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ARTICLE

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Density-dependent changes in elk resource selection over successional time scales following forest disturbance

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Abstract

There is an increasing need to understand how animals respond to modifications of their habitat following landscape-scale disturbances such as wildfire or timber harvest. Such disturbances can promote increased use by herbivores due to changes in plant community structure that improve forage conditions, but can also cause avoidance if other habitat functions provided by cover are substantially reduced or eliminated. Quantifying the total effects of these disturbances, however, is challenging because they may not fully be apparent unless observed at successional timescales. Further, the effects of disturbances that improve habitat quality may be density dependent, such that the benefits are (1) less valuable to high-density populations because the per-capita benefits are reduced when shared among more users or, alternatively, (2) more valuable to animals living in high densities because resources may be more depleted from the greater intraspecific competition. We used 30 years of telemetry data on elk occurring at two distinct population densities to quantify changes in space use at diel, monthly, and successional timescales following timber harvest. Elk selected logged areas at night only, with selection strongest during midsummer, and peak selection occurring 14 years post harvest, but persisting for 26–33 years. This pattern of increased selection at night following a reduction in overhead canopy cover is consistent with elk exploiting improved nutritional conditions for foraging. The magnitude of selection for logged areas was 73% higher for elk at low population density, consistent with predictions from the ideal free distribution. Yet elk avoided these same areas during daytime for up to 28 years post logging and instead selected untreated forest, suggesting a role for cover to meet other life history requirements. Our results demonstrate that while landscape-scale disturbances can lead to increased selection by large herbivores and suggest that the improvement in foraging conditions can persist over short-term successional timescales, the magnitude of the benefits may not be equal across population densities. Further, the enduring avoidance of logging treatments during the daytime indicates a need for structurally intact forests and suggests that a mosaic of forest patches of varying successional stages and structural completeness is likely to be the most beneficial to large herbivores.

KEYWORDS
density dependence, forest management, ideal free distribution, large herbivore, logging, resource selection function, timber harvest, ungulate nutrition

INTRODUCTION

Understanding how animals respond to habitat modifications will be increasingly important in the Anthropocene given that more frequent natural and human-caused disturbances to landscapes are expected (Newman, 2019). The resulting habitat modifications from disturbances can have both positive and negative effects on wildlife, such that understanding the conditions that lead to increased versus decreased use of altered habitats will be key to informing conservation and management actions (Fisher & Burton, 2018). For example, land conversion often causes animals to either leave the disturbed areas entirely or remain in suboptimal habitats when emigration is not possible (Martínez-Abraín & Jiménez, 2016), both of which can have fitness consequences. Alternatively, landscape alterations causing successional changes to plant communities can have positive effects on primary consumers that prefer conditions associated with early seral stages (Hayes et al., 2022). This is often the case when disturbances reduce the overhead canopy cover in dense forests and stimulate the growth of understory vegetation, leading to increased biomass comprised of nutritious forage for large herbivores (Cook et al., 2016). Given that landscape disturbances have the potential to both positively and negatively influence wildlife over multidecadal time series, the total effects must therefore be considered wherein the costs and benefits perceived by animals can be proxied by disproportionately low or high use of the altered areas compared with baseline conditions.

A challenge in assessing the response of wildlife to disturbance is that resource selection by animals is confounded by the density-dependent nature of habitat selection (Avgar et al., 2020; Mobæk et al., 2009; van Beest et al., 2014). That is, density-dependent habitat selection theory and the ideal free distribution predict that, as population density increases (expected if habitat quality improves), per-capita use of higher quality habitat declines concomitant with an increase in the use of lower quality resources (Fretwell & Lucas, 1969; Morris, 2003). This occurs because the per-capita value of high-quality habitats is less when shared by more consumers, therefore beyond some threshold of competitor density, lower quality habitats with fewer competitors become more profitable and disincentivize the use of the highest quality habitats (Morris, 2003). This leads to a general pattern in which it is optimal to be a specialist in high-quality habitats at low population densities, but a habitat generalist at high population densities (Fortin et al., 2008). Alternatively, if animals living at high densities experience a scarcity of forage due to high intraspecific competition (as expected in a high-density population), landscape changes that stimulate forage growth may be more valuable than for low-density populations.

Although previous research has shown that landscape-scale habitat disturbances can create high-quality habitat patches that animals select disproportionately (Oeser et al., 2021; Spitz et al., 2018), the influence of population density is seldom considered. Because there are contrasting mechanisms by which population density can affect the selection of habitat treatments (i.e., utilization by more animals could more quickly erode the value of habitat treatments, but could also be more valuable to high-density populations with depleted resources), failing to quantify the effects of population density on the magnitude and duration of increased selection of habitat treatments reduces our understanding of the potential benefits that disturbances may have. The magnitude of nutritional benefits to animals arising from disturbance may also depend on the size of the disturbed area relative to population density. For example, a disturbance of a given size may produce sufficient biomass of nutritious forage for a small population, but may not be enough to sustain a large population.

Anthropogenic disturbances such as timber harvest and prescribed burning that reset forest stands to early seral conditions can confer nutritional benefits to large herbivores and are often used by wildlife managers to improve habitats. This is particularly true in areas where historical fire suppression has caused forest canopies to become enclosed, reducing the mosaic of forested versus nonforested habitats in which many species thrive. A reduction in overhead canopy cover through such management interventions increases forage biomass (Irwin & Peek, 1979) as well as forage quality, as the plant community transitions from shade-tolerant to shade-intolerant species that are typically associated with higher digestible energy when consumed by large herbivores (Cook et al., 2016; Rowland et al., 2018). For example, logging in temperate forests in the western USA was associated with an increase in the dietary-digestible energy available to elk (*Cervus canadensis*) that remained high for 1–4 decades depending on forest type (Cook et al., 2016). In harvested lodgepole pine stands in Alberta, forage biomass peaked at ~9 years after logging,

but palatable browse species remained dominant to unpalatable species for ~30 years (Visscher & Merrill, 2009). In northwestern Washington, the biomass of the most nutritious forage for deer (*Odocoileus hemionus* and *Odocoileus virginianus*) increased for ~14 years post harvest (Hull et al., 2020). Additional disturbance through the application of prescribed fire following canopy reduction can further improve the availability of plant species that are nutritious to large herbivores and beyond what can be achieved by timber harvest alone (Franklin & Dyrness, 1973).

While a substantial body of literature indicates many ungulate species disproportionately use areas in which overhead canopy cover has been reduced through logging and/or burning ostensibly due to the nutritional benefits (Churchill, 1982; Spitz et al., 2018; Stewart et al., 2002), studies have generally been hampered by short time series of animal location data from which to draw inference on the duration of increased use, and without an assessment of how or whether the selection of disturbed areas is mediated by animal population density. More convincing research would therefore measure animal resource selection both before habitat manipulations have occurred and at successional timescales following the disturbance, and measure the response of animal selection at different population densities. Studies should further assess the response of large herbivores to forest treatments in contrast with areas left untreated, and examine the potential avoidance of treated areas during nonfeeding hours, given the need for structurally complex habitats for other requirements including safety cover and thermoregulation (Churchill, 1982; Hebblewhite et al., 2009; Spitz et al., 2018). In particular, in heat-sensitive species the use of disturbed areas may come at a greater cost of thermoregulation, because reduced overhead canopy cover increases solar radiation and prevents heat dissipation (Verzuh et al., 2023). This may cause ungulates to forage in open-canopy disturbances only during the nighttime hours during the summer months to avoid heat stress (Lamont et al., 2019). Further, although larger disturbances may lead to overall greater biomass of nutritious forage, forest-dwelling species may be less willing to use areas that are far from forest cover (Hammond, 1980); thus some intermediate size in forest openings may exist wherein forage acquisition and safety are optimized (Hammond, 1980; Thomas, 1979). Thus, much remains to be learned about how large herbivores respond to forest disturbances at diel, seasonal, and successional temporal scales, and whether this is mediated by population density, as well as how characteristics of disturbed landscapes such as their size and configuration influence the degree to which they are used.

