e., use predicted from the BBMM) values within each bin. We then calculated Spearman's rank correlation coefficient between the 20 summed probabilities and the prediction class, similar to model evaluation methods commonly described in the literature (Boyce et al. 2002, Coe et al. 2011).

RESULTS

We used UDs from 341 hunters in our analyses after filtering telemetry data by numbers of locations (≥20) and minimum size (20 ha) of individual core areas (Table 1). Numbers of hunters by hunt type were similar, with 110 each for archery elk and rifle deer hunts and 121 for rifle elk; successful hunters were less common than were unsuccessful. Across years, success rates ranged from <5% for archers to 30% for rifle deer and 34% for rifle elk hunters, rates comparable to those in adjacent WMUs (ODFW, unpublished data; Table 1). Locations, summed across years by hunt type and outcome, varied from 620 for successful archers to 18,105 for unsuccessful archers. Because we truncated location data after harvest and there were fewer successful hunters, total locations were always fewer for successful hunters except for rifle deer hunters in 2013 (Table S1).

Core Area Size and Space-Use Overlap

At all scales of analysis (i.e., individual hunter, yearly mean, and 6-year composite UDs) patterns of core area size and overlap were similar. For concision, we focus on results for yearly mean UDs and refer the reader to supplemental material for summaries at other scales (Fig. S1 and Table S3, available online in Supporting Information). Hunter space use was compressed, with the largest core area (1,178 ha, unsuccessful rifle elk hunters in 2011; Fig. 2) encompassing <16% of the area available to hunt. For all hunt types, core area sizes of unsuccessful hunters were generally similar, with those of rifle elk hunters largest, followed by rifle deer, then archers (Fig. 2). Core areas were nearly always smaller for successful hunters, sometimes markedly so (Fig. 2). Mean core areas of successful rifle elk hunters ($\bar{x} = 240$ ha) were about a third of the size of those for unsuccessful hunters ($\bar{x} = 801$ ha; Fig. 2), but differences were less pronounced for rifle deer hunters (Figs. 2 and 3). Although unsuccessful hunters had more locations than did successful hunters for all hunt types, the number of locations was not related to core area size (Table S1 and Fig. S2, available online in Supporting Information). Combined cores, representing the joint footprint within a hunt type of unsuccessful and successful hunters afield, also differed across hunt types. The mean combined core size for archery elk hunters was 625 ha, nearly half that of rifle deer hunters

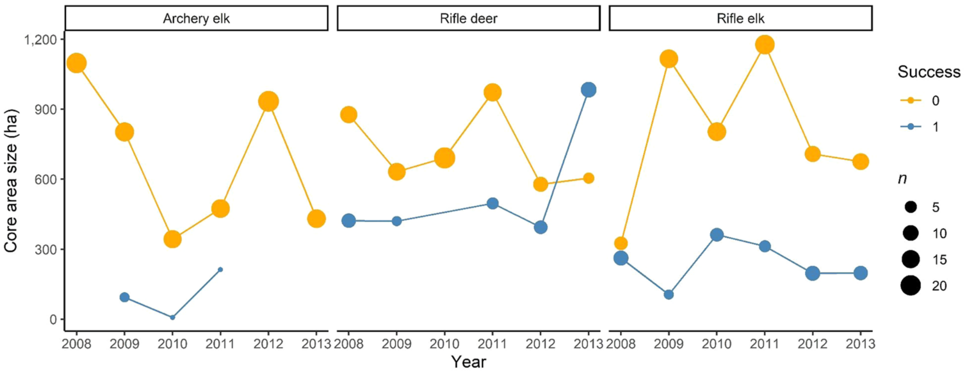

Figure 2. Yearly mean core area sizes of archery elk and rifle mule deer and elk hunters in Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013, created by averaging 50% contours of individual hunter utilization distributions (UDs). Success = 0 for unsuccessful hunters and 1 for successful. There were no successful archers in 2008, 2012, and 2013 or successful rifle deer hunters in 2010. Point size reflects the number of individual hunters (n) used to create each mean UD.

($\bar{x} = 1,148$ ha) and roughly 30% smaller than that of rifle elk hunters ($\bar{x} = 893$ ha; Appendix A).

Successful and unsuccessful hunters were spatially separated, reflected in the minimal 2-dimensional overlap between them in core areas (Fig. 3; Appendix A). Overlap was smallest for archers and greatest for rifle deer hunters. But even for the latter, the largest yearly overlap was only 226 ha (Appendix A). Values for the PHR overlap statistic were also most similar for rifle deer hunters but remained small, and unsuccessful hunters of all hunt types were less likely to be found in the cores of successful hunters than the converse (i.e., $PHR_{1,0} < PHR_{0,1}$; Fig. 4; Appendix A). Mean UDOI for rifle deer hunters (0.67) was nearly twice that of remaining hunt types, corroborating the comparatively greater space-use sharing for this group (Fig. 4; Appendix A). Most yearly values for UDOI were <0.5, and only 2 exceeded 1.0 for any hunt-year combination (Appendix A), indicating strong dissimilarities in shared space between successful and unsuccessful hunters within a hunt type (Figs. 3 and 4).

Models of Hunter Space Use by Hunt Type and Outcome

Landscape characteristics associated with space use of the 6 hunter groups varied across Starkey, with differences generally more pronounced among the 3 hunt types than by hunt outcome. Marginal plots for successful archers indicated that intensity of use increased on steeper slopes, farther from streams, and with increasing percentage of cover in a 600-m radius. Use declined farther from ATV trails and cover-forage edges; for ATV trails the decline was attenuated somewhat, as indicated by inclusion of a quadratic term (Fig. 5; Table S4 and Fig. S3, available online in Supporting Information). The best model for unsuccessful archers resembled that of successful archers with greater use farther from streams, with increasing cover, and closer to cover-forage edges. Predicted use for this group declined with higher values of sine of aspect, reflecting greater use of west-facing slopes, and with increasing distance from open roads (Fig. 5).

For successful rifle deer hunters, relative probability of use declined with increasing distance from streams, cover percentage within 600 m, distance from both open and closed roads, and slope (Fig. 5). The relationship for slope was nonlinear, with predicted use peaking at approximately 20% slope. The best model for unsuccessful rifle deer hunters included the same 5 covariates but declines in predicted use compared to successful hunters were less pronounced for increasing distance from streams and were steeper as percent cover and slope increased (Fig. 5).