We used a 30-year time series of telemetry locations of Rocky Mountain elk to elucidate the patterns of use in areas that had undergone intensive logging ($N = 27$ years) compared with pre-treatment conditions ($N = 3$ years). For the last 23 years of the study, the study area was divided into two zones in which elk were held at low or high density, allowing the influence of population density on resource selection to be quantified. Our objectives were to (1) use selection ratios (i.e., metrics describing whether a discrete resource is used more or less than its availability) and resource selection functions (RSFs) to clarify diel and (2) monthly patterns of selection for or against treated areas, (3) determine the duration of these effects, (4) assess whether the selection of treated areas was mediated by elk density, and (5) at the level of the harvest unit, determine whether prescribed burning or (6) the size of the treatment influenced the amount of use they received by elk. Because reductions in canopy cover associated with logging increase the quantity and quality of forage for elk (Cook et al., 2016), we hypothesized that elk would exhibit increased selection of areas that had undergone logging treatments and this would be (H1) stronger during the night than the day in summer months because of the need to avoid direct solar radiation that prevents heat dissipation (Ager et al., 2003; Lamont et al., 2019; Roberts et al., 2017; Verzuh et al., 2023); (H2) that the selection of logged areas would be strongest during midsummer when grasslands (the other available open habitat type in our study area) were senesced relative to early spring and late fall green-up periods (Skovlin, 1967); and (H3) that the selection of logging treatments would persist for at least 10–20 years, because forage biomass and digestible energy typically remain high for this duration or sometimes longer following logging (Cook et al., 2016). Further, consistent with the ideal free distribution, we hypothesized (H4) that the areas of treated forest would not be enough to sustain all individuals in the high-density elk population and that some individuals would, instead, be forced to utilize other vegetation types. Consequently, we predicted that individual selection of treated forest would be more variable in elk at high densities relative to elk at low densities, and that overall, the high-density population would exhibit lower selection of treated forest than elk at low densities. Alternatively, we hypothesized ($H4_A$) that, due to resource depletion caused by high intraspecific competition in the high-density elk population, habitat improvements would provide more value to elk at high densities, and that the selection of treated forest would thus be greater for elk at high densities than low densities. Finally, when considering the use of individual patches of harvested forest, we hypothesized (H5) that elk would utilize those that were burned more than those left unburned, because post-logging burning has the

potential to increase forage quantity and quality beyond that achieved through logging alone (Cook et al., 2016; Franklin & Dyrness, 1973), and (H6) that harvest units of intermediate size would be most favored by elk because small patches would not provide as much biomass as larger ones (Hammond, 1980), but that the largest patches would not offer elk access to hiding cover, thereby disincentivizing use (Hammond, 1980; Thomas, 1979). Our results provide insight into the degree and duration of space use by ungulates following timber harvest and similar disturbances that establish open-canopy forests that typically result in substantial increases in forage biomass and quality (Cook et al., 2016) and elk selection (Cook et al., 2018; Rowland et al., 2018). The 30-year time series, study design with pre-treatment and post-treatment data, consideration of both treated and untreated stands, and the assessment of density-dependent responses allowed us to achieve robust insight into how a large herbivore responds to disturbance over successional time scales.

METHODS

Study area

Our study took place in the Syrup Creek study area within the Starkey Experimental Forest and Range (Starkey) in the Blue Mountains of northeastern Oregon, USA (Figure 1). The study area was composed largely of dry mixed-conifer forests dominated by Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and ponderosa pine (*Pinus ponderosa*) interspersed by thin-soiled grasslands. Between 1989 and 1997, elk in the Syrup Creek study area were allowed to roam freely within the 14.5 km^2 study area, enclosed by a 2.4 m ungulate-proof fence and separated from the rest of the Starkey. However, in 1997 an additional 2.4 m fence was erected to divide the Syrup Creek study area into two zones (Rowland, 1997), the western zone in which elk were held at low densities ($\bar{x} = 2.9$, standard deviation [SD] = 0.4 adult females/km^2 between 1998 and 2020), and the eastern zone in which elk were held at high

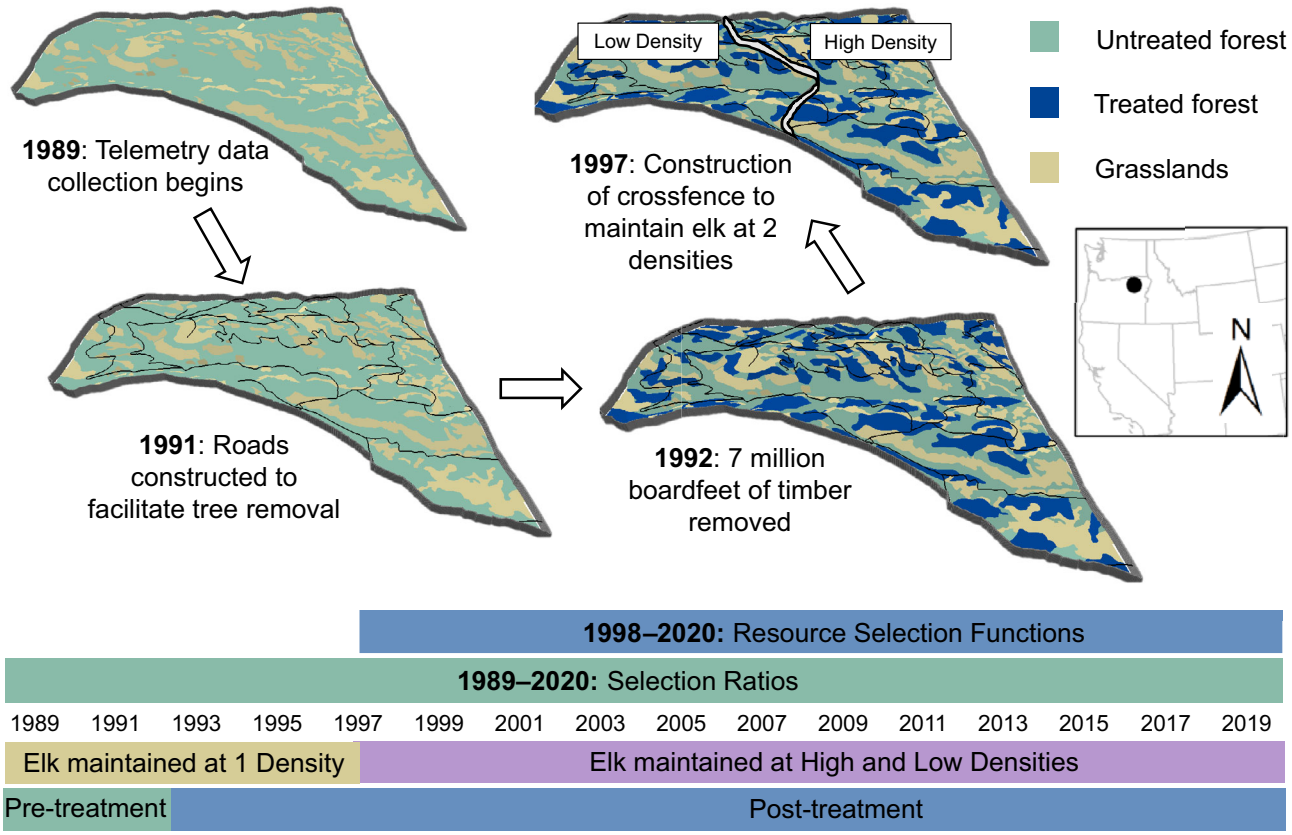

FIGURE 1 Schematic and timeline of the study area in northeastern Oregon, USA. Telemetry data collection began in 1989, roads were constructed in 1991, and logging occurred in 1992. In 1997 a fence was constructed to maintain elk at two contrasting densities. The study concluded in 2020. We analyzed elk telemetry data using selection ratios for the entire time series (1989–2020) and with resource selection functions only during the time in which elk were maintained at two densities (1998–2020).

densities ($\bar{x} = 7.9$, SD = 1.4 adult females/km^2 between 1998 and 2020). Relatively constant elk densities could be maintained because each fall (typically November), elk in Starkey are baited with alfalfa into a winter feeding area (where they are counted, individual data are collected, telemetry collars are attached, etc.) and their subsequent release (typically in April) to the summer study areas is regulated (Rowland, 1997). Public entry to the Syrup Creek study area was prohibited, except for controlled hunts that occurred in the fall between 1989 and 1996, and during a recreation study that occurred for 2 weeks each year between 2002 and 2004. At all other times, roads were open to administrative use only and received only light traffic.

Between November 1991 and the end of 1992, ~7 million board feet of timber was removed through logging within the Syrup Creek study area through a salvage sale that focused on the removal of grand fir and Douglas fir killed by drought and insects (Wisdom et al., 2004). Logging occurred in 63 harvest units, ranging in size from 0.012 to 0.22 km^2 and encompassing 4.9 km^2 total, which was roughly half of the forested areas in the study area. Even-aged regeneration harvest that removed >90% of the overstory trees was the silvicultural prescription applied to 60 of the 63 harvest units (Figure 1). Overstory trees were >16 inches in diameter at breast height, and their harvest resulted in an overstory canopy cover of <10%. Commercial thinning was applied to the other three units, resulting in an overstory canopy cover of <30%. Overall, 40% of the harvest units were treated with prescribed burns in 1993, the year following tree removal. The remaining forested areas were left intact to provide cover for elk and to serve as a baseline from which the effect of timber harvest on elk could be measured. Throughout, we refer to forested areas that were logged (and possibly burned) as treated forest, and forested areas that were neither logged nor burned as untreated forest. Because the experiment was designed to measure the response of ungulates to timber harvest, the harvest units were dispersed throughout the area in which elk were confined, and ungulate-proof fencing prevented elk from leaving the area where logging occurred (Wisdom et al., 2004). Apart from treated and untreated forests (together representing all forested areas in the study area), thin-soiled grasslands represented the only remaining land cover type occurring in significant quantities. Thus, we classified all areas within the study area into one of three landcover types: treated forest, untreated forest, or grassland.

Telemetry data

We used telemetry data from 187 adult female elk, representing 414 animal years. Between 1989 and 2005, elk were fitted with collars that collected data using a rebroadcast civilian long-range navigation system (LORAN-C) that was automated to relocate animals using triangulation based on a series of fixed radio tower beacons (Findholt et al., 1996). From 2003 to 2020, elk were equipped with Global Positioning System (GPS) collars. For both LORAN-C and GPS telemetry collars, we subset data to a consistent hourly schedule (Spitz et al., 2018) and only used locations between May and October each year. Telemetry data were censored from all analyses during periods in which public access was permitted in the study, for hunting during the autumn periods of 1989–1996 (Wisdom et al., 2004) or to implement treatment periods of a nonconsumptive recreation study during short intervals of spring through fall 2002–2004 (Preisler et al., 2013), because space use by elk could have been influenced by these human activities.

LORAN-C telemetry data have a higher positional error than modern GPS collars ($\bar{x} = 45$–51 m; Findholt et al., 1996). While positional error in LORAN-C and similar very high-frequency telemetry data typically does not bias inference in habitat selection studies involving spatially correlated continuous covariates (Findholt, 2002; Garton et al., 2001), our primary objective involved characterizing use versus availability of discrete landcover types. We were therefore concerned about the potential for imprecision of telemetry locations to influence the correct classification of used resource units within landcover types and, ultimately, inference on selection or avoidance of these areas. To assess this possibility, we conducted a simulation study to determine whether the misclassification of telemetry locations could lead to a biased inference of animal selection (Appendix S1). After adding positional error to simulated datasets commensurate to that known for LORAN-C collars in our study area, we determined that 24%–31% of the locations observed in patches of treated forest would be misclassified into other landcover types (Appendix S1: Table S1). However, our simulations demonstrated that this level of misclassification led to an underestimation of the strength of selection or avoidance (i.e., it shrunk selection ratios or coefficients toward 1) but, importantly, it did not bias inference in the opposite direction (Appendix S1: Figure S1). This means that for our results that solely used LORAN-C data (1989–2002), the true selection or avoidance of a landcover type was stronger than that observed, as positional error obscured some of the true signals. Thus, our results using data from this period should be considered conservative due to the presence of type II errors.

Selection ratios

We first calculated selection ratios to investigate patterns of use of treated forest, untreated forest, and grasslands.

Selection ratios, $s(i)$, determine whether a discrete landcover type i is used more ($s(i) > 1$), less ($s(i) < 1$), or equal ($s(i) = 1$) to its availability, and are defined as

$$s(i) = \frac{\%\,\text{use}_i}{\%\,\text{available}_i},$$

where $\%\,\text{use}_i$ refers to the percent of telemetry locations falling in landcover type i and $\%\,\text{available}_i$ refers to the percentage of the total landscape covered by landcover type i (Manly et al., 2002).

We constructed a series of selection ratios to elucidate patterns at diel, monthly, and successional timescales. Following Spitz et al. (2018) who found that using crepuscular time periods obscured elk selection of burned areas in an adjacent study area, yet found marked differences between day and night, we first combined data from both high-density and low-density elk populations across all years to calculate selection ratios at a diel scale to test circadian patterns of selection. We then constructed selection ratios on monthly and annual timescales. Finally, we constructed selection ratios using data from all months and years following the construction of the cross-fence separating the study area into high-density and low-density elk zones to assess overall differences in selection of grasslands, treated forest, and untreated forest based on elk density (Figure 1). For all selection ratio analyses, we considered the entire area in which elk were enclosed to be available to elk, therefore selection ratios for treated forest were given with respect to all other landcover types. We calculated selection ratios by telemetered individuals that were then averaged using a weighted mean (weighted by the number of telemetry locations corresponding to that individual in the given time period) to estimate population-level responses (Spitz et al., 2018).