As found for the 2 groups of rifle deer hunters, the best models for successful and unsuccessful rifle elk hunters contained identical covariates, demonstrating strong similarities in predictors of space use: distance from open and closed roads, sine of aspect, cover percentage (600 m), and distance from cover-forage edge (Figs. 5 and S3; Table S4). Relationships between predicted use and covariate values were generally similar between the models for successful and unsuccessful rifle elk hunters but differed in rates of change. For example, predicted use 1.5 km away from cover-forage edges was substantially lower for unsuccessful rifle elk hunters versus successful (~0.50 vs. 0.75, respectively). Likewise, predicted use by successful rifle elk hunters remained higher as distance from open roads increased, reflected by the quadratic term, and their use was higher at all distances from closed roads than for unsuccessful hunters (Figs. 5 and S3A). Across all models, a majority of coefficients had confidence intervals that did not include zero (Table S4; Fig. S3), indicating generally consistent relationships in our final models.

All RUF models included 5 covariates, indicating that AIC_c values continued to decline as more covariates were included until we reached our stopping rule of 5 covariates (Figs. 5 and S3; Table S4). Percentage cover in a 600-m radius occurred in all 6 models (Fig. 5), and 4 distance covariates occurred in ≥4 models: open roads, closed roads, streams, and cover-forage edge (Fig. 5). Only 8 of 17 covariates considered (Table S2) occurred in the 6 best RUF models (Table 2).

Patterns of space use across hunters were markedly consistent for some covariates, such as distance from closed roads and cover-forage edges (Fig. 5), but exceptions occurred. For example, probability of use increased with

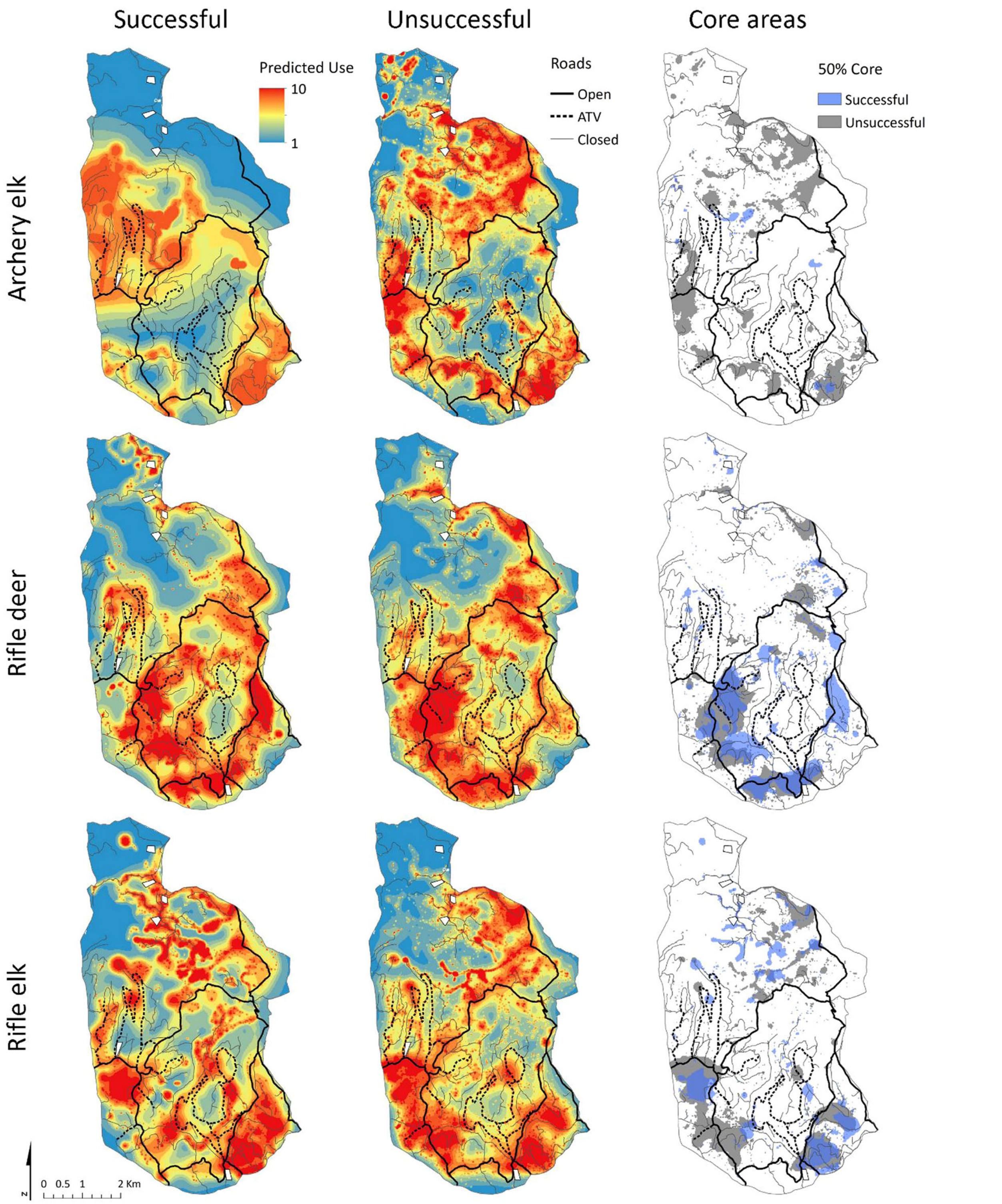

Figure 3. Predicted relative probability of use and 50% core areas of use for successful and unsuccessful hunters estimated with a Brownian bridge movement model and averaged across 6 years. Predicted use is displayed in 10 equal-area bins reflecting hunter distributions during controlled archery elk, rifle deer, and rifle elk hunts at the Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013. Lines denote the road and all-terrain vehicle (ATV) trail system in place during the hunts.

increasing cover for archery and rifle elk hunters but declined for rifle deer hunters (Fig. 5). Moreover, successful archers were more likely to be in sites with steeper slopes, in contrast to rifle deer hunters (Fig. 5). Predicted use in relation to open roads was consistent, declining with increasing distance from roads for all groups except successful archers, whose model lacked this covariate (Fig. 5). Use away from open roads declined most sharply for rifle deer hunters; at 1 km, predicted use was only approximately 0.60, but remained near 1.0 for successful rifle elk and