Resource selection functions

Because selection ratios are univariate analyses and appropriate for discrete landcover types only (Manly et al., 2002), we additionally constructed RSFs to control for other covariates and to formally assess how the selection of treated and untreated forest changed over time, and also how this varied between the high-density and low-density elk populations. Due to different domains of availability between the high-density and low-density elk populations (i.e., available resource units in the high-density population were not available to elk in the low-density population, and vice versa), we opted to fit separate models for each population. We considered both the linear and quadratic effects of the time since the treatment occurred (hereafter, Time) and compared models using AIC (Burnham & Anderson, 2002). Our RSFs with a linear effect of Time took the form:

$$w(x) = \exp(\beta_1 \times \text{Treatment} + \beta_2 \times \text{Time} + \beta_3 \times \text{Treatment} \times \text{Time} + \boldsymbol{\beta} \times \boldsymbol{X}),$$

while models with a quadratic formulation of Time took the form:

$$w(x) = \exp(\beta_1 \times \text{Treatment} + \beta_2 \times \text{Time} + \beta_3 \times \text{Time}^2 + \beta_4 \times \text{Treatment} \times \text{Time} + \beta_5 \times \text{Treatment} \times \text{Time}^2 + \boldsymbol{\beta} \times \boldsymbol{X}),$$

where $w(x)$ is the relative probability of selection by elk, Treatment is a binary variable indicating whether each pixel corresponded to the treated forest (1) or the untreated forest (0), Time refers to the number of years since the treatment occurred, and $\boldsymbol{X}$ is a vector of additional landscape covariates influencing elk probability of selection (described below). The interaction between Treatment and Time allowed us to interpret how the selection of treated forest differed as a function of time since the treatment occurred. A positive, linear effect of Time would suggest that the selection of treated areas had not yet peaked, whereas a negative, linear effect would indicate that selection was highest immediately following timber harvest and subsequently declined. Alternatively, a quadratic effect would suggest that the selection of treated forest peaked at an intermediate time period following timber harvest.

We fitted RSFs in a used-available design (Manly et al., 2002), using generalized linear mixed models with a logit link and a binomial error distribution in which used locations were coded 1 and available locations were coded 0. Available locations were generated randomly within the entire enclosure in which elk resided at a ratio of 1:1 for used versus available points. Because we were interested in both the individual-level and population-level responses of elk toward timber harvest, we pooled telemetry locations across individuals within each study area (high and low elk density) to fit RSFs and included a random intercept and random slope for the effect of Treatment for each elk-year. This structure allowed us to estimate a population-level effect for the selection of treated forest, but also allowed us to extract annual individual-level coefficients for the selection of treated forest. We tested for differences in the strength of selection of treated forests between high-density and low-density populations using a Z-test (Clogg et al., 1995), comparing the coefficient estimates of the fixed effect for treated forest by population. To quantify differences in individual-level variation in the selection of

treated forest between populations, we calculated the SD and coefficient of variation of individual selection coefficients from the random effect for treated forest for each population. During the years in which both GPS and LORAN-C collars were deployed in our study area (2003–2005), we also compared individual selection coefficients for the selection of treated forest at night between collar types to assess the potential differences arising from the greater imprecision in the LORAN-C collars.

We additionally controlled for other landscape variables that could influence resource selection based on findings from previous studies of elk resource selection in the area, including continuous variables measuring the cosine of aspect (a metric to identify north-facing slopes), distance to the nearest permanent water source (natural log-transformed), distance to nearest road open to administrative use (natural log-transformed), and a binary variable classifying each pixel as grassland (1) or not (0). Continuous variables were standardized to have a mean of zero and an SD of one, and all spatial covariates had a 30 × 30 m resolution.

Elk use of different treatment types

Finally, we assessed whether prescribed burning or the size of harvest units influenced the amount of use harvest units received from elk. To do this we related the total number of nighttime (the period spanning 30 min after sunset until 30 min before sunrise) telemetry locations in each harvest unit to burn status (binary; 0 = not burned, 1 = burned) and area (km^2) of the harvest unit using negative binomial regression with an offset term for the natural log of the area of each harvest unit. The offset term converted the raw counts of telemetry locations in each harvest unit to a density (i.e., number of telemetry locations per unit area). By including area as both an offset term and a covariate, we could assess whether the size of the harvest unit influenced the use by elk, while also controlling for the fact that the raw number of telemetry locations falling within the bounds of a harvest unit would be expected to be greater in larger harvest units. We compared models with linear and quadratic terms of area using AIC (Burnham & Anderson, 2002). We fitted separate models to telemetry data for elk in (1) the early period in the 5 years immediately following logging in which elk could roam freely in the whole study area (1993–1997), and (2) the late period post construction of a fence separating the Syrup Creek study area by elk density (1998–2020). In the late period, we pooled data between the high-density and low-density elk zones and included a binary variable for "density" in which high density was the reference category.

RESULTS

Selection ratios

On diel timescales prior to timber harvest (i.e., between 1989 and 1991, May–October), elk avoided grasslands during daylight hours but selected them in the evening before transitioning to indifference and finally avoidance by morning. During daylight hours, elk exhibited a strong selection for forest stands that would later be harvested, yet were largely indifferent to the forest that has since remained intact (Figure 2). However, in the years post timber harvest, elk avoided treated forest (and selected untreated forest) during the day, and selected treated forest (and avoided untreated forest) during evening and night (Figure 2). Identifying this overwhelming contrast between daytime and nighttime selection and avoidance of treated areas motivated us to consider daytime and nighttime locations separately for all subsequent analyses. We defined daytime to be the period spanning 30 min after sunrise until 30 min before sunset, and nighttime to be the period spanning 30 min after sunset until 30 min before sunrise (Spitz et al., 2018).

On monthly timescales, elk consistently selected untreated forest during the daytime between May and October. This contrasted with avoidance or indifference to treated forest during the day for all months. At night, however, elk selected treated forest during all months, with a notable peak in July, and consistently avoided untreated forest. During both day and night, elk selected grasslands in May and October, and avoided them during the summer months (Figure 3).

On successional timescales, elk avoided treated forest during the day, beginning almost immediately after logging occurred in 1992, and lasting until the mid-2010s, and selected untreated forest during diurnal hours during the same time period. But, at night, elk selected treated forest consistently in the period post logging, although selection began to wane at the very end of the time series. The untreated forest was avoided at night in all years post timber harvest, but tended toward indifference by the late 2010s (Figure 4).

Resource selection functions

Fitting RSFs allowed us to formally model the effect of time since treatment on the probability of selection of logging treatments for elk at both high and low densities.

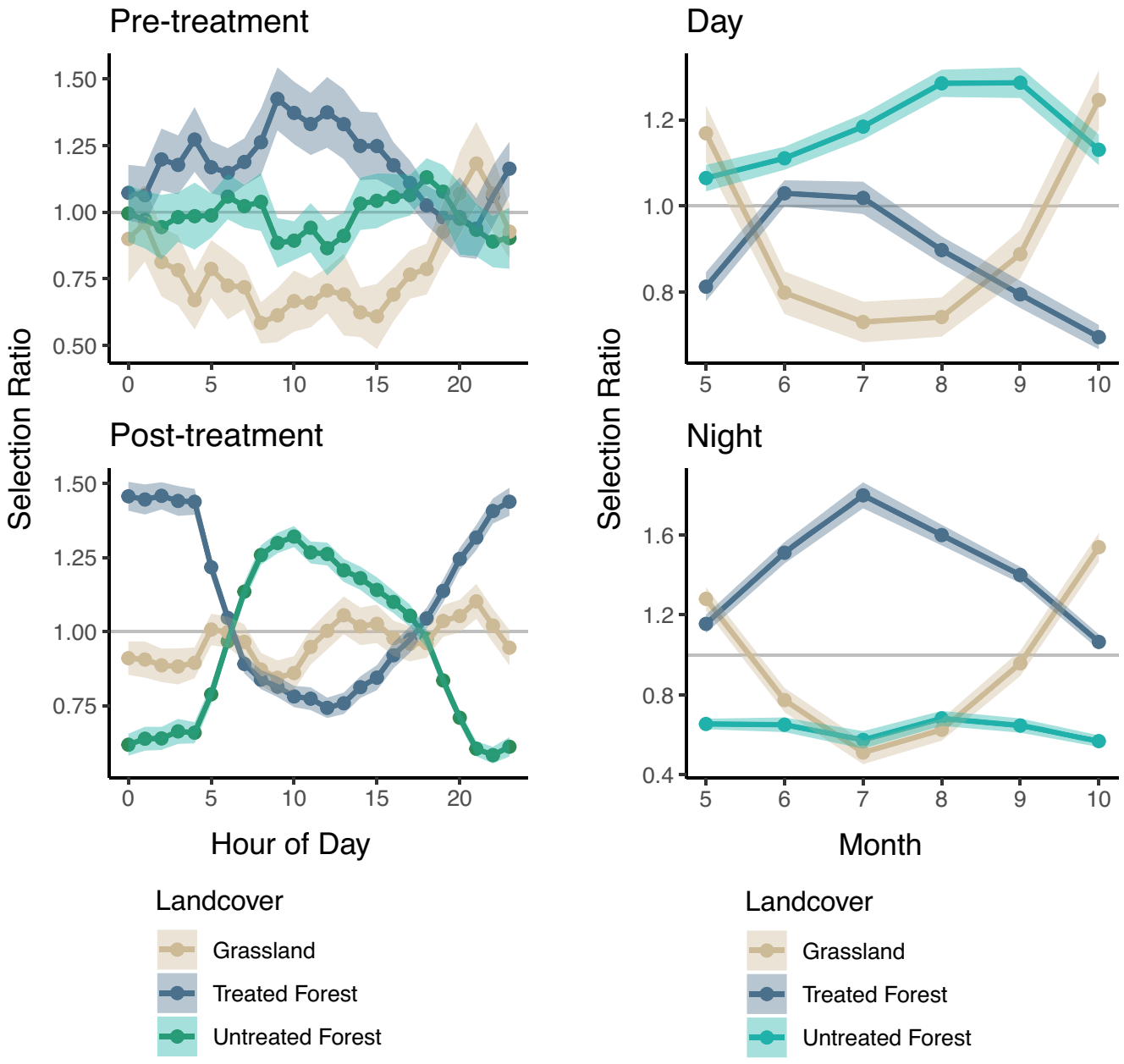

FIGURE 2 Diel selection patterns by elk before and after timber harvest in northeastern Oregon, USA, as measured by selection ratios. Blue points indicate estimated selection of treated forest (i.e., forest that was logged and possibly burned), green points indicate estimates for untreated forest (i.e., forest that was left intact), and tan points indicate estimates for grasslands. Shaded regions indicate 95% CI. The gray horizontal line at $y = 1$ is the line of indifference; values above that line indicate increased use relative to availability and values below it indicate decreased use relative to availability. The *x*-axis measures a 24-h cycle in which 0 corresponds to midnight. Note that "treated forest" in the pre-treatment period represents the stands targeted for tree removal that had not yet been harvested.

FIGURE 3 Monthly selection patterns by elk following timber harvest in northeastern Oregon, USA, as measured by selection ratios. Blue points indicate the estimated selection of treated forest (i.e., forest that was logged and possibly burned), green points indicate estimates for untreated forest (i.e., forest that was left intact), and tan points indicate selection of grassland. Shaded regions indicate 95% CI. The gray horizontal line at $y = 1$ is the line of indifference; values above that line indicate increased use relative to availability and values below it indicate decreased use relative to availability.

For nighttime locations, models with a quadratic effect of time since treatment were favored over models with a linear time effect for both high-density and low-density populations ($\Delta AIC = 5.0$ and $\Delta AIC = 42.6$, respectively). Terms for Treatment × Time ($\beta = 0.38$, $p = 0.05$ [high density]; $\beta = 0.60$, $p < 0.001$ [low density]) and Treatment × Time^2 ($\beta = -0.49$, $p = 0.02$ [high density]; $\beta = -0.74$, $p < 0.001$ [low density]) indicated that selection of logged

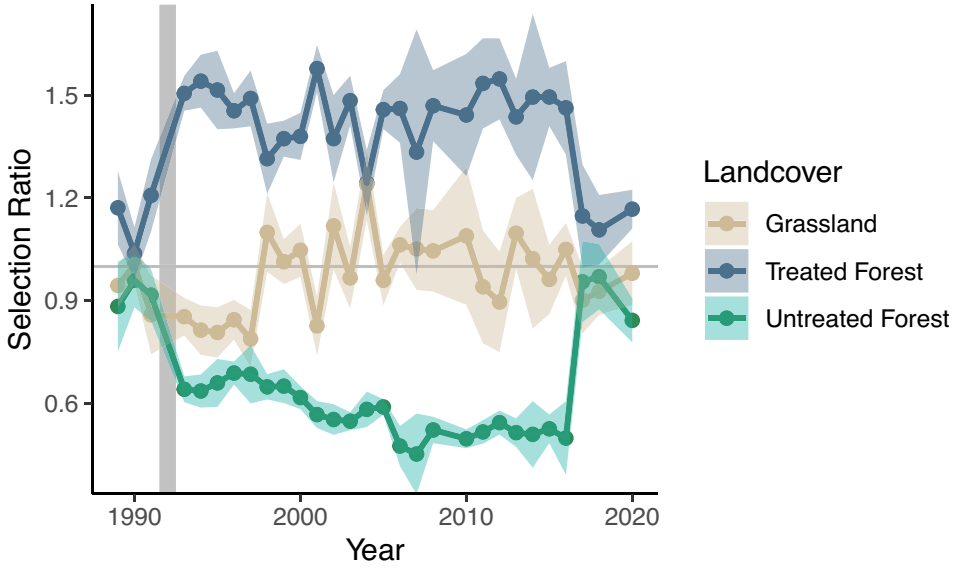

FIGURE 4 Annual nighttime selection patterns by elk in northeastern Oregon, USA, as measured by selection ratios. The vertical bar indicates the time of logging. Blue points indicate estimated selection of treated forest (i.e., forest that was logged and possibly burned), green points indicate estimates for untreated forest (i.e., forest that was left intact), and tan points indicate estimates for grassland. Shaded regions indicate 95% CIs. The gray horizontal line at $y = 1$ is the line of indifference; values above that line indicate increased use relative to availability and values below it indicate decreased use relative to availability.

areas initially rose following treatments, then peaked and subsequently declined, and that the magnitude of the effect differed by elk density (Figure 5a; Appendix S2: Table S1). Specifically, peak selection in both high-density and low-density populations occurred 14 years post logging, although the relative probability of selection remained above 1 (indicating selection) for 26 years in the high-density population and for 33 years in the low-density population (Figure 5a). The relative probability of selection of logged areas at its peak was 73% higher for elk in the low-density zone than in the high-density zone (Figure 5a). A Z-test confirmed that the difference in selection coefficients for the treated forest was significantly different between populations ($Z = 2.30$, $p = 0.021$). In contrast with the treated forest, elk avoided untreated forests at night (Figure 5c). At night, elk selected grasslands ($\beta = 0.55$, $p < 0.001$ [high density]; $\beta = 0.36$, $p < 0.001$ [low density]), north-facing slopes ($\beta = 0.25$, $p < 0.001$ [high density]; $\beta = 0.076$, $p < 0.001$ [low density]), and areas closer to permanent water sources ($\beta = -0.10$, $p < 0.001$ [high density]; $\beta = -0.002$, $p = 0.66$ [low density]). The effect of distance to the nearest road differed by population; elk at high densities selected areas closer to roads, while elk at low densities selected areas farther from roads ($\beta = -0.026$, $p < 0.001$ [high density]; $\beta = 0.044$, $p < 0.001$ [low density]; Appendix S2: Table S1, Figure S1).