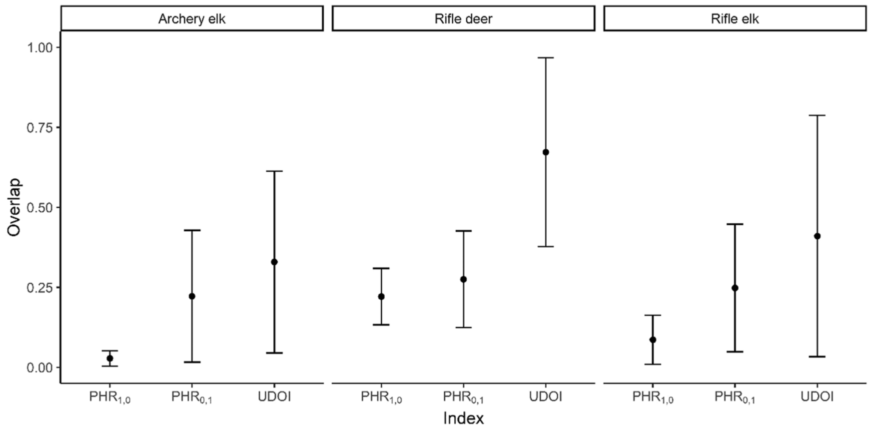

Figure 4. Patterns of space-use sharing between successful and unsuccessful mule deer and elk hunters during controlled hunts in Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013, characterized by mean (± 1 SD) overlap indices for core areas (defined as 50% contours of yearly mean utilization distributions). PHR = probability of home range overlap, and UDOI = utilization distribution overlap index. $PHR_{1,0}$ values indicate the probability of an unsuccessful hunter (0) being in the core area of a successful hunter (1), given that the unsuccessful hunter is already in their own core, whereas $PHR_{0,1}$ indicates the probability of a successful hunter (1) being in the core area of an unsuccessful hunter (0), given that the successful hunter is already in their own core ($n = 3$ years for archery elk, $n = 5$ for rifle deer, and $n = 6$ for rifle elk).

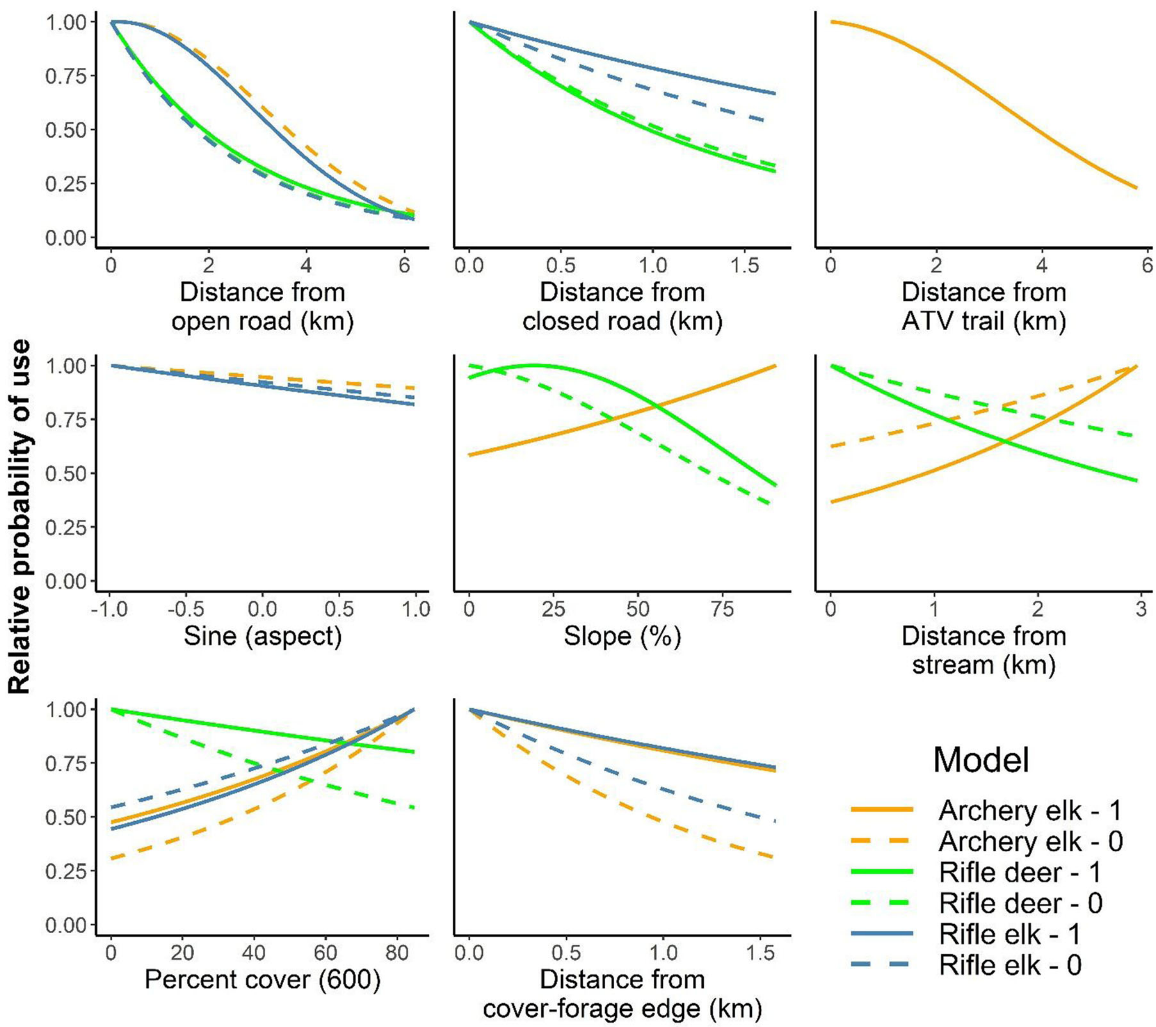

Figure 5. Marginal plots of predicted changes in relative probability of use by hunters in relation to covariates occurring in the best resource utilization function models for each of 3 hunt types (archery elk, rifle deer, rifle elk) and 2 outcomes (successful = 1, unsuccessful = 0) during controlled, 5-day hunts for antlered mule deer and elk at the Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013. Each plot represents a covariate occurring in ≥1 of the best models. Percent cover (600) denotes percentage of a 600-m-radius circle composed of forest cover, and ATV refers to all-terrain vehicles.

Table 2. Description of environmental covariates (grouped by category) included in final resource utilization models to evaluate space use by hunters during controlled mule deer and elk hunting seasons in Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013.

Category	Description
Abiotic	Distance to nearest perennial stream (km)
	Aspect converted to sine value
	Percentage slope from a digital elevation model
Access	Distance to nearest trail restricted to motorized use by all-terrain vehicles or foot traffic during the hunt (km)
	Distance to nearest closed road during the hunt (km)
	Distance to nearest road open to motorized use by the public during the hunt (km)
Vegetation	Percentage of pixels in a 600-m-radius circle with tree canopy cover >20%
	Distance to nearest edge between cover-forage patches, with cover defined as patches with >40% tree canopy cover (km)

unsuccessful archery elk hunters (Fig. 5). Binned maps of predicted use and core areas using the composited UDs affirmed patterns of modeled space use in relation to open roads (Fig. 3). In a *post hoc* analysis of the 6 composite UDs, we summed probability of use within distance bands from open roads and ATV trails and divided those sums by the proportion of area within each band (use, or selection, ratio; Table S5, available online in Supporting Information). Rifle deer hunters and unsuccessful rifle elk hunters demonstrated high use of sites <250 m of an open road (ratios = 1.23–2.46). Despite the opening of 34 km of ATV trails during the hunts, use in relation to trails was less evident than for open roads, except for successful archers at distances of 500–2,000 m (1.66–2.21; Table S5).