The RSFs for daytime locations were also best explained with a quadratic term for time since treatment, relative to models with a linear effect (ΔAIC = 4.1 [high density], ΔAIC = 10.8 [low density]). These models indicated that, in the high-density elk zone, selection of treated forest during the day began decreasing immediately post logging, with peak avoidance occurring 17 years later, and returning to selection at 28 years post logging (Figure 5b). A similar pattern was observed for elk in the low-density zone, with daytime avoidance of treated forest peaking 14 years post logging and returning to selection after 25 years (Figure 5b). In contrast with treated forest, the untreated forest was generally selected during the day (Figure 5d). During the day, elk avoided grassland ($\beta = -0.23$, $p < 0.001$ [high density], $\beta = -0.16$, $p < 0.001$ [low density]), north-facing slopes ($\beta = -0.10$, $p < 0.001$ [high density], $\beta = -0.23$, $p < 0.001$ [low density]), and areas farther from permanent water sources ($\beta = -0.023$, $p < 0.001$ [high density], $\beta = -0.15$, $p < 0.001$ [low density]), while selecting areas farther from roads ($\beta = 0.093$, $p < 0.001$ [high density], $\beta = 0.05$, $p < 0.001$ [low density]; Appendix S2: Table S2, Figure S1).

We extracted individual-level coefficient estimates to assess differences in selection of treated forests between elk at high and low density. For nighttime locations, the means (and SD) of individual selection coefficients for the treated forest were 0.61 (SD = 0.40) for the high-density population and 0.74 (SD = 0.35) for the low-density population (Figure 6). The coefficient of variation (the ratio of the SD to the mean, thus provided a better measure of the variation of individual selection coefficients, given the difference in mean selection between

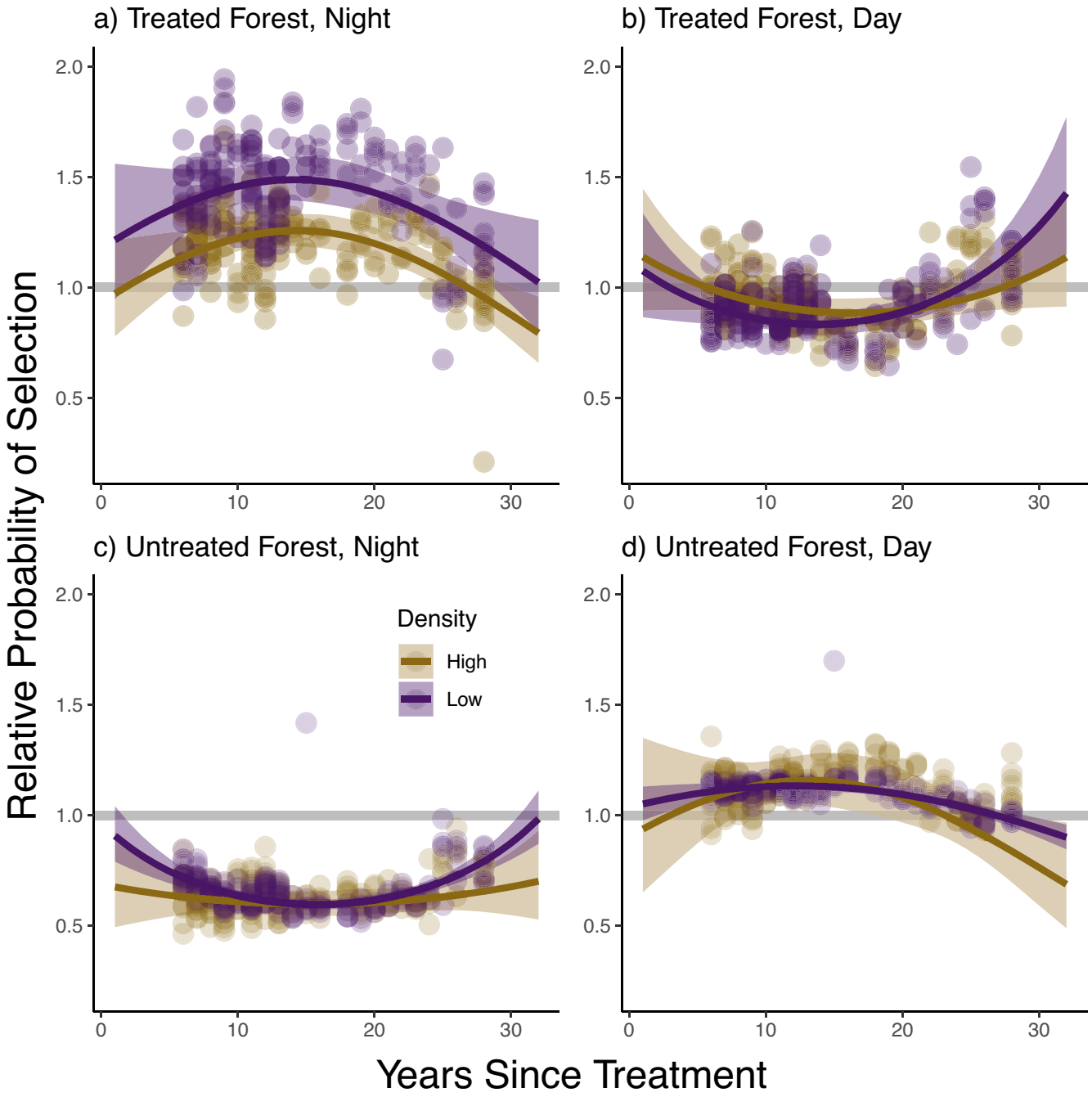

FIGURE 5 The predicted relative probability of selection for elk in northeastern Oregon, USA, as estimated from resource selection functions using data between 1998 and 2020. Plots show the selection of treated (i.e., logged and possibly burned) forest (a, b, top row), untreated forest (c, d, bottom row), at night (a, c, left column), and during the day (b, d, right column), in relation to the number of years since forest treatments occurred. Tan lines indicate the selection by elk in the high-density population and purple lines indicate the low-density population. Shaded bands indicate 95% CIs. Points represent individual-level selection coefficients with tan points representing individuals in the high-density population and purple points representing individuals in the low-density population.

populations) was 0.64 for elk at high density and 0.35 for elk at low density, indicating that elk in the high-density population were more variable in their selection of treated forest. As expected from our simulation study (Appendix S1), the mean of individual selection coefficients for treated forest at night was higher in elk wearing GPS collars than those wearing LORAN-C collars during the period in which both collar types were deployed (2003–2005). Specifically, selection coefficients of GPS-collared individuals were 16% or 30%

higher for elk at low and high densities, respectively, than for elk wearing LORAN-C collars (Appendix S1: Figure S2).

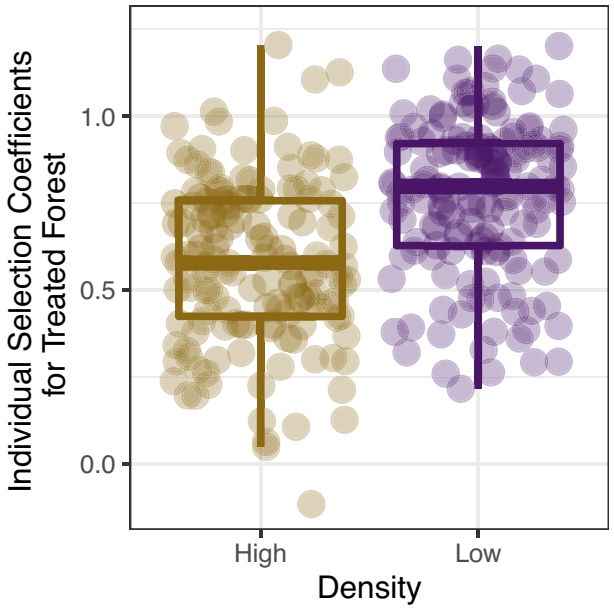

FIGURE 6 The distribution of elk selection coefficients for treated forest (i.e., forest that was logged and possibly burned) extracted from resource selection functions using data between 1998 and 2020 at two population densities. Individual selection coefficients are represented by points. Boxplot horizontal lines represent the 0.25, 0.5, and 0.75 quantiles, and the vertical "tails" extend to 1.5 times the interquartile range. For both points and boxplots, tan colors represent the high-density elk population and purple colors represent the low-density population. The figure is intended to visualize the weaker and more variable response to logging treatments for elk in the high-density population.

Elk use of different treatment types

We used negative binomial regression to assess whether nighttime elk use of treated areas was influenced by characteristics of the harvest unit during two time periods, the early period from 1993 to 1997, when elk were maintained at one density in our study area, and the late period from 1998 to 2020, when elk were kept at high and low densities. Both models were better explained using a quadratic term (as opposed to a linear only term) for the area of the harvest unit (ΔAIC = 0.75 and 5.69 in early and late models, respectively), suggesting that elk use did not increase monotonically with the size of the harvested area (Appendix S2: Figure S2). Specifically, the models predicted that elk use of harvest units would be greatest when the area logged was between 0.17 and 0.21 km^2 (Appendix S2: Figure S2). Harvest units that underwent prescribed burning were used 1.5 times more than those left unburned ($\beta = 0.42$, $p = 0.017$; Table 1), although this was only the case in the <5 years post logging treatments and not during the following period ($\beta = 0.19$, $p = 0.16$; Table 1).

DISCUSSION

More than a century of fire suppression in the western USA has caused the prevalence of closed-canopy forests to proliferate across massive spatial scales. Because this has created conditions favorable to catastrophic wildfires that are exacerbated by ongoing climate change, over 50 million acres of fire-prone lands in the western USA are now being managed for fire resiliency using prescribed burning and timber harvest (Ager, 2022). While these actions are intended to restore landscapes that had

TABLE 1 Parameter estimates for negative binomial regression models constructed to explain how variation in the characteristics of each harvest unit influenced the intensity of use (i.e., number of elk telemetry locations) by elk each harvest unit received in the Starkey Experimental Forest and Range, Oregon, USA.

	Coefficient		Standard error		*p*-value	
Parameter	**1993–1997**	**1998–2020**	**1993–1997**	**1998–2020**	**1993–1997**	**1998–2020**
Intercept	6.861	9.187	0.274	0.203	<0.001	<0.001
Burned	0.424	0.189	0.177	0.135	0.017	0.163
Area	13.300	15.005	6.039	4.432	0.028	0.001
Area^2	−44.456	−59.954	26.298	20.107	0.091	0.003
Elk density	NA	0.370	NA	0.128	NA	0.004

Note: Results are presented for two models, one constructed using data from 1993 to 1997 in which elk were held at a single density, and another constructed using data from 1998 to 2020 in which elk were held at both a high and low density. "Density" identifies the low and high elk density zones (the reference category was high density). "Burned" is a binary variable indicating whether each harvest unit was burned after timber harvest and the quadratic term for "Area" indicates whether the area of the harvest unit (in km^2) influenced the amount of use received by elk. An offset term for the natural log of area of the harvest unit was additionally included to control for the fact that larger harvest units should receive more use by elk due to chance alone.

lost natural recurrent disturbance regimes, the extent to which these actions will alter the space use and behavior of terrestrial vertebrates has not been adequately quantified. Here we assessed the response of a culturally and ecologically important large herbivore to anthropogenic, landscape-scale disturbances. We found that disturbance through logging treatments led to persistent changes in patterns of elk resource selection that varied across diel, monthly, and successional timescales, and that the magnitude and duration of these differences were density dependent. Elk selection of logged areas occurred at night only, which aligned with our first hypothesis (H1) and supported earlier research on elk responding to habitat manipulations (Spitz et al., 2018). Although elk selected treated forest during all months for which we had telemetry data (May–October), there was a notable peak in July. This supported our prediction that forest treatments would be most valuable when grasses in our study area had senesced relative to spring and fall green-up (H2). Our prediction that elk would continue to select the treated forest for at least 10–20 years post logging, because forage biomass and digestible energy remains high for at least this duration (H3), was also supported. Specifically, peak selection of treated forest occurred 14 years post harvest, and persisted for 26–33 years. Yet elk avoided the same areas during the day for 25–28 years after logging had occurred, and instead selected untreated forest with greater cover. Our ability to observe changes in selection across successional timescales was possible because of our 30-year dataset of elk telemetry locations. Because GPS collars were not available at the onset of the study, our inference between 1989 and 2002 relied solely on LORAN-C telemetry collars, which are known to be less precise than modern GPS collars, and our simulations demonstrated that the strength of selection and avoidance was likely to have been underestimated during this time span (Appendix S1). Therefore, although we caution that our results for this time period should be considered conservative because of the potential for type II errors, we were still able to observe overarching patterns in a large herbivore's resource selection that tracked forest succession following timber harvest over a multidecadal time series.

Our study design was unique in that, between 1998 and 2020, elk were enclosed in different study areas at either a high or low density, permitting us to explore the mediating effect that population density played on the patterns of selection of landscape-scale habitat disturbances. Consistent with the ideal free distribution and density-dependent habitat selection theory (Fretwell & Lucas, 1969; Morris, 2003) and H4, elk in the low-density zone exhibited stronger selection of high-quality habitat during feeding hours (i.e., treated forest at night; Figures 5 and 6), whereas the relatively lower magnitude of selection of treated forest observed for elk in the high-density zone was ostensibly due to that habitat type being of less value when shared with more users. Our alternative hypothesis ($H4_A$) posited that, due to resource depletion occurring because of greater intraspecific competition, the high-density population of elk would respond more strongly to the habitat improvements than would the low-density population. However, this hypothesis was not supported and our results were aligned more closely with predictions from the ideal free distribution.