Spearman's rank correlation coefficients using bins of predicted use indicated the models performed well, with $r = 0.99$ for all models except successful archery elk ($r = 0.67$). Pearson's correlation coefficients were lower and more variable. Values were higher for rifle hunter models (successful rifle deer, 0.66; unsuccessful rifle deer, 0.75; successful rifle elk, 0.61, unsuccessful rifle elk, 0.74) than for archers (successful archery elk, 0.58; unsuccessful archer elk, 0.51). Models for unsuccessful hunters generally performed better than those for successful hunters.

DISCUSSION

Our approach using 6 years of telemetry data analyzed at multiple scales revealed diverse patterns of hunter space use among hunt types, hunt outcomes, and targeted species. As predicted space use differed among hunt types. Core areas of rifle hunters, especially successful ones, tended to be larger at all scales of analysis than those of archers, and distance from closed roads occurred in rifle but not archery models. Space use also varied by hunt outcome, supporting our second hypothesis; core areas of successful hunters were consistently and markedly smaller than those of their unsuccessful counterparts and were spatially separated (e.g., unsuccessful hunters were highly unlikely to be in core areas of successful hunters). Multiple findings supported our hypothesis that successful hunters would seek out habitats selected by their prey (e.g., predicted use by successful elk hunters was greatest near cover-forage edges, aligning with prior evidence that elk select sites closer to edges; Benkobi et al. 2004, Rowland et al. 2018). Notably, Starkey hunters concentrated their use in a relatively small percentage of the available landscape, regardless of hunt type, outcome, or scale, possibly reflecting their focus on areas that constitute habitat for deer and elk and are readily accessible.

Differences in Space Use Among Hunt Types

The larger footprint of rifle hunters versus archers likely reflects contrasts in weapon choice and hunting modes (e.g., stalking vs. active searching; Schmitz 2008). Rifle hunters, analogous to coursing predators (Cleveland et al. 2012), often traverse large, open landscapes to locate prey and quickly place a killing shot from up to 300 m or more because rifles are effective weapons for shooting animals alerted to or actively fleeing hunters. By comparison, archers are akin to stalking or ambush predators (Cleveland et al. 2012) requiring closeness (≤50 m) and sufficient cover to successfully approach and harvest an animal (Heurich et al. 2016). Greater core area sizes for rifle versus archery hunters also suggest a potentially broader influence on animal distribution and behavior, including non-targeted segments of the population (Spitz et al. 2019, Brown et al. 2020). In Colorado, USA, however, the spatial scale of effects of hunting on elk resource selection was deemed larger for archery than for rifle hunters, though effects were more diffuse (Ranglack et al. 2017).

Our prediction that archers would be farther from motorized routes than that of rifle hunters was partially supported. Use by unsuccessful archers was highest near open roads but remained relatively high up to about 2 km distant for this group and for successful rifle elk hunters; however, open roads did not enter the model for successful archers. Use by archers increased with canopy cover as predicted, but this was also true for rifle elk hunters. Ostensibly use of cover affords hunters a close approach to elk and places them in habitats preferred by elk during archery and rifle seasons (Ranglack et al. 2017).

Unlike archers, higher predicted use by rifle hunters near closed roads may facilitate rapid access into more remote locations in open landscapes compared to walking cross-country (Lyon and Burcham 1998). By contrast, the RUF model for successful archers was the only one incorporating distance from ATV trails, which archers may have walked to enter more remote areas than accessible by closed roads at Starkey; successful archers spent more time hunting on foot than any other group in our study (>90%; ODFW, unpublished data). Predicted use by successful archers also increased with slope, suggesting that archers may have used topographic relief as cover when stalking elk, unlike rifle hunters who benefit from conditions that maximize long-distance viewing opportunities. By contrast, deer hunters at Starkey used areas with gentler slopes, as found for deer hunters in Pennsylvania, USA (Diefenbach et al. 2005).

Differences in Space Use by Hunt Outcome

The smaller core areas of successful hunters versus those of unsuccessful hunters at all scales possibly reflected their superior knowledge of prey behavior and habitat use, leading to greater efficiency in harvest. Moreover, a substantially larger proportion of successful rifle hunters scouted prior to the start of the hunt compared to unsuccessful hunters (ODFW, unpublished data), likely boosting hunting efficiency. Successful deer hunters in West Virginia, USA, used a smaller area per hour and returned to the same area multiple times (Thomas et al. 1973). Although successful Starkey hunters had fewer locations, number of locations did not affect core area size; thus, more concentrated use of successful hunters was not an artifact of sample size but a valid difference in how they used the landscape.

The minimal spatial overlap at multiple scales of successful and unsuccessful rifle deer and rifle elk hunters suggests that these groups sought those features in different locales within Starkey, despite similarities in covariates predicting space use. Unsuccessful hunters were highly unlikely to be found in the core areas of successful hunters, but on average about 25% of predicted use for successful hunters was in the core of unsuccessful hunters. The relatively low UDOI for all 3 hunt types further corroborated distinct spatial separation of hunters by outcome within each type. These findings may denote a greater efficiency, experience, and knowledge of successful hunters about fine-scale habitat features selected by deer and elk. Yuan et al. (1991) reported that successful rifle elk hunters spent significantly less time road hunting and more time calling and in areas affording a long (up to 400 m) sighting range than did unsuccessful hunters.

Humans hunt for many reasons, including resource acquisition, tradition, and maintaining social networks (Decker and Connelly 1989, Bhandari et al. 2006, Hamilton et al. 2007). The top motivations for Oregon deer hunters were being close to nature and with family and friends (ODFW 2019). Starkey deer hunters often use the same camps yearly, and the area lacks the cachet for trophy deer that it holds for trophy elk, as revealed by the substantially longer time required to draw a Starkey male elk versus male deer tag despite tag numbers being identical (ODFW, unpublished data). In combination these factors may help explain the strong similarities in space use of Starkey deer hunters compared to other hunt types, from spatial overlap to model covariates. We found no studies describing attitudes or behavior of mule deer hunters, especially in relation to roads, in contrast to several for white-tailed deer hunters (Bhandari et al. 2006, Harper et al. 2012, Serenari et al. 2019).