Individual selection coefficients for treated forest among elk in the high-density population were, on average, not only weaker than those in the low-density population, but were also more variable (coefficient of variation = 0.35 and 0.64 for low-density and high-density populations, respectively; Figure 6). This further accords with the ideal free distribution that predicts weaker and more variable selection of high-quality habitat when it becomes saturated at high population densities and results in "spillover" selection of alternative habitats that become equally favorable. Indeed, elk at high densities selected grasslands more than did elk at low densities (Appendix S2: Table S1), suggesting that the resources within treated forest could not fully meet the nutritional requirements of all individuals, and thus grasslands served as a spillover resource (particularly in the summer months when grasses are less nutritious than during green-up). This idea is consistent with previous research in our study area that indicated that elk in the high-density population exhibited greater dietary breadth, including forage species of lower quality and palatability than observed in the low-density population (Stewart et al., 2011). Such empirical tests of density-dependent habitat selection are rare in large mammals. Our results support previous findings that selection of the highest quality habitat by elk (van Beest et al., 2016), moose (*Alces alces*) (van Beest et al., 2014), and domestic sheep (*Ovies aries*) (Mobæk et al., 2009) waned as conspecific population density increased, coincident with an increase in selection of lower quality habitats. This accords with the theory of density-dependent habitat selection, in that generalist strategies optimize fitness in high-density populations whereas, at low densities, fitness would be optimized by specialization on the highest quality resources (Fortin et al., 2008).

Our study did not measure how or whether forage quality or quantity had changed post logging. However, a substantial body of literature suggests that the nutritional landscape is improved following the opening of forest canopy associated with logging (Cook et al., 2016; Hammond, 1980; Hull et al., 2020; Irwin & Peek, 1979; Long et al., 2008; Rowland et al., 2018), so we expect this was also the case in our study area. We thus infer that

the selection of treated forest post logging was due to elk exploiting the increased availability of nutritional resources. Our finding that, at night, elk selected logged areas suggests they were feeding nocturnally, which is consistent with another study adjacent to ours that found strong nocturnal selection of burned areas by elk (Spitz et al., 2018). Elk are generally believed to concentrate feeding during crepuscular hours (Green & Bear, 1990), but we suggest that they deviate from this pattern and feed nocturnally in hot summer months, when forage resources are concentrated in open canopies, such as those post fire or logging. The frequent use of open areas at night, and subsequent retreat into closed-canopy forests during the day, has been observed in many other studies of elk prior to ours, and this has been attributed to the need to thermoregulate (Ager et al., 2003; Lamont et al., 2019), reduce risk of predation (Kohl et al., 2019), or avoid human disturbance (Smith et al., 2022; Spitz et al., 2019). The fact that we observed an increase in the strength of daytime selection of untreated (i.e., high canopy cover) forest, coinciding with the progression of hot summer months, provides evidence that elk were seeking thermal cover (Long et al., 2014; Millspaugh et al., 1998). Although our study area was closed to the public and received only light human traffic for administrative use, our RSFs nonetheless indicated that elk avoided roads during daylight hours. Consequently, we cannot entirely rule out human disturbance as the mechanism causing elk to avoid open, logged areas during the day, although we consider it unlikely, given the low levels of background human activity. Also, because cougars (*Puma concolor*), and not wolves (*Canis lupus*), are the primary predators of elk in this study area, it is unlikely that retreating into dense canopy would yield any reduction in predation risk, given that cougars typically use structurally complex cover to approach prey (Atwood et al., 2009; Laundré & Hernández, 2003). Given the lack of coursing predators in open areas and the low levels of human disturbance (including hunting) in this study area, the most likely explanation why elk selected higher canopy cover during the day may have been to reduce thermal stress.

Regressions modeling elk intensity of use as a function of harvest unit characteristics revealed that, in the first 5 years following logging treatments, harvest units that were burned after timber harvest were used by elk 1.5 times more than those that were not burned. Although this finding supported our hypothesis (H5) that burning would improve palatable forage for elk beyond what is achieved by logging (Cook et al., 2016; Franklin & Dyrness, 1973), we were somewhat surprised that the effect did not persist >5 years post logging treatments. However, the near-term enhancement of fire on forage characteristics for ungulates is well established (Greene et al., 2012; Proffitt et al., 2019; Sittler et al., 2014), but does not preclude the potential long-term benefits of mechanical disturbance that we documented for elk selection of both burned and unburned logged areas. Finally, the quadratic term for the area of harvest units indicated that elk use of harvest units peaked when logging treatments were between 0.17 and 0.21 km^2, which supported our hypothesis (H6) that harvest units of intermediate sizes would be preferred (Appendix S2: Figure S2). However, we suggest caution against overinterpreting these values, given that the harvest units in this study were all relatively small (averaging 0.081 km^2) and the low variation in size meant that we lacked the power to precisely describe the relationship. Further, the models with quadratic effects of area were not overwhelmingly supported over a positive, linear effect of area that would indicate that use by elk would monotonically increase as harvest units became larger ($\Delta AIC = 0.75–5.69$). However, we concur with Thomas (1979), who suspected that some threshold must exist in which large harvest units would lead to decreased use because of the lack of proximity to hiding cover. Similarly, Hammond (1980) suggested that, although large clear cuts increased forage quantity, the overall benefit was negated because of the unwillingness of elk to venture far from forest cover. Wisdom et al. (1986) and Thomas et al. (1988) also documented higher elk use in forage areas closer to cover and vice versa. In contrast, timber harvest in our study area resulted in a mosaic of small patches of treated forest, untreated forest, and grasslands. This mosaic of vegetation conditions allowed elk to make choices on the landscape to best meet varying needs throughout the daily cycle. Had timber harvest been restricted to a single or few large homogenous patches, the value of logging treatments to elk would probably have been less than that observed.

Although we found a persistent effect of increased selection by elk to logged areas at night, we caution that this pattern was mirrored by daytime avoidance of the same areas, suggesting that intact forest is also critical to elk. Indeed, guidelines for optimal landscape composition for elk suggest that hiding cover should constitute 40% of the landscape (Thomas, 1979), so patchy disturbances such as nonstand-replacing wildfire and smaller fuels treatments interspersed with higher canopy cover units to create a heterogeneous landscape, are more likely to benefit elk and other large herbivores. Large herbivores typically avoid roads (Johnson et al., 2000; Rowland et al., 2000, 2018), which also come with increased mortality risk from hunters (Frair et al., 2007), so the construction of roads to facilitate logging may reduce the benefits relative to natural disturbances. Thus, we do not

suggest that logging universally benefits wild herbivores, but that disturbance is valuable in closed-canopy forests when this results in a mosaic of habitat types, while readily offering access to security cover. Disturbance in wet forest types may have greater nutritional benefits than that in less productive dry forests (Proffitt et al., 2016), which is of particular relevance as many forest treatments focusing on fire resiliency are more likely to target dry forest types. Strategic closures of roads, whether seasonally or permanently, following disturbance may allow large herbivores to more fully realize the ensuing forage benefits. Finally, both anthropogenic and natural disturbances should be considered within the context of restoring landscape resiliency to stand-replacing wildfire, while also meeting multiple land management objectives, including biodiversity maintenance and the productivity of wildlife habitat.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ruprecht et al., 2023) are available in Dryad at https://doi.org/10.5061/dryad.r4xgxd2js.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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