Space Use in Relation to Targeted Prey

As predicted, use by successful, but also unsuccessful, deer hunters was greater near open roads compared to elk hunters. Mule deer at Starkey consistently select areas close to open roads, possibly reflecting interference competition with elk (Johnson et al. 2000, Ager et al. 2003, Wisdom et al. 2005). Researchers in eastern Oregon also reported mule deer closer to open roads than expected (Curtis and Du Toit 2017). By contrast, probability of use by successful rifle elk hunters remained high (>0.50) up to 3 km from open roads and use ratios remained above 1.0 up to 2 km, corroborating a large body of evidence that elk avoid open roads at Starkey and elsewhere, especially during hunting seasons (Rowland et al. 2000, Montgomery et al. 2013, Spitz et al. 2019, Lamont et al. 2020). In Idaho the most successful elk hunters selected the least roaded areas, where elk were more likely to occur (Gratson and Whitman 2000*a*).

Predicted use by successful rifle deer hunters peaked at about 20% slope, equivalent to slopes used by mule deer at Starkey in spring through fall (Stewart et al. 2002, Ager et al. 2003). Second, the increasing use on steeper slopes by archers aligned with daytime movements of elk toward steeper slopes during Starkey archery hunts (Ager et al. 2003) and selection by elk of moderate slopes in archery hunts in Colorado (Ranglack et al. 2017). Last, predicted use by successful rifle deer hunters remained high at low levels of cover, mirroring findings of Ager et al. (2003) that mule deer in Starkey selected areas with lower canopy cover during daytime hours.

Hunter Space Use and Roads

Models of space use revealed strong links of most Starkey hunters, especially rifle deer hunters, with open roads during shooting hours, a behavior well-documented for elk (Lyon and Burcham 1998, Gratson and Whitman 2000*b*, Lamont et al. 2020) and white-tailed deer (Stedman et al. 2004) hunters. In Pennsylvania, nearly 90% of deer hunters remained within 0.5 km of a road (Diefenbach et al. 2005). We observed very limited use by hunters in the northern third of Starkey, where motorized vehicle access was most restricted, and spatial overlap between successful and unsuccessful hunters, especially rifle deer, often occurred along roads and ATV trails. The relatively high use ratios in the 0–50-m category for open roads (>1.4 for 5 of 6 hunter groups) likely reflect traveling along roads to hunt or scout for prey, rather than actively hunting. Motorized routes serve as a primary access point by hunters, and can even constrain hunter movements (Plante et al. 2017). Consistent with the concept of human hunters as central place foragers (Rosenberg and McKelvey 1999, Papworth et al. 2012), roads may function as a central place anchoring hunter movements. This concept can be further extended by considering hunter behavior as representing multiple orders of selection (Johnson 1980), with hunters first choosing an access point along an open road (first-order selection) and then using their knowledge of prey behavior and habitat to guide their movements while actively hunting (second-order selection; Wszola et al. 2019). Collectively, our findings illustrate the importance of roads in hunter distributions across the landscape, as emphasized by Ranglack et al. (2017).

Despite strong published evidence about effects of roads on deer and elk distributions and vulnerability to harvest, stakeholders sometimes oppose policies that restrict access, leading to management challenges in meeting habitat and population objectives (Serenari et al. 2019). An evaluation of ODFW Travel Management Areas that incorporated road closures during mule deer hunts reported that deer remained even farther from open roads in the Travel Management Areas than adjacent areas and noted that road closures were difficult to enforce, especially when physical blockage is lacking (Curtis and Du Toit 2017). Rodgers et al. (2020) suggested limiting motorized use on summer and migratory ranges for mule deer in Wyoming, USA, to reduce effects of hunting disturbance. Balancing hunter opportunity with herd objectives, especially considering declining mule deer populations in Oregon (Coe et al. 2015) and elsewhere (Unsworth et al. 1999) remains a challenge for land and wildlife managers.

Model Performance, Limits of Inference, and Future Research

Both forms of evaluation suggested that our RUF models performed well, bolstering their utility for managing hunters and landscapes in northeastern Oregon and beyond. The superior performance of unsuccessful hunter models in most comparisons may have stemmed from their larger sample size (i.e., hunter numbers) in nearly all year-hunt combinations. Likewise, the small number of successful archers likely factored into that model's lower performance. Hunter densities and success rates at Starkey resembled those in nearby WMUs, further lending support for application of our models.

Limitations of our study include the variable fix rate of hunter GPS units, resulting in our use of UDs created with BBMMs as a more coarse modeling method to characterize general space use, in contrast to more fine-scale estimates of use such as with resource selection functions. Missing fixes may be less of an issue under very frequent fix schedules if the subject's rate of movement between fixes suggests little divergence from the observed locations. For hunters in our study, however, the degree of divergence between fixes was unknown but likely high in some instances. Last, our small sample size for successful archers ($n = 5$) warrants caution for interpreting results from this group.

Future research that explicitly considers the role of ATVs in hunting, including their spatial interaction with deer and elk and influence on hunter success, would provide needed information about this increasingly dominant recreational activity. The paucity of research on attitudes and behavior of mule deer hunters points to the need for additional investigation of this important and large segment of the hunting population. Last, understanding landscape features influencing distributions of successful hunters has implications for meeting harvest objectives and vulnerability of animals to harvest; likewise, knowing where the more ubiquitous unsuccessful hunters concentrate their use can advance knowledge of their spatial and temporal influence on prey distributions and ramifications such as foregone foraging opportunities (DeVoe et al. 2019, Brown et al. 2020). Studies like ours that investigate hunter behavior and landscape use will ultimately benefit hunters and land and wildlife agencies.

MANAGEMENT IMPLICATIONS

Knowledge of hunter space use, including core areas of use and across landscapes, has direct relevance for managing hunter opportunity and harvest for deer, elk, and other prey species. Our results suggest that strategic control of motorized access can either facilitate or reduce hunter access and use near open roads, depending on objectives. Closing roads can lessen hunter pressure given that open roads serve as conduits for hunters, while simultaneously facilitating success of hunters choosing non-motorized travel on closed roads, such as rifle elk hunters in our study. Such closures may also lower success rates of mule deer hunters; overharvest of mule deer poses a special management challenge when open road density is high and mule deer populations are declining or below population objectives. Spatial separation of successful hunters from their more numerous unsuccessful counterparts results from myriad nuanced differences in environmental conditions and could be accounted for in hunting season designs. Future efforts should investigate cumulative distributions of archery and rifle hunters across the entire hunting season, which in Oregon spans late August through mid-November, to fully account for effects on deer and elk and the contrasting space use of archery versus rifle hunters. Integrated management of forest cover in tandem with roads and trails open to motorized use can promote hunter opportunity while maintaining herd numbers and composition at desired levels. Moreover, our methods contrasting how successful versus unsuccessful hunters navigate landscapes, and space-use overlap between these groups, can be applied to other hunt types, including for other large ungulate species or small game.

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LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076–1088.

Andersen, O., H. K. Wam, A. Mysterud, and B. P. Kaltenborn. 2014. Applying typology analyses to management issues: deer harvest and declining hunter numbers. Journal of Wildlife Management 78: 1282–1292.

Apollonio, M., V. V. Belkin, J. Borkowski, O. I. Borodin, T. Borowik, F. Cagnacci, A. A. Danilkin, P. I. Danilov, A. Faybich, F. Ferretti, et al. 2017. Challenges and science-based implications for modern management and conservation of European ungulate populations. Mammal Research 62:209–217.

Barker, K. J., M. S. Mitchell, K. M. Proffitt, and J. D. DeVoe. 2019. Land management alters traditional nutritional benefits of migration for elk. Journal of Wildlife Management 83:167–174.

Bengston, D. N., and D. P. Fan. 1999. Roads on the U.S. National Forests: an analysis of public attitudes, beliefs, and values expressed in the news media. Environment and Behavior 31:514–539.

Benkobi, L., M. A. Rumble, G. C. Brundige, and J. J. Millspaugh. 2004. Refinement of the Arc-Habcap Model to predict habitat effectiveness for elk. U.S. Forest Service, Rocky Mountain Research Station, Research Paper RP-51, Fort Collins, Colorado, USA.

Benson, J. F., and B. R. Patterson. 2015. Spatial overlap, proximity, and habitat use of individual wolves within the same packs. Wildlife Society Bulletin 39:31–40.

Bhandari, P., R. C. Stedman, A. E. Luloff, J. C. Finley, and D. R. Diefenbach. 2006. Effort versus motivation: factors affecting antlered and antlerless deer harvest success in Pennsylvania. Human Dimensions of Wildlife 11:423–436.

Bolon, N. A. 1994. Estimates of the values of elk in the Blue Mountains of Oregon and Washington: evidence from the existing literature. U.S. Forest Service, Pacific Northwest Research Station, PNW-GTR-316, Portland, Oregon, USA.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157: 281–300.

Brown, C. L., J. B. Smith, M. J. Wisdom, M. M. Rowland, D. B. Spitz, and D. A. Clark. 2020. Evaluating indirect effects of hunting on mule deer spatial behavior. Journal of Wildlife Management 84:1246–1255.

Bryant, L. D., J. W. Thomas, B. K. Johnson, and J. H. Noyes. 1991. Hunter and Rocky Mountain elk (*Cervus elaphus nelsoni*) interactions in the Starkey Experimental Forest and Range. Pages 168–173 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of elk vulnerability—a symposium. Montana State University, Bozeman, USA.

Burnham, K. P., and D. R. Anderson. 2004. Multi-model inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Cerveny, L. K., D. J. Blahna, M. J. Stern, M. J. Mortimer, S. A. Predmore, and J. Freeman. 2011. The use of recreation planning tools in U.S. Forest Service NEPA Assessments. Environmental Management 48:644–657.

Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Coe, P. K., B. K. Johnson, M. J. Wisdom, J. G. Cook, M. Vavra, and R. M. Nielson. 2011. Validation of elk resource selection models with spatially independent data. Journal of Wildlife Management 75:159–170.

Coe, P. K., R. M. Nielson, D. H. Jackson, J. B. Cupples, N. E. Seidel, B. K. Johnson, S. C. Gregory, G. A. Bjornstrom, A. N. Larkins, and D. A. Speten. 2015. Identifying migration corridors of mule deer threatened by highway development. Wildlife Society Bulletin 39:256–267.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926–940.

Cordell, H. K. 2012. Outdoor recreation trends and futures: a technical document supporting the Forest Service 2010 RPA Assessment. U.S. Forest Service, Southern Research Station, General Technical Report SRS-150, Asheville, North Carolina, USA.

Curtis, A. M., and J. T. Du Toit. 2017. Efficacy of travel management areas for reducing disturbance to mule deer during hunting seasons. Wildlife Society Bulletin 41:309–312.

Davidson, G. A., B. K. Johnson, J. H. Noyes, B. L. Dick, and M. J. Wisdom. 2012. Effect of archer density on elk pregnancy rates and conception dates. Journal of Wildlife Management 76:1676–1685.

Decker, D. J., and N. A. Connelly. 1989. Motivations for deer hunting: implications for antlerless deer harvest as a management tool. Wildlife Society Bulletin 17:455–463.

DeVoe, J. D., K. M. Proffitt, M. S. Mitchell, C. S. Jourdonnais, and K. J. Barker. 2019. Elk forage and risk tradeoffs during the fall archery season. Journal of Wildlife Management 83:801–816.

Diefenbach, D. R., J. C. Finley, A. E. Luloff, R. Stedman, C. B. Swope, H. C. Zinn, and G. J. San Julian. 2005. Bear and deer hunter density and distribution on public land in Pennsylvania. Human Dimensions of Wildlife 10:201–212.

Diekert, F. K., A. Richter, I. M. Rivrud, and A. Mysterud. 2016. How constraints affect the hunters decision to shoot a deer. Proceedings of the National Academy of Sciences 113:14450–14455.

Eckrich, C. A., P. K. Coe, D. A. Clark, R. M. Nielson, J. Lombardi, S. C. Gregory, M. J. Hedrick, B. K. Johnson, and D. H. Jackson. 2020. Summer habitat use of female mule deer in Oregon. Journal of Wildlife Management 84:576–587.

Ferrari, S., and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31:799–815.

Festa-Bianchet, M., M. Douhard, J.-M. Gaillard, and F. Pelletier. 2017. Successes and challenges of long-term field studies of marked ungulates. Journal of Mammalogy 98:612–620.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. Journal of Wildlife Management 69:1346–1359.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.

Gerrits, A. P., P. H. Wightman, J. R. Cantrell, C. Ruth, M. J. Chamberlain, and B. A. Collier. 2020. Movement ecology of spring wild turkey hunters on public lands in South Carolina, USA. Wildlife Society Bulletin 44:260–270.

Good, P. I., and J. W. Hardin. 2009. Common errors in statistics (and how to avoid them). Wiley-Interscience, Hoboken, New Jersey, USA.

Gratson, M. W., and C. L. Whitman. 2000*a*. Characteristics of Idaho elk hunters relative to road access on public lands. Wildlife Society Bulletin 28:1016–1022.

Gratson, M. W., and C. L. Whitman. 2000*b*. Road closures and density and success of elk hunters in Idaho. Wildlife Society Bulletin 28:302–310.

Hamilton, M. J., B. T. Milne, R. S. Walker, and J. H. Brown. 2007. Nonlinear scaling of space use in human hunter–gatherers. Proceedings of the National Academy of Sciences 104:4765–4769.

Harper, C. A., C. E. Shaw, J. M. Fly, and J. T. Beaver. 2012. Attitudes and motivations of Tennessee deer hunters toward quality deer management. Wildlife Society Bulletin 36:277–285.

Havlick, D. 2002. No place distant: roads and motorized recreation on America's public lands. Island Press, Washington, D.C., USA.

Hebblewhite, M., M. Percy, and E. H. Merrill. 2007. Are all Global Positioning System collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. Journal of Wildlife Management 71:2026–2033.

Heurich, M., K. Zeis, H. Küchenhoff, J. Müller, E. Belotti, L. Bufka, and B. Woelfing. 2016. Selective predation of a stalking predator on ungulate prey. PLoS One 11:e0158449.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2002. Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. Holocene 12:597–604.

Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Alldredge. 2013. Reconciling resource utilization and resource selection functions. Journal of Animal Ecology 82:1146–1154.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Johnson, B. K., A. A. Ager, J. H. Noyes, and N. Cimon. 2005. Elk and mule deer responses to variation in hunting pressure. Pages 127–138 *in* M. J. Wisdom, editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Alliance Communications Group, Lawrence, Kansas, USA.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kardos, M., G. Luikart, and F. W. Allendorf. 2018. Predicting the evolutionary effects of hunting requires an understanding of genetics. Journal of Wildlife Management 82:889–891.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Elsevier, New York, New York, USA.

Lamont, B. G., M. J. Kauffman, J. A. Merkle, T. W. Mong, M. M. Hayes, and K. L. Monteith. 2020. Bark beetle-affected forests provide elk only a marginal refuge from hunters. Journal of Wildlife Management 84:413–424.

Lebel, F., C. Dussault, A. Massé, and S. D. Côté. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. Journal of Wildlife Management 76:1431–1440.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.
Lyon, L. J., and M. G. Burcham. 1998. Tracking elk hunters with the Global Positioning System. U.S. Forest Service, Rocky Mountain Research Station, Research Paper RMRS-RP-3, Ogden, Utah, USA.
Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411–1427.
McCulloch, C. E., S. R. Searle, and J. M. Neuhasu. 2008. Generalized, linear, and mixed models. Second edition. Wiley-Interscience, Hoboken, New Jersey, USA.
Meisingset, E. L., L. E. Loe, Ø. Brekkum, B. Van Moorter, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181–191.
Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994–1003.
Millspaugh, J. J., R. A. Gitzen, B. J. Kernohan, M. A. Larson, and C. L. Clay. 2004. Comparability of three analytical techniques to assess joint space use. Wildlife Society Bulletin 32:148–157.
Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.
Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2013. Variation in elk response to roads by season, sex, and road type. Journal of Wildlife Management 77:313–325.
Neumann, W., and G. Ericsson. 2018. Influence of hunting on movements of moose near roads. Journal of Wildlife Management 82: 918–928.
Nielson, R. M., B. F. Manly, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. Ecology 90:2956–2962.
Nielson, R. M., H. Sawyer, and T. L. McDonald. 2013. BBMM—Brownian bridge movement model. R Foundation for Statistical Computing, Vienna, Austria.
O'Brien, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality & Quantity 41:673–690.
Oregon Department of Fish and Wildlife [ODFW]. 2019. Summary report: Oregon deer and elk hunters' attitudes toward big game management and hunting opportunities. ODFW, Salem, USA.
Papworth, S. K., N. Bunnefeld, K. Slocombe, and E. J. Milner-Gulland. 2012. Movement ecology of human resource users: using net squared displacement, biased random bridges and resource utilization functions to quantify hunter and gatherer behaviour. Methods in Ecology and Evolution 3:584–594.
Pauli, B. P., E. R. Sun, Z. K. Tinkle, J. S. Forbey, K. E. Demps, and J. A. Heath. 2019. Human habitat selection: using tools from wildlife ecology to predict recreation in natural landscapes. Natural Areas Journal 39:142–149.
Pereira, G. H. A. 2019. On quantile residuals in beta regression. Communications in Statistics—Simulation and Computation 48:302–316.
Plante, S., C. Dussault, and S. D. Côté. 2017. Landscape attributes explain migratory caribou vulnerability to sport hunting. Journal of Wildlife Management 81:238–247.
Proffitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdonnais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. Journal of Wildlife Management 74:210–218.
Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology 52:137–154.
R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Ranglack, D. H., K. M. Proffitt, J. E. Canfield, J. A. Gude, J. Rotella, and R. A. Garrott. 2017. Security areas for elk during archery and rifle hunting seasons. Journal of Wildlife Management 81: 778–791.
Robert, K., D. Garant, and F. Pelletier. 2012. Keep in touch: does spatial overlap correlate with contact rate frequency? Journal of Wildlife Management 76:1670–1675.
Roberts, D. R., V. Bahn, S. Ciuti, M. S. Boyce, J. Elith, G. Guillera-Arroita, S. Hauenstein, J. J. Lahoz-Monfort, B. Schröder, and W. Thuiller. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929.
Rodgers, P. A., H. Sawyer, T. W. Mong, S. Stephens, and M. J. Kauffman. 2020. Sex-specific behaviors of hunted mule deer during rifle season. Journal of Wildlife Management 85:215–227.
Rosenberg, D. K., and K. S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63:1028–1038.
Rowland, M. M., L. D. Bryant, B. K. Johnson, J. H. Noyes, M. J. Wisdom, and J. W. Thomas. 1997. The Starkey Project: history, facilities, and data collection methods for ungulate research. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-396, Portland, Oregon, USA.
Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.
Rowland, M. M., M. J. Wisdom, B. K. Johnson, and M. A. Penninger. 2005. Effects of roads on elk: implications for management in forested ecosystems. Pages 42–52 *in* M. J. Wisdom, editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Alliance Communications, Lawrence, Kansas, USA.
Rowland, M. M., M. J. Wisdom, R. M. Nielson, J. G. Cook, R. C. Cook, B. K. Johnson, P. K. Coe, J. M. Hafer, B. J. Naylor, D. J. Vales, et al. 2018. Modeling elk nutrition and habitat use in Western Oregon and Washington. Wildlife Monographs 199:1–102.
Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.
Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319:952–954.
Serenari, C., J. Shaw, R. Myers, and D. T. Cobb. 2019. Explaining deer hunter preferences for regulatory changes using choice experiments. Journal of Wildlife Management 83:446–456.
Singer, F. J., and L. C. Zeigenfuss. 2002. Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep. Journal of Mammalogy 83:682–698.
Smith, D., and M. Yuan. 1991. Modeling the effects of hunter caused elk mortality. Pages 204–208 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of elk vulnerability—a symposium. Montana State University, Bozeman, USA.
Spitz, D. B., M. M. Rowland, D. A. Clark, M. J. Wisdom, J. B. Smith, C. L. Brown, and T. Levi. 2019. Behavioral changes and nutritional consequences to elk (*Cervus canadensis*) avoiding perceived risk from human hunters. Ecosphere 10:e02864.
Stedman, R., D. R. Diefenbach, C. B. Swope, J. C. Finley, A. E. Luloff, H. C. Zinn, G. J. S. Julian, and G. A. Wang. 2004. Integrating wildlife and human-dimensions research methods to study hunters. Journal of Wildlife Management 68:762–773.
Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.
Stine, R. A. 1995. Graphical interpretation of variance inflation factors. American Statistician 49:53–56.
Thomas, J. W., J. D. Gill, J. C. Pack, W. M. Healy, and H. R. Sanderson. 1976. Influence of forestland characteristics on spatial distribution of hunters. Journal of Wildlife Management 40:500–506.
Thomas, J. W., J. C. Pack, W. M. Healy, J. D. Gill, and H. R. Sanderson. 1973. Territoriality among hunters: the policy implications. Transactions of the North American Wildlife and Natural Resources Conference 38:274–280.
Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. Journal of Wildlife Management 57:495–502.
Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.
Vieira, M. E. P., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management 67:717–728.

Visscher, D. R., I. Macleod, K. Vujnovic, D. Vujnovic, and P. D. Dewitt. 2017. Human risk induced behavioral shifts in refuge use by elk in an agricultural matrix. Wildlife Society Bulletin 41:162–169.

Ward, K. J., R. C. Stedman, A. E. Luloff, J. S. Shortle, and J. C. Finley. 2008. Categorizing deer hunters by typologies useful to game managers: a latent-class model. Society & Natural Resources 21:215–229.

Wattles, D. W., K. A. Zeller, and S. DeStefano. 2018. Response of moose to a high-density road network. Journal of Wildlife Management 82:929–939.

Wertz, T. L., A. Blumton, L. E. Erickson, L. M. Kemp, T. Thomas, and K. E. Evans. 1996. Strategies to keep wildlife where you want them—do they work? Pages 70–72 *in* K. E. Evans, editor. Sharing common ground on western rangelands: Proceedings of a livestock/big game symposium. U.S. Forest Service, Intermountain Research Station, General Technical Report INT-GTR-343, Ogden, Utah, USA.

White, E., J. Bowker, A. E. Askew, L. L. Langner, J. R. Arnold, and D. B. English. 2016. Federal outdoor recreation trends: effects on economic opportunities. U.S. Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-945, Portland, Oregon, USA.

Wilson, R. R., M. B. Hooten, B. N. Strobel, and J. A. Shivik. 2010. Accounting for individuals, uncertainty, and multiscale clustering in core area estimation. Journal of Wildlife Management 74:1343–1352.

Wisdom, M. J. 2005. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Alliance Communications Group, Lawrence, Kansas, USA.

Wisdom, M. J., N. J. Cimon, B. K. Johnson, E. O. Garton, and J. W. Thomas. 2005. Spatial partitioning by mule deer and elk in relation to traffic. Pages 53–66 *in* M. J. Wisdom, editor. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Alliance Communications, Lawrence, Kansas, USA.

Wisdom, M. J., R. M. Nielson, M. M. Rowland, and K. M. Proffitt. 2020. Modeling landscape use for ungulates: forgotten tenets of ecology, management, and inference. Frontiers in Ecology and Evolution 8:1–19.

Wszola, L. S., E. F. Stuber, C. J. Chizinski, J. J. Lusk, and J. J. Fontaine. 2019. Prey availability and accessibility drive hunter movement. Wildlife Biology 2019:1–9.

Yen, S.-C., Y. Wang, P.-H. Yu, Y.-P. Kuan, Y.-C. Liao, K.-H. Chen, and G.-J. Weng. 2019. Seasonal space use and habitat selection of sambar in Taiwan. Journal of Wildlife Management 83:22–31.

Yuan, M., D. Smith, and P. Zager. 1991. Examining the components of the elk hunter model: the relationship between successful and unsuccessful hunters. Pages 209–217 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of elk vulnerability—a symposium. Montana State University, Bozeman, USA.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A: HUNTER OVERLAP INDICES

Table A1. Yearly summary metrics and overlap indices of successful and unsuccessful hunters using core areas (i.e., 50% contours of yearly mean utilization distributions) to characterize patterns of space-use sharing by archery (elk) and rifle (mule deer and elk) hunters in Starkey Experimental Forest and Range, northeastern Oregon, USA, 2008–2013. Combined core areas represent the union of core areas for unsuccessful and successful hunters.

Hunt type	Year	Combined core area (ha)	Core area overlap (ha)	$PHR_{1,0}$[a]	$PHR_{0,1}$[b]	UDOI[c]
Archery elk	2009[d]	863.91	31.86	0.04	0.41	0.50
	2010	350.64	NA	NA	NA	NA
	2011	660.42	26.46	0.04	0.26	0.49
Rifle deer	2008	1,190.07	109.08	0.15	0.32	0.64
	2009	966.69	85.59	0.26	0.24	1.11
	2011	1,243.44	225.99	0.22	0.52	0.78
	2012	916.92	54.72	0.13	0.15	0.34
	2013	1,423.53	163.53	0.35	0.15	0.49
Rifle elk	2008	575.73	12.6	0.04	0.04	0.06
	2009	1,211.31	11.16	0.01	0.10	0.14
	2010	1,044.72	121.14	0.14	0.33	0.50
	2011	1,398.6	91.62	0.08	0.37	0.50
	2012	882.27	22.05	0.03	0.10	0.17
	2013	767.16	105.93	0.21	0.55	1.08

[a] PHR = probability of home range overlap. Values in this column indicate the probability of an unsuccessful hunter (0) being in the core area of a successful hunter (1), given that the unsuccessful hunter is already in their own core.
[b] Probability of a successful hunter (1) being in the core area of an unsuccessful hunter (0), given that the successful hunter is already in their own core.
[c] Utilization distribution overlap index. Values typically range from 0 to 1 but can exceed 1 if the 2 utilization distributions are non-uniformly distributed but have a high degree of overlap.
[d] Some year-hunt combinations are not reported because data were missing from ≥1 group to calculate space-use sharing metrics (e.g., there were no successful archery elk hunters in 2008). For archery hunters in 2010, core areas did not overlap and thus overlap indices could not be calculated (NA = not applicable